Dental Macrowear Reveals Ecological Diversity of *Gorilla Spp.*

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Abstract

Size and shape variation of molar crowns in primates plays an important role in understanding how species adapted to their environment. Gorillas are commonly considered to be folivorous primates because they possess sharp cusped molars which are adapted to process fibrous leafy foods. However, the proportion of fruit in their diet can vary significantly depending on their habitats. While tooth morphology can tell us what a tooth is capable of processing, tooth wear can help us to understand how teeth have been used during mastication. The objective of this study is to explore if differences in diet at the subspecies level can be detected by the analysis of molar macrowear. We analysed a large sample of second lower molars of Grauer’s, mountain and western lowland gorilla by combining the Occlusal Fingerprint Analysis method with other dental measurements. We found that Grauer’s and western lowland gorillas are characterised by a macrowear pattern indicating a larger intake of fruit in their diet, while mountain gorilla’s macrowear is associated with the consumption of more folivorous foods. We also found that the consumption of herbaceous foods is generally associated with an increase in dentine and enamel wear, confirming the results of previous studies.

Introduction

Gorillas have been traditionally described as specialised folivorous primates based on the early behavioural studies from populations of the Virunga Mountains[1,2]. However, additional ecological studies have shown that the most common gorillas, who inhabit western lowland rainforests, eat a considerable variety of foods including large amounts of fruits[3,4] (Fig. 1).

Gorillas are found in Central and Western Equatorial Africa, and they are separated by the Congo River into western and eastern gorillas[6]. The western gorillas are divided into two subspecies, the western lowland gorillas (*Gorilla gorilla gorilla*; Savage, 1847) and the Cross River gorillas (*Gorilla gorilla diehli*; Matschie, 1904)[7]. The western lowland gorillas are distributed in southern Cameroon, Equatorial Guinea, Gabon, Republic of Congo, northern Angola, and western Democratic Republic of Congo, while the Cross River gorillas can be found in a small region of highland forests located along the borders of Cameroon and Nigeria[6,8]. Cross River gorillas are vastly understudied, but data suggests they have diets similar to other western lowland gorillas[9].

The eastern gorillas consist of two subspecies: mountain gorillas (*Gorilla beringei beringei*; Matschie, 1903), and eastern lowland gorillas, or Grauer’s gorillas (*Gorilla beringei graueri*; Matschie, 1914)[7]. The mountain gorillas live in the high-altitude rainforests of Virunga Volcanoes, along the borders between Rwanda, Democratic Republic of Congo and Uganda, and in the Bwindi Impenetrable Forest between the southwest of Uganda and northwest Rwanda[6]. Grauer’s gorillas can be found in eastern forests of the Democratic Republic of Congo[6,8].

When rainfall is low and fruit is scarce, gorillas inhabiting lowlands rely on more herbaceous foods, including leaves, stems, pith and barks[10]. These foods fall into the general categories of terrestrial herbaceous vegetation (THV) and aquatic herbaceous vegetation (AHV). While less common, other foods, like the woody endocarps of the *Coula edulis* seeds, are incorporated in the diets of some populations of western lowland gorillas, indicating a broader dietary spectrum than previously thought[11]. Both western lowland gorillas and Grauer's gorillas prefer relatively soft, ripe fruits[10,12]. However, the percentage of THV consumed by western lowland gorillas and Grauer's gorillas differs, with a larger amount of fibrous food eaten by the eastern populations[13]. On the other hand, mountain gorillas mostly rely on THV foods, which is available year-round, while fruit, especially in the high-altitude forests of the Virunga Mountains, are relatively scarce throughout the year[2,14,15].

