


RESEARCH ARTICLE

Understanding dietary ecology in great apes from dental macrowear analysis

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Abstract

Objectives: Dietary diversity in primates is reflected in their dental morphology, with differences in size and shape of teeth. The objective of this study is to investigate the relationship between molar morphology and macrowear patterns in *Pongo*, *Gorilla*, and *Pan* to obtain dietary information.

Methods: We have examined 68 second lower molars using the Occlusal Fingerprint Analysis method including 18 chimpanzees, 28 gorillas, and 22 orangutans. We selected only molars from wildshot specimens characterized by a moderate degree of wear. High-resolution digital models of teeth were created using a white scanning light system with a resolution of 45 μm .

Results: The macrowear patterns of *Pan* were significantly different from those of *Gorilla* and of *Pongo*, differences that are mostly due to shearing wear. *Gorilla* and *Pongo* macrowear patterns are dominated by phase II areas, followed by lingual phase I facets, while in *Pan* we observe a significant increase in buccal phase I facets. The latter group also displays the highest macrowear variation across the sample examined in this study.

Conclusions: The molar macrowear patterns of the great apes analyzed in this study did not confirm our initial hypothesis of finding larger crushing and grinding areas in *Pongo* and more shearing wear in *Gorilla*. *Pan* shows the most variable macrowear, which is probably associated with their more flexible diet. The similarity between *Pongo* and *Gorilla* macrowear patterns may be due to a larger intake of mechanically challenging foods that could obfuscate dietary wear signals generated by softer foods.

KEYWORDS

dental functional morphology, fallback foods, occlusal fingerprint analysis, primate diets, wear facets

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1 | INTRODUCTION

Size and shape variation of molar crowns in human and non-human primates play an important role for testing phylogenetic hypotheses and for better understanding how species are dentally adapted to their environment. Primate teeth have evolved to improve mechanical efficiency in eating a variety of different types of foods (Lucas, 2004). Thus, differences in tooth shape and size reflect the mechanical properties of foods that primates eat (Kay & Hiiemae, 1974; Teaford & Ungar, 2007). For instance, primates that rely on the consumption of hard and brittle foods generally display flat and thick enameled molars with smooth and blunt cusps, while insectivorous primates possess sharp and tall cusps with well-developed shearing crests specialized for cutting and perforating insect exoskeletons (Fleagle, 2013; Teaford & Ungar, 2007). However, some primates, especially those who live in highly seasonal environments, show a lack of correspondence between diet and morphology, a phenomenon called Liem's paradox (Liem, 1980; Robinson & Wilson, 1998). Although these species have a specialized dentition to fracture foods with specific textural and physical properties, they tend to prefer foods for which they are not adapted (Ungar, 2015). For example, although gorillas and chimpanzees have significantly different primary tooth morphology, they both prefer ripe and sweet fruits during periods of resource abundance (Conklin-Brittain et al., 1998; Marshall & Wrangham, 2007; Masi et al., 2009; Rogers et al., 1990; Williamson et al., 1990). However, when fruit availability is scarce or completely absent, the sharp cusped molars of gorillas allow them to more efficiently consume fibrous leafy foods, a strategy less common among chimpanzees, whose dentition is less adapted for this

type of diet (Marshall & Wrangham, 2007; Ungar, 2015). These seasonal foods with poor nutritional values and which are more difficult to digest (also called fallback foods) seem to have exerted a large influence on dental morphology in primates (Lambert, 2007; Marshall et al., 2009; Marshall & Wrangham, 2007; Rosenberger & Kinzey, 1976; Taylor, 2006; Vogel et al., 2008). Thus, we should be cautious when we use tooth shape alone to reconstruct the dietary spectrum of a species (Ungar, 2015).

1.1 | Dental morphology

Gorilla lower molars are commonly characterized by a relatively thin enamel layer throughout the crown, a large talonid basin and five tall and sharp cusps that are separated by a Y-5 fissure pattern, or one of its several modifications (Kono, 2004; M'Kirera & Ungar, 2003; Shellis et al., 1998; Smith et al., 2005; Swindler, 2002; Ungar & M'Kirera, 2003) (Figure 1). The occlusal separation between metaconid and entoconid is wide and it shows a deep notch, a condition that is not found in other apes (Swindler, 1976; Swindler, 2002). Moreover, *Gorilla* mandibular molars differ also from those of orangutans and chimpanzees due to the presence of a well-expressed protostylid (Swindler, 2002; Whitehead et al., 2005). *Pongo pygmaeus* possesses large low-cusped molars with relatively thick enamel (but relatively thin toward the basal cervical region) and a Y-5 pattern (Kono, 2004; Smith et al., 2005; Vogel et al., 2008). The occlusal surface of the posterior teeth in orangutans is usually covered with complex wrinkles (or crenulations), and in unworn molars the crenulated surface can obscure the primary fissure system, forming complex structural