Dental functional studies have found that mountain and Grauer's gorillas are characterised by molars with duller cusps compared to western lowland gorillas[16]. When duller cusps wear, they create longer compensatory crests, increasing the contact areas between the sharp blade-like crests on the molars and the food particles. This provides a functional advantage compared to molars with sharper cusps, as it increases the cutting surfaces for processing fibrous foods[17]. Another study utilised the Dirichlet Normal Energy (DNE; a dental topographic method) to analyse the diet of seven groups of great apes, finding a positively correlation between DNE and fibre content in apes among sympatric pairs[18]. Significant differences were observed between Grauer's and mountain gorillas, and between western lowland and Grauer's gorillas. DNE is a measure of surface curvature, meaning higher DNE values are found in curvier, or sharper, teeth, providing a mechanical advantage for breaking down foods with a high fibre content[19].

Moreover, a study based on buccal microwear signals found geographic differences between various populations of Grauer's gorillas which were attributed to ecological conditions[20]. Dental microwear texture analyses have compared western lowland gorillas with mountain gorillas without finding any clear differences between the two groups[21]. This is probably due to dietary overlap between mountain and lowland gorillas, that may be larger enough that microwear differences are not observable. In addition to this, tooth microwear signatures can change very rapidly, yielding information only about an individual's diet in the weeks or even days before its death[22]. In turn, a recent study in chimpanzees revealed that dental microwear texture can provide information about short-dietary changes, such as seasonality, but are less effective in providing long-term dietary signals[23]. Elgart[24] correlated the toughness of food with the amount of dental wear in *Gorilla*, finding some inconclusive results in relation to their diet, potentially due to complications in gathering dietary mechanical property data[25]. Galbany and colleagues[26] measured the percentage of dentine exposure (PDE) in permanent molars of mountain gorillas from the Volcanoes National Park (Rwanda), finding a significant relationship between the degree of tooth wear with the consumption of plant roots at the individual level.

However, we still do not comprehensively understand if ecological constraints and dietary differences observed in gorilla subspecies are reflected in tooth wear. The aim of this study is to explore if differences in diet in gorillas can be detected at the subspecies level by using molar macrowear analyses in combination with various dental measurements.

Dental macrowear, as opposed to dental microwear, is a cumulative process, which occurs during the individual's lifetime and thus reflects long-term dietary and environmental history[27,28]. Here we examine the macrowear patterns of second lower molars (M2s) in a large sample of western lowland gorilla, Grauer's gorillas and mountain gorillas by combining the Occlusal Fingerprint Analysis method (OFA)[29], a well-established digital approach tracking changes in dental function by examining occlusal wear facets (planar areas with well-defined edged boundaries produced by the attritional and abrasional contact between upper and lower teeth), with other dental measurements, including the occlusal relief index (OR), PDE and percentage of enamel wear (PEW). OR has been widely used to reconstruct primate diets, and it is based on the assumption that folivorous species should be characterised by a high relief because it increases the efficacy in processing fibrous and tough foods such as leaves[30].

We expect to find differences in molar macrowear patterns between the folivorous mountain gorillas with the more frugivorous eastern and western lowland gorillas. We also expect to find a more complex occlusal morphology with sharper cusps in mountain gorillas enhancing comminution of fibrous foods such as leaves and stems. Finally, we also explore if there are any differences in molar macrowear between males and females of western lowland gorillas. Gorillas are characterised by a marked sexual dimorphism, with adult males often weighting twice as much as females[31]. This marked body size difference is reflected also in the nutritional requirements, with males spending more time in feeding than females[32]. Because prolonged chewing times have an effect on tooth wear, we expect to find a greater amount of wear in males than in females.

Results

Overall, gorillas are characterised by small buccal phase I facets, and larger phase II and lingual phase I facets (Table 1). During the earlier wear stages, the macrowear patterns of the three gorilla groups look similar, with differences emerging only at the later wear stages (Fig. 2).

The macrowear pattern of mountain gorillas is dominated by large phase II facets (between 51% and 67%), followed by lingual (between 30% and 40%) and buccal phase I facets (between 3% and 6%). The macrowear pattern of Grauer's gorillas is rather homogenous compared to the other two groups and is characterised by large lingual phase I facets (between 33% and 53%), followed by phase II facets (between 42% and 49%), and by buccal phase facets (between 7 and 11%). Finally, western lowland gorillas show the most variable molar macrowear pattern, with large lingual phase I facets (between 38% and 44%) and phase II facets (between 47% and 48%), and small buccal phase I facets (between 5% and 9%).