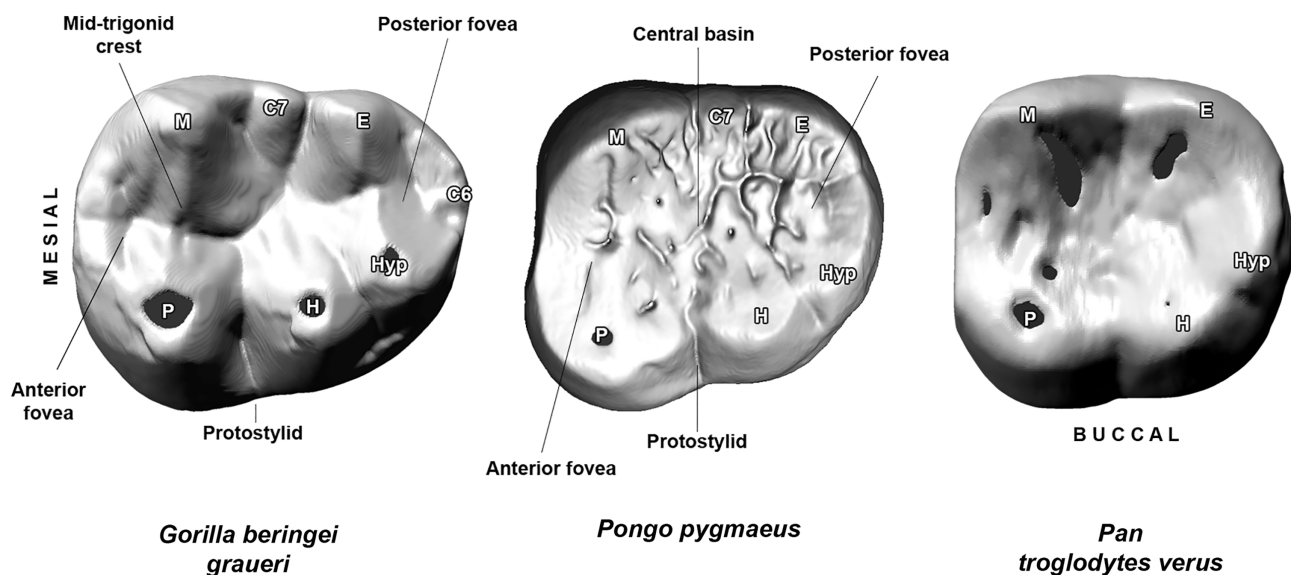


FIGURE 1 Digital 3D models in occlusal view of second lower molars of *Gorilla gorilla*, *Pongo pygmaeus*, and *Pan troglodytes*, not to scale. C6, cusp 6; C7, cusp 7; E, entoconid; H, hypoconid; Hyp, hypoconulid; M, metaconid; P, protoconid

patterns along the marginal ridges and at the end of the basins (Swindler, 2002; Whitehead et al., 2005).

Finally, *Pan troglodytes* molars show intermediate features between gorillas and orangutans: the thickness of the enamel layer is average, but particularly thin in the occlusal basin while the occlusal surface is generally flat but it maintains cusp angularity (Kono, 2004; M'Kirera & Ungar, 2003; Shellis et al., 1998; Smith et al., 2005; Swindler, 2002; Ungar & M'Kirera, 2003; Vogel et al., 2008; Whitehead et al., 2005). Chimpanzee molars are dominated by a large talonid basin; they often show a Y-5 pattern and sometimes a protostylid, which is not as complete as the one found in gorillas (Swindler, 2002; Whitehead et al., 2005).

1.2 | Diet and feeding ecology in great apes

African (*Pan troglodytes* and *Gorilla gorilla*) and Asian (*Pongo pygmaeus*) great apes rely on significantly different diets (Morgan, 2017). Their habitats are among the most floristically diverse in the world and most apes prefer ripe and sweet fruits when available (Morgan, 2017). *Gorilla* is commonly described as a folivorous primate, with a diet consisting of leaves, stems, roots, fresh shoots and bark (Doran & McNeillage, 1998; Watts, 1996). However, the proportion of fruit in their diet can change significantly depending on their habitats, with the western lowland gorillas (who inhabit lowland rain forests) being more frugivorous than the mountain gorillas (who live in high-altitude montane forests) (Doran & McNeillage, 1998; Watts, 1996; Yamagiwa et al., 1994; Yamagiwa et al., 1996). Direct observations from a longitudinal study from the Kahuzi-Biega National Park (Democratic Republic of Congo) indicate that the diet of eastern lowland gorillas (*Gorilla beringei graueri*) consists for the major part of leaves, pith, and barks (70.2%), and therefore they can be considered as folivorous primates (Berthaume, 2014; Yamagiwa et al., 2005).

Orangutans are primarily considered as frugivorous, but rely heavily on tough and highly fibrous fallback foods consisting of fibrous and unripe fruits, leaves, nuts, bark, and on rare occasion wood (Delgado Jr. & van Schalk, 2000; Kanamori et al., 2010; Mackinnon, 1974, 1979; Taylor, 2006; Wich et al., 2009). Finally, chimpanzees are characterized by the largest dietary variation among apes, ranging from fruits, insects, leaves to occasionally meat (Basabose, 2002; McGrew et al., 1988; Newton-Fisher, 1999; Nishida et al., 1983; Potts et al., 2011; Wrangham, 1986). Despite this, chimpanzees are mostly considered as a frugivorous species. In periods of fruit scarcity chimpanzees tend to eat fallback foods consisting of leaves, seeds, stems, and resin (Conklin-Brittain et al., 1998; Wrangham et al., 1998). In particular, western chimpanzees (*Pan troglodytes verus*) eat less fruit and more low-quality food compared with other chimpanzees (McGrew et al., 1988; Pruett, 2006).

1.3 | Molar macrowear in great apes

The examination of tooth wear can provide additional information on how teeth have been used during mastication (Teaford, 2007). There

is in fact a strict relationship between masticatory movements, tooth wear, and physical properties of the food eaten (Kay & Hiiemae, 1974). The study of dental microwear and microtexture analysis in particular, has become one of the most widely used approaches for the reconstruction of human and non-human primate diet (Scott et al., 2005). However, it is well understood that interpretations based on microwear alone can be problematic because of the "last supper" phenomenon (Grine, 1986). Microwear features can change quickly, usually yielding information about an individual's diet in the days just before its death (Wood & Schroer, 2012). A recent study that combined the analysis of microscopic and macroscopic tooth wear in chimpanzees have further demonstrated that the examination of microwear can address short-term dietary changes such as seasonality, but not long-term dietary signals (Stuhlträger et al., 2021).

The aims of this study are to analyze molar macrowear patterns in *Pongo*, *Gorilla*, and *Pan* to obtain information about their feeding ecology, and ultimately to advance our understanding of the relationship between masticatory function, dental wear, and diet in non-human primates. Here we examine the general occlusal wear patterns in great ape lower molars using a well-established method called occlusal fingerprint analysis (OFA; Kullmer et al., 2009; Kullmer et al., 2020), which has been successfully employed to reconstruct the chewing behavior and diet of extinct species and of past human populations (Fiorenza et al., 2011, 2019; Fiorenza et al., 2018; Fiorenza et al., 2020). This approach is based on the analysis of macrowear patterns that describe the major movements of occlusal interaction between upper and lower teeth in three-dimensional (3-D) space (Kullmer et al., 2009). We combine this method with recent advances in the OFA approach to track changes in dental function, jaw movements, and diet in living great apes. Preliminary studies on great ape dental macrowear detected significant differences between the three genera analyzed (*Pongo*, *Gorilla*, and *Pan*), and demonstrated the power of the OFA method to interpret the relationship between food items, mastication, and tooth wear processes in living primates (Fiorenza et al., 2014; Fiorenza & Kullmer, 2016; Knight-Sadler & Fiorenza, 2017).

In this study, we test two main hypotheses: firstly, we examine if molar macrowear patterns of great apes reflect their feeding behavior by comparing the proportions of shearing, crushing, and grinding wear areas (hypothesis 1). Specifically, we expect to find a larger proportion of shearing wear in the folivorous gorillas, and a larger proportion of grinding and crushing wear in orangutans, who rely more on a diet consisting of hard and brittle foods. Secondly, we will test if the dietary variation found in great apes is reflected in the macrowear patterns of these species (hypothesis 2). Because of their more flexible diet, we expect to find a more variable macrowear patterns in chimpanzees compared to those of gorillas and orangutans, who consume more specialized diets.

2 | MATERIAL AND METHODS

We have examined 18 chimpanzees (all *Pan troglodytes verus*), 28 gorillas (21 *Gorilla gorilla gorilla*, 5 *Gorilla beringei graueri*, and

2 *Gorilla beringei beringei*, and 22 orangutans (9 *Pongo abelii* and 13 *Pongo pygmaeus*) from various museum skeletal collections including the Max Planck Institute (Leipzig, Germany), Natural History Museum (London, UK), Royal Museum for Central Africa (Tervuren, Belgium), Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science (Berlin, Germany), Senckenberg Research Institute and Natural History (Frankfurt, Germany); Naturalis Biodiversity Center (Leiden, Netherlands) (Table S1). Here, we analyzed moderately worn lower second molars from wild shot individuals characterized by full cusp removal and moderate dentine patches (wear stages 2 and 3 after Smith, 1984), which showed a complete set of wear facets (Maier & Schneck, 1981). According to Kay (1973), analyses of second molars in primates provide a good general overview of the development of masticatory functions within a species. Negative impressions of the original specimens were taken using a light viscosity silicone material (Provil. Novo Light Regular C.D.2, Heraeus Kulzer GmbH). Dental molds were filled at a later stage with a high-quality die stone material (Alpha-Rock, Alphabond Dental Pty Ltd.) characterized by a smooth non-reflective surface that is ideal for three-dimensional (3D) scanning (Fiorenza et al., 2009). Digital polygonal models of teeth were generated using a white-light scanning system with a xy resolution of 45 µm (smartSCAN3D C-5, Breuckmann GmbH), and multiple scans were aligned with the integrated scanning software (optoCAT, Breuckmann GmbH). Data post-processing, identification and analyses of wear facets were carried out using Polyworks® V12 (InnovMetric Software), a 3-D metrology software.

2.1 | Occlusal fingerprint analysis

In this study, we grouped together the wear facets by chewing cycle phases, which correspond to specific masticatory processes of the occlusal power stroke that are necessary to reduce the food bolus into

smaller pieces before swallowing (Kay & Hiiemae, 1974). Specifically, during the initial phase (I) of the power-stroke, the lower molars move into occlusion and the food is broken down by a shearing action (where the masticatory stresses are directed almost parallel to the planes of contact). Subsequently, when upper and lower molars reach maximum intercuspation, the food is processed by a crushing action (where the stress is distributed in a perpendicular direction to the occlusal plane). Finally, the lower molars move out of occlusion in the second phase of the power-stroke (II), and the food is mechanically reduced into smaller pieces by grinding (that is the resulting action of the combination of parallel and perpendicular stresses to the contact plane). We further divide the shearing facets into buccal and lingual phase I areas because their shape and size are associated with the consumption of foods characterized by the different physical properties (Fiorenza et al., 2011; Janis, 1990).