No statistically significant differences were found when comparing molars with wear stage 1 (Table S1).

Table 1
Summary statistics (median and SD) of relative wear facet areas divided by wear stages.

		Buccal P I		Lingual P I		PII	
Wear 1	**N**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**
G. b. beringei	5	0.04	0.05	0.39	0.07	0.51	0.08
G. b. graueri	3	0.11	0.06	0.33	0.05	0.49	0.03
G. g. gorilla	13	0.05	0.04	0.38	0.08	0.48	0.08
Wear 2 & 3	**N**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**
G. b. beringei	4	0.06	0.07	0.40	0.04	0.51	0.09
G. b. graueri	18	0.11	0.04	0.45	0.04	0.45	0.06
G. g. gorilla	54	0.09	0.06	0.44	0.06	0.47	0.05
Wear 4	**N**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**
G. b. beringei	1	0.03	-	0.30	-	0.67	-
G. b. graueri	4	0.07	0.06	0.53	0.05	0.42	0.03
G. g. gorilla	10	0.08	0.13	0.44	0.06	0.48	0.08

Statistically significant differences were found when comparing lingual phase I facets of mountain gorillas with those of Grauer's gorillas ($p = 0.040$; Wear stage 2 & 3). No differences have been found between molars with wear stage 4. However, the only mountain gorilla with wear 4 included in this analysis looks very different compared to Grauer's and western lowland gorillas (Fig. 2).

Gorilla molars are generally characterised by steep facets, with average angles of phase I and phase facets comprised between 26 and 47 degrees (Table 2). Tip crush areas are relatively flat, with values comprised between 8 and 16 degrees. Phase II facets show much steeper angles if compared to phase I facets, especially in slightly worn molars. The opposite situation is found in more heavily worn molars with phase I facets characterised by higher values if compared to the planes of phase II facets. The mountain gorillas generally display the steepest wear facets, while western lowland and Grauer's gorillas tend to have more variable inclinations depending on the wear stage considered. We could not statistically test if mountain gorillas facet inclinations differ from those of Grauer's and western lowland gorillas, because we could not group together molars with wear stage 2 with molars with wear stage 3. We could only compare the wear facet angles of molars with wear stage 1, which did not produce any statistically significant difference 1 (Table S2). The only statistically significant difference has been found between the buccal phase I facets of Grauer's and western lowland gorillas ($p = 0.016$; Wear 2).

Table 2
Summary statistics (median and SD) of wear facet inclinations divided by wear stages.

		Buccal P I		Lingual PI		Phase II		Tip crush	
Wear 1	**N**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**
G. b. beringei	5	32.76	6.54	38.03	4.56	46.5	6.01	16.42	7.32
G. b. graueri	3	32.00	7.84	36.66	3.90	41.94	1.88	0.00	12.48
G. g. gorilla	13	29.43	6.02	40.55	4.40	44.75	4.70	0.00	9.54
Wear 2	**N**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**
G. b. beringei	2	24.23	0.35	31.49	1.44	41.98	1.040	11.87	16.78
G. b. graueri	9	35.01	2.55	36.74	5.75	38.97	5.08	11.36	8.17
G. g. gorilla	27	29.40	5.17	38.62	5.40	37.4	4.63	15.94	7.37
Wear 3	**N**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**
G. b. beringei	2	39.58	10.63	37.00	14.26	32.83	2.46	10.06	3.49
G. b. graueri	9	31.90	8.96	35.68	2.56	34.83	4.62	12.12	1.73
G. g. gorilla	27	32.73	7.44	37.30	3.72	32.23	5.53	13.13	5.99
Wear 4	**N**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**
G. b. beringei	1	36.81	***	30.64	***	33.40	***	7.75	***
G. b. graueri	4	28.40	15.49	37.57	2.64	28.70	1.59	11.46	5.50
G. g. gorilla	10	26.64	8.12	34.71	3.42	29.28	7.73	14.49	4.67

Mountain gorillas display lower OR values compared to those of western lowland gorillas (Table 3).