The analysis of the polygonal models follows a well-established protocol that can be summarized into three major steps: model orientation (1), wear facet identification (2), measurement of relative surface areas of wear facets (3) (Kullmer et al., 2009) (Figure 2). Each individual 3D model was loaded onto Polyworks® V12 and oriented using a reference Cartesian plane that is created along its cervical line through the least square best-fit method (Kullmer et al., 2009). The cervical plane is then rotated to the xy plane which is automatically obtained from the original coordinate system.

Wear facets are manually outlined onto the polygonal surface according to Maier and Schneck (1981), who recognized a maximum of 13 wear facets in hominoid molars. Facets 1, 2, 2.1, 3, & 4 form on the buccal slopes of protoconid, hypoconid, and hypoconulid, while facets 5, 6, 7, and 8 develop along the slopes of the metaconid and entoconid. Finally, facets 9, 10, 11, 12, and 13 are created during the phase II of the chewing cycle, and they form along the lingual slopes of protoconid, hypoconid, and hypoconulid. We also identify worn areas that form on the tips of the molar cusps, known as tip

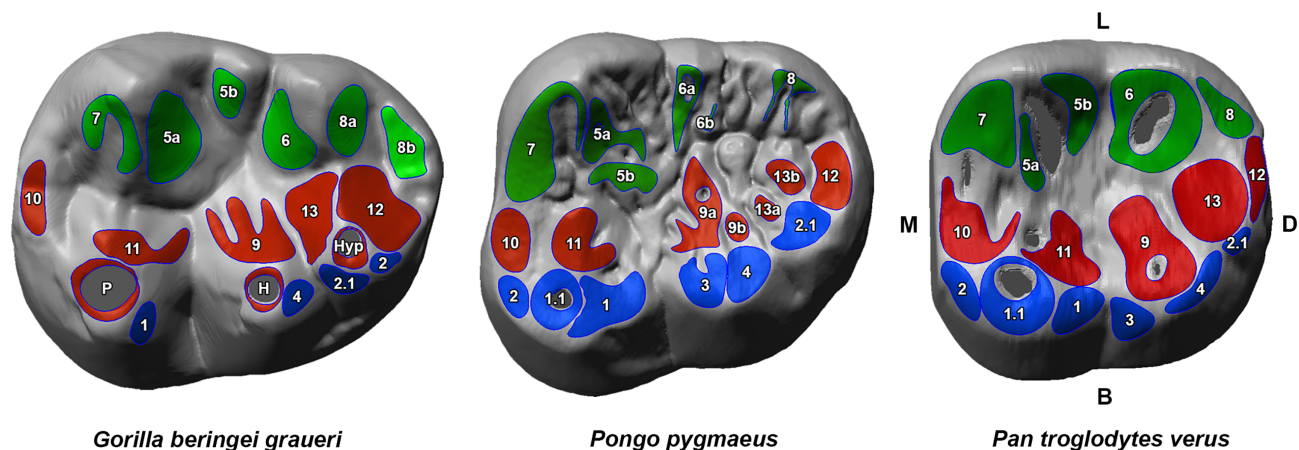


FIGURE 2 Maps of molar macrowear patterns of *Gorilla beringei graueri* (ZMB-31626), *Pongo pygmaeus* (ZMB-83515), and *Pan troglodytes verus* (MPITC-13439). The wear facets have been labeled according to Kullmer et al. (2009) and grouped based on the chewing cycle power stroke phases (Kay & Hiiemae, 1974). Buccal phase I (in blue): Facets 1, 1.1, 2, 2.1, 3 and 4. Lingual phase I (in green): Facets 5, 6, 7 and 8. Phase II (in red): Facets 9, 10, 11, 12 and 13. Tip crushing areas, those worn areas on the tips of the molar cusps that are formed during puncture-crushing (Gordon, 1984) were included in phase II areas (Fiorenza et al., 2011). B, buccal; D, distal; H, hypoconid; Hyp, hypoconulid; L, lingual; M, mesial; P, protoconid

crush areas (Gordon, 1984; Janis, 1990). These areas are characterized by a circular shape without any dominant occlusal movement, and they are probably produced during puncture-crushing (Fiorenza et al., 2020).

We use the proportion of shearing, crushing, and grinding wear to understand the functional relationship between tooth macrowear and food processing abilities, which is ultimately related to the diet of a species or of a population (Fiorenza et al., 2020; Kay & Hiiemae, 1974; Kullmer et al., 2009, 2020). To facilitate the analysis of molar macrowear we grouped phase II facets together with tip crushing areas, and divided the phase I facets into buccal and lingual facets (Fiorenza et al., 2011).

Because larger teeth likely develop larger facets than smaller teeth, we use relative wear facet areas considering solely the proportions of buccal and lingual phase I facets, and phase II facets. These relative values are obtained by dividing the areas of buccal, lingual, and phase II facets by the total occlusal wear area, which was calculated as the sum of absolute area of each occlusal wear facet (Fiorenza et al., 2011).