Table 3
Summary statistics (median and SD) of occlusal relief index (OR), percentage of dentine exposure (PDE) and percentage enamel wear (PEW).

		OR		PDE		PEW	
Groups	**N**	**Median**	**SD**	**Median**	**SD**	**Median**	**SD**
G. b. beringei	10	1.895	0.133	0.245	3.156	20.215	8.540
G. b. graueri	25	1.990	0.190	1.660	3.550	24.290	6.600
G. g. gorilla	77	2.040	0.268	0.760	3.400	26.830	7.760

This is also confirmed by the statistical comparative analysis ($p = 0.006$) (Table S3). Overall, western lowland gorillas are also characterised by the highest degree of variation in OR, while the least variable are the mountain gorillas.

Grauer's gorillas display intermediated OR values.

In terms of PDE, Grauer's gorilla show the highest values, followed by western lowland gorillas and mountain gorillas (Table 3). No statistically significant differences have been found when comparing PDE values between the gorillas examined in this study (Table S2).

Western lowland gorillas are generally characterised by the highest PEW values, followed by Grauer's and mountain gorillas (Table 3). We found statistically significant differences in PEW values between western lowland and Grauer's gorillas ($p = 0.039$) and between mountain and western lowland gorillas ($p = 0.023$) (Table S2). Finally, no statistically significant differences have been found between males and females of western lowland gorillas for all variables considered in this study (Tables S4, S5 and S6).

Discussion

We have found significant differences in molar macrowear patterns between mountain gorillas and lowland gorillas, confirming our initial hypothesis. Grauer's and western lowland gorilla molar macrowear patterns are dominated by lingual phase I facets, which is probably associated with a larger intake of fruit in their diet. Previous studies of molar macrowear on various ungulate mammals and of colobus monkeys suggested that lingual phase I facets are linked to the consumption of softer food items such as fruit[27]. However, we found that the eastern lowland gorillas display the largest lingual phase I facets, especially at the most advanced wear stages. We would have expected to find the largest lingual phase I facets in western lowland gorillas, considering their more frugivorous diet[33]. We observe this trend only when examining slight worn molars, while at intermediate levels of wear the proportion of lingual phase I facets in eastern and western lowland gorillas is similar. Larger lingual phase I facets are possibly correlated with greater transverse mandibular movements, which may also indicate the consumption of foods other than fruit such as roots, seeds and gums[27,34]. Mountain gorilla molars are characterised by largest phase II facets which seem to be associated with a greater consumption of THV foods. Contrary to previous findings, where higher degrees of folivory was linked to larger buccal phase I facets[27], here we found that the consumption of herbaceous food is associated with an increase of the proportion of phase II facets and tip crush areas. Buccal phase I facets are very small in all gorillas examined in this study at any given wear stage. This seems to be very common in all great apes, which would indicate a distinctive masticatory behaviour compared to early and late hominins[35]. The functional significance of phase II facets is still highly debated[36]. Phase II facets are used during both phases of mastication, including crushing (phase I) and grinding (phase II)[37]. Grinding is a combination of forces that act parallel and perpendicular to the contact planes producing a more horizontal shear force[38]. Consequently, the consumption of THV foods, which requires prolonged exposure to repetitive mastication[39], probably promote the formation of large phase II facets.

As expected, the western lowland gorillas show the highest degree of macrowear variation, suggesting a more flexible diet if compared to those of eastern gorillas. Western lowland gorillas occupy a large geographical area, ranging between the southern part of Cameroon to North Angola[8]. They also inhabit a variety of lowland forest types, including open and closed-canopy forests, and vast swamps in northern Congo[6]. Western lowland gorillas eat a wide variety of fruit, preferring ripe, succulent, sweet fruits that are low in proteins and fat[4]. However, fruit productivity is highly seasonal, and therefore the preferred food of western lowland gorillas is not always available. During these periods of fruit scarcity, western lowland gorillas consume larger quantity of THV, including pith, shoots, leaves and barks[33]. Moreover, some populations of western lowland gorillas regularly consume AHV, which are high in essential vitamins and minerals[4,8], while evidence of seasonal hard-object feeding has been documented in one population of western lowland gorillas from Loango National Park, Gabon[11].