2.2 | Statistical analysis

In order to examine the macrowear results we initially employed summary statistical analyses, such as median, SD, and inter-quartile ranges. We visually describe the proportions of buccal phase I, lingual phase I, phase II (together with tip crush areas) facets using the ternary and box plots. Ternary plots are based on a triangular system that illustrates the ratios of three variables that sum to 1 or 100% (Hammer & Harper, 2006). We compared the macrowear patterns of *Gorilla*, *Pongo*, and *Pan* molars using the one-way PERMANOVA test, a non parametric test of significant differences between two or more groups, which is calculated directly from any asymmetric distance or dissimilarity matrix (Anderson, 2001). Statistical significance was computed with a permutation test of group membership ($n = 9999$). The Mann-Whitney pairwise comparisons between all pairs of groups are provided as a post-hoc test. The Mann-Whitney test is used to test whether the medians of two independent samples are different, and it does not assume normal distribution. Intergroup variability (between *Pan*, *Gorilla*, and *Pongo*) was assessed by calculating pairwise Euclidean distances between all specimens and testing for the presence of significant differences using Permutational Multivariate ANOVA (Permanova, n . permutations = 999) using the function `adonis` in the package `vegan` in R version 4.0.1 (Oksanen et al., 2020; R Core

Team, 2021). Multivariate homogeneity of group dispersions, also based on the previously calculated distance matrix, was calculated using the function `betadisper` in the same R package and adding bias correction for small samples. Heteroscedasticity was assessed through permutation ($n = 999$) using the function `permutest` (also in the same package), while pairwise differences between groups were calculated using a post-hoc Tukey Honest Significance Difference test. The descriptive statistical analysis and ternary diagram were performed using the software PAST v.3.22 (PALaeontological Statistics) (Hammer et al., 2001), while for the box plots and all other statistical analyses we used the R package (R Core Team, 2021).

3 | RESULTS

The macrowear pattern of *Pan* is dominated by phase II areas, followed by lingual phase I, and buccal phase I facets (Table 1). *Gorilla* tooth wear is characterized by large phase II and lingual phase I facets, and by small buccal phase I facets. Finally, *Pongo* shows a similar macrowear pattern of those of *Gorilla*. In general, *Pan* shows a higher

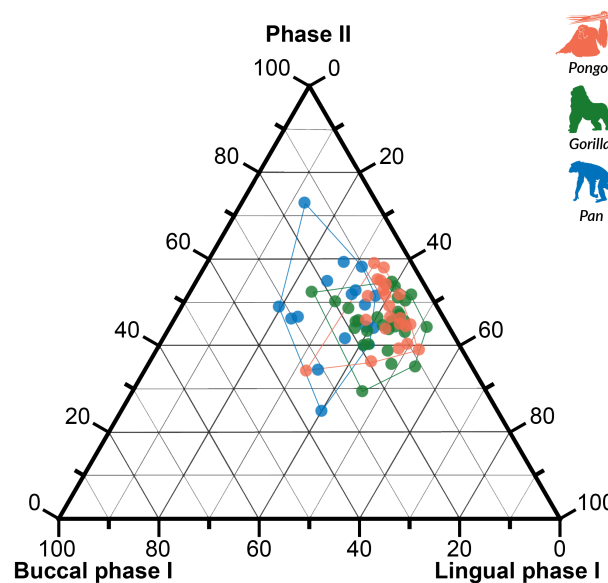


FIGURE 3 Ternary plot showing the proportions of relative wear facet areas in great ape lower molars (*Pongo* in orange, *Gorilla* in green, and *Pan* in blue). The three variables (buccal phase I, lingual phase I, and phase II) are positioned in an equilateral triangle

TABLE 1 Descriptive statistical analysis of wear facet areas with median, SD, and interquartile range (IQR)

Taxon	N	Buccal phase I			Lingual phase I			Phase II		
		Median	SD	IQR	Median	SD	IQR	Median	SD	IQR
<i>Pan</i>	18	16.91	7.84	14.89	34.04	8.19	13.58	47.91	10.92	12.16
<i>Gorilla</i>	28	12.10	5.79	9.471	43.23	6.07	6.50	45.64	5.86	6.50
<i>Pongo</i>	22	8.67	5.92	4.42	41.81	5.44	9.17	46.55	7.00	10.13

degree of variation for all chewing cycle facets considered in this study (Figure 3).

The one-way PERMANOVA test shows significant differences between *Pan* and *Gorilla* ($p = 0.0003$) and between *Pan* and *Pongo* ($p = 0.0009$). No statistically significant differences have been found between *Gorilla* and *Pongo* ($p = 1$). If we considered each chewing cycle phase individually, we can notice that statistically significant differences affect only the buccal and lingual phase I facets (Table 2). Specifically, statistically significant differences have been found

TABLE 2 Between-group comparisons (Mann–Whitney pairwise post-hoc test) of the relative areas of Buccal phase I, Lingual phase I, and phase II facets

Buccal phase I	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>
<i>Pan</i>	–	0.01749	1.02E-04
<i>Gorilla</i>	0.005831	–	0.5811
<i>Pongo</i>	3.39E-05	0.1937	–
Lingual phase I	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>
<i>Pan</i>	–	0.0002344	0.001583
<i>Gorilla</i>	7.81E-05	–	1
<i>Pongo</i>	0.00005278	0.6045	–
Phase II	<i>Pan</i>	<i>Gorilla</i>	<i>Pongo</i>
<i>Pan</i>	–	0.8551	1
<i>Gorilla</i>	0.285	–	0.6224
<i>Pongo</i>	0.9242	0.2075	–

Note: Significant p values (<0.005) are highlighted in bold. Corrected p values (Bonferroni correction multiplies the p values with the number of comparisons) are shown in the top right corner.

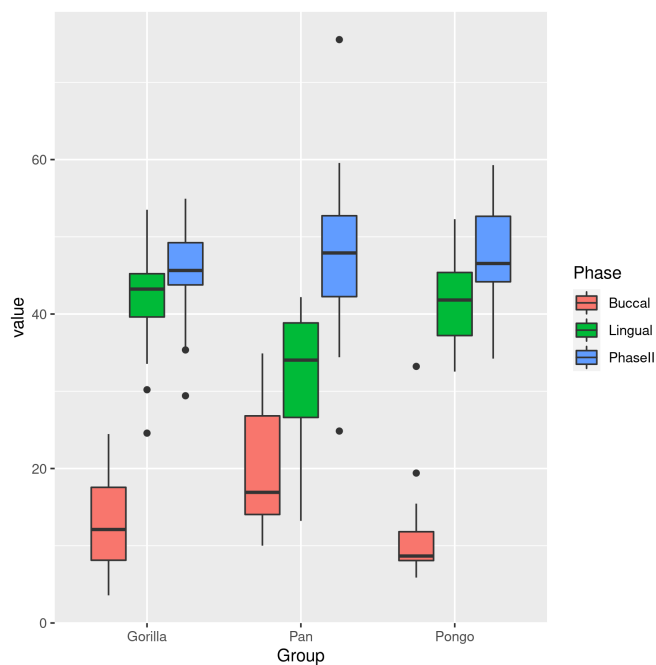


FIGURE 4 Box and whiskers plot showing the distribution of all buccal phase I, lingual phase I, and phase II wear facets across the three analyzed groups (*Gorilla*, *Pan*, and *Pongo*)

between *Pan* and *Pongo* and between *Pan* and *Gorilla* for buccal and lingual phase I facets. No differences have been found when we compared the relative phase II facet areas between *Gorilla*, *Pongo*, and *Pan*.

Although the sample size is reasonably balanced across the three analyzed groups, intragroup variability is not homogeneous. The distribution of individual values (Figure 4) exhibits a different

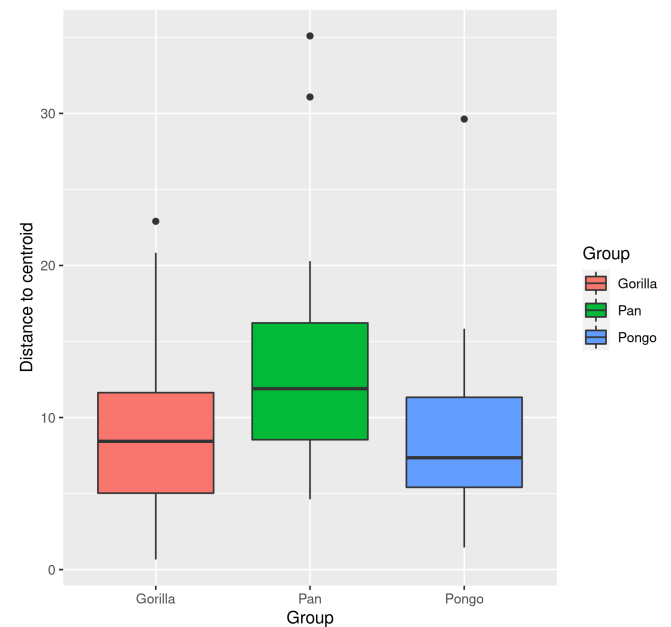


FIGURE 5 Box and whiskers plot showing the distribution of individual distances to group centroid. Measures are calculated on the principal coordinates obtained from multivariate homogeneity of group dispersions

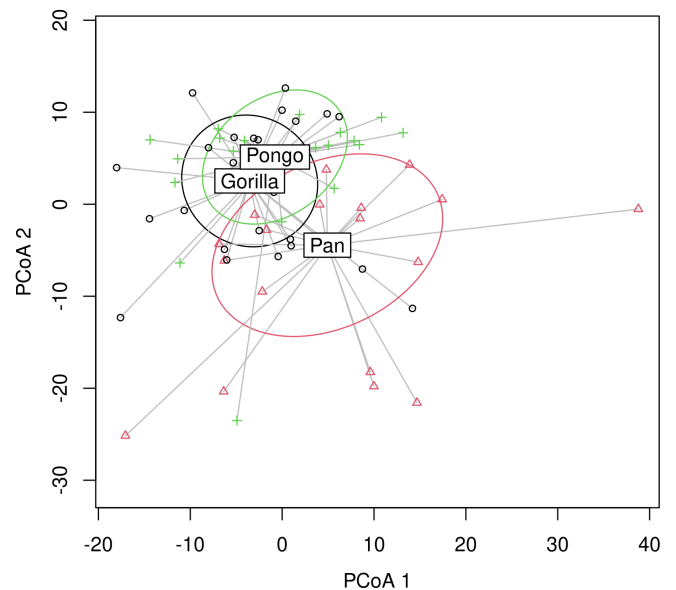


FIGURE 6 Projection of individual specimens and group centroids on the first two principal coordinate dimensions obtained from multivariate homogeneity of group dispersions. Confidence ellipses are calculated at one SD for the centroids

pattern in *Pan* compared to the other two groups, with higher Inter Quartile Dispersion in all variables. Phase II seems to be more consistently distributed across groups, while buccal and lingual phase I sections show marked differences across groups. The distribution of Euclidean distances to each group centroid (Figure 5 and Figure 6) exhibits higher values for *Pan* specimen than for either *Gorilla* or *Pongo*, although *Gorilla* specimens show a longer tail toward higher distances around the spatial median. These exploratory results are confirmed by the results of permutation test (Table 3) and Tukey test (Table 4) both of which suggest a significant difference between the variance of *Pan* and those of the remaining two groups, supporting the hypothesis of a higher variability within the former. Results of Permanova suggest a significant difference between *Pan* and the other groups in the distribution of distances based on all three dental wear variables (Table 5), although this result should be interpreted in the light of the possible confounding effect of heteroscedasticity.

4 | DISCUSSION

The molar macrowear results did not confirm our initial hypothesis of having larger crushing and grinding areas in *Pongo*, and more developed shearing areas in *Gorilla*. Although gorillas displays the larger shearing areas, these are not significantly larger than those of *Pongo*.

The macrowear pattern of *Pan*, on the other hand, differs significantly from those of *Gorilla* and *Pongo*, especially for the low lingual phase I values, mirroring its highly versatile diet, and confirming thus our second hypothesis. Unexpectedly, our results show closer similarities between *Pongo* and *Gorilla*, despite the exploitation of

significantly different foods, and despite differences in the primary morphology of their molars. This is probably due to the intake of mechanically challenging foods, highly fibrous in nature, which probably have a stronger effect on the formation of occlusal wear facets.

A recent study documented that western lowland gorillas can eat more mechanically challenging foods than expected including the endocarps of the seeds of *Coula edulis* (Van Casteren et al., 2019). This feeding behavior is generally not associated with a molar morphology characterized by thin enamel and high crests because of the risk of damage (Taylor, 2002). However, as suggested by a recent study, tooth strength in *Gorilla* is higher than in *Pongo* despite their significantly thinner enamel layer, indicating that gorillas could include hard seeds in their diets (Schwartz et al., 2020). Both *Pongo* and *Gorilla* are characterized by very large lingual phase I facets which indicate an increase in transverse mandibular movements. Previous macrowear studies have suggested that larger lingual facets are associated with an increased reliance on hard, abrasive foods including roots, seeds, gums, and other plant materials (Fiorenza et al., 2011; Janis, 1990), which could partly explain our results. In addition to this, the functional significance of phase II areas is still not clear (Krueger et al., 2008). Phase II facets are used during both phases of mastication, including crushing toward the end of phase I, and grinding during phase II (Kay & Hiiemae, 1974). Grinding is a combination of forces that act parallel and perpendicular to the contact planes producing a more horizontal and low-angled shear force (Wall et al., 2006). It is therefore possible that the consumption of terrestrial herbaceous foods, which requires prolonged exposure to repetitive mastication (Glowacka et al., 2017), can promote the formation of large phase II facets. It is also possible that differences in primary tooth morphology between *Gorilla* and *Pongo* molars, and more specifically in relief height, may affect the formation of wear facets (Knight-Sadler & Fiorenza, 2017). For instance, the presence of steeper phase I facets in gorillas may contribute to the formation of larger contact areas that are produced by lateroretrusive movements (Kullmer et al., 2009).

Moreover, although gorillas are traditionally portrayed as folivorous primates, they also consume large amounts of fruits (Grueter et al., 2013; Masi et al., 2009; Ostrofsky & Robbins, 2020). Specifically, there is a large dietary variation among gorillas, with the lowland gorillas being more frugivorous and the mountain gorillas

TABLE 3 Results of permutation test (N = 999) to assess for homogeneity of variances across the analyzed groups

Taxon	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>
<i>Gorilla</i>	-	0.21	0.94
<i>Pan</i>	0.02	-	0.033
<i>Pongo</i>	0.94	0.045	-

Note: Significant p values (<0.005) are highlighted in bold. Observed p values below the diagonal, permuted p values above the diagonal.

TABLE 4 Results of Tukey honest difference test showing pairwise differences between groups with corrected p-values

	Diff	Lower	Upper	p adjusted
<i>Pongo-Gorilla</i>	0.123786	-4.338374	4.585946	0.9975621
<i>Pan-Gorilla</i>	4.892078	0.1604116	9.623745	0.0411475
<i>Pan-Pongo</i>	4.768292	-0.2094556	9.74604	0.0632225

TABLE 5 Results of permutational multivariate ANOVA

	Df	SumSq	MeanSq	F	R ²	N. perm.	p-value
Groups	2	2153.3	1076.63	7.4211	0.18	999	0.001
Residuals	65	9430	145.08		0.81		
Total	67	11583.3			1		

relying more on herbaceous vegetation. Consequently, the heterogeneity of the gorilla sample examined in this study (Table S1) may be a confounding factor. Previous dental morphological and tooth wear studies have indicated a high degree of variation across the gorilla groups, which is probably related to ecological and dietary differences (Berthaume, 2016; Berthaume & Schroer, 2017; Elgart, 2010; Galbany et al., 2009; Galbany et al., 2016).

Several studies highlighted the importance of fallback foods in the diet, ecology, and evolution of non-human primates and early hominins (Cerling et al., 2011; Constantino et al., 2009; Ungar et al., 2008; Ungar & Sponheimer, 2011). Morphological specializations for fallback foods may have offered the possibility to consume a wider range of foods, especially important when preferred foods are in short supply (Constantino & Wright, 2009). Fallback foods are those foods of low nutritional values and more difficult to digest, which are eaten when preferred foods are scarce or unavailable (Wood & Schroer, 2012). Because these low-quality foods are more difficult to process, aspects of cranio-dental morphology, such as a general architectural robusticity, enamel thickness, and dental topography, are viewed as an adaptive response to evolutionary pressure imposed by fallback foods (Lambert, 2007; Marshall et al., 2009).

Preferred foods among chimpanzees (*Pan troglodytes*), Bornean orangutans (*Pongo pygmaeus*) and lowland gorillas (*Gorilla gorilla gorilla* and *Gorilla beringei graueri*) appears to be relatively soft, ripe fruits (Constantino et al., 2009). However, Bornean orangutans live in highly seasonal environments where the preferred foods are often unavailable (Fleming et al., 1987; Kanamori et al., 2010). Thus, during periods of ripe fruit scarcity, Bornean orangutans mostly rely on the consumption of fibrous and unripe fruits (such as wild figs), leaves, nuts, bark and, on rare occasions, wood and animal proteins (Kanamori et al., 2010; Knight-Sadler & Fiorenza, 2017; Mackinnon, 1974; Rijksen, 1978; Rodman, 1977; Sugardjito & Nurhuda, 1981; Taylor, 1998, 2002, 2006; Utami Atmoko & Van Hoff, 1997). Some of the fallback foods eaten by orangutans can be extremely hard and mechanically challenging to process. For example, laboratory tests on fracture toughness of certain foods consumed by orangutans in the wild, such as *Mezzetia* seeds, estimated a maximum bite force of 6000 N in order to break them down, a force that probably exceeds the orangutans' capacities (Lucas et al., 1991; Lucas et al., 1994). It is probably for this reasons that *Pongo* is frequently characterized by chipped teeth, suggesting that they frequently use high forces to process hard foods such as seeds and nuts (Constantino et al., 2012). Western lowland gorillas generally prefer soft and ripe fruits, while Grauer's and mountain gorillas rely more on terrestrial herbaceous vegetation (THV) such as leaves, barks, and pith (Yamagiwa et al., 2005). THV foods are characterized by high fracture toughness due to the amount of fibers they contain (Lucas et al., 2000), and bark and woody pith are among some of the toughest material eaten by living great apes (Constantino et al., 2009; Dominy, 2001; Elgart-Berry, 2004).

Tooth wear is caused by different mechanisms acting together, each with varying intensity and duration, producing, thus, a multitude of different wear patterns (Kaidonis, 2008). It is therefore difficult to

either determine the major cause of wear or to evaluate how different wear mechanisms have interacted (Addy & Shellis, 2006). It is possible that even the chewing of small quantities of mechanically demanding foods may play a larger role in the formation of molar macrowear patterns, masking the signals generated by the consumption of softer foods.

Chimpanzees are the most frugivorous of great apes, and differently from gorillas and orangutans, it tends to continue searching out ripe fruits expanding their home range (Furuichi et al., 2001), rather than heavily relying on fallback foods during periods of fruit scarcity. However, fruit in savannah habitats is less abundant and more widely distributed. Thus, western chimpanzees look also for alternative resources, consuming larger amount of low-quality and leafy foods than other chimpanzee populations (McGrew et al., 1988; Pruetz, 2006).

Tooth wear is the enamel loss produced by different mechanisms acting over the occlusal surface, such as attrition, abrasion, and erosion (e.g., Kaidonis, 2008; Kaifu et al., 2003). Analyses of macrowear patterns help to reconstruct the attritional movements generated during the mastication of food, and therefore they provide indirect evidences of individual's diet (e.g., Fiorenza et al., 2011; Kullmer et al., 2009; Silvester et al., 2021). At the same time, tooth wear helps in maintaining masticatory efficiency throughout the lifetime of an individual (Lee et al., 2021), by reducing the gaps between antagonistic contacts, and by changing the stress distribution and decreasing the tensile stress acting over the tooth surface (Benazzi, Nguyen, Kullmer, & Hublin, 2013; Benazzi, Nguyen, Schulz, et al., 2013).

Finally, it is important to underline some limitations in our current study. First, the analysis is limited to a relatively small sample size. Moreover, the sample used in this study is rather heterogenous and it consists of museums specimens where often the information about the age of the individual was unknown, and the geography was frequently uncertain, especially for *Gorilla* and *Pongo*. Consequently, our interpretations about the diet of these ape groups should be taken with caution. It is desirable to extend this work including more specimens and considering other tooth types and different wear stages to see if macrowear patterns change throughout the life of an individual. Future studies could investigate if dietary difference exist at the subspecies level in the African and Asian apes. Moreover, the integration of OFA with biomechanical methods could provide more information for a better interpretation of diet and ecology in great apes (Benazzi, Nguyen, Kullmer, & Hublin, 2013; Benazzi, Nguyen, Schulz, et al., 2013; Fiorenza et al., 2015).

AUTHOR CONTRIBUTIONS

Luca Fiorenza: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (lead); investigation (lead); methodology (equal); project administration (lead); resources (equal); software (equal); supervision (equal); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (lead). **Teagan Harty:** Formal analysis (supporting); investigation (supporting). **Marcel M. Janocha:** Formal analysis (supporting); investigation (supporting). **Ottmar Kullmer:** Conceptualization (supporting);

data curation (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); resources (supporting); software (equal); supervision (supporting); validation (supporting); writing – review and editing (supporting). **Huynh N. Nguyen:** Conceptualization (supporting); formal analysis (equal); investigation (supporting); methodology (equal); software (equal); supervision (supporting); validation (supporting); visualization (supporting); writing – review and editing (supporting). **Eugenio Bortolini:** Formal analysis (supporting); visualization (supporting); writing – review and editing (supporting). **Stefano Benazzi:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (supporting); resources (equal); software (equal); supervision (equal); validation (equal); visualization (equal); writing – review and editing (supporting).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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