Grauer's gorillas and the mountain gorillas show a less variable macrowear pattern suggesting the intake of a less diverse diet if compared to western lowland gorillas. Mountain gorillas occupy high altitude forests, which are characterised by a significant lower diversity of plants and fewer fruits[39]. Grauer's gorilla's diet is more variable than those of mountain gorillas. At higher altitude the diet mostly consists of THV foods, like mountain gorillas, while the populations from lower elevations incorporate more fruit in their diets[3,6].

Mountain gorillas are generally characterised by steeper phase II facets, probably increasing the shearing capabilities, which is functionally advantageous in processing tough and pliant foods such as leaves[28]. This is very different from the wear patterns observed in late *Homo*, where phase II facets are significantly flatter than buccal and lingual phase I facets[40]. Significant differences in inclination of buccal phase I facets between eastern and lowland gorillas are probably linked to the consumption of THV foods. Although the buccal phase I facets play a little role in gorilla chewing behaviour, their steeper planes in Grauer's gorillas increase their shearing capacity, more suitable for processing herbaceous vegetation. We observe the same pattern in mountain gorillas, but because of the small sample size we could not test if there were any statistically significant differences with western lowland gorillas.

While the percentage of dentine exposure is negligible in slightly worn molars, we noticed larger PDE values in more advanced wear stages in the mountain and eastern lowland gorillas. This could be correlated with the increased amount of THV foods included in their diet. Feeding time in primates increases as toughness increases[41]. A previous study has shown that PDE in mountain gorillas from the Virunga National Park was positively correlated with the time spent consuming plant roots[26]. This was also probably correlated with the amount of exogenous material accidentally introduced in their diet, which is more likely to cause increased tooth wear[42]. It has been observed that mountain gorillas pull out the plants out from the soil to access the roots without properly eliminating all the gritty particles that cover the plants[26]. We have also observed that the molars of western lowland gorillas are generally characterised by a higher occlusal relief index compared to those of mountain and Grauer's gorillas, partially confirming the results of Berthaume's study[16] who found that western lowland gorillas were characterised by sharper cusps compared to mountain and Grauer's gorillas.

Mountain gorillas are characterised by the least amount of wear (PEW) compared to western lowland and Grauer's gorillas, confirming the results of previous studies[24,26]. This would indicate that mountain gorilla molars maintain a good chewing efficiency throughout the life of an individual despite the mechanically demanding diet[24]. Similarly, the high PEW values of western lowland gorillas are in agreement with Elgart's study[24], where it was found that the western populations showed the highest quantities of wear.

Finally, dental topographic and macrowear analyses of western lowland gorilla molars did not reveal any difference between males and females, rejecting thus out initial hypothesis. Previous studies support these results as it was found that there were no differences in occlusal relief and in the amount of wear between males and females of western lowland gorillas[24,30]. Previous studies have also identified that western lowland gorilla males in Bai Hoköu, Central African Republic, spend less time feeding and more time resting compared to females and immatures in their group[33].

It is important to consider some limitations in our current study. First of all, the sample size of mountain gorillas is rather small, and therefore our interpretations need to be taken with caution. Unfortunately, most of the museum collections we examined included only a small number of mountain gorillas. Their teeth were often heavily worn and chipped, preventing thus their inclusion for the occlusal fingerprint analysis. Moreover, because our sample mostly consists of museum specimens, the age of the individual was often unknown, and the geography was frequently uncertain. This additional information could have been very useful with the interpretation of the results. For example, a recent study of dental wear patterns in chimpanzee populations from precise geographic locations revealed previous information for the ecological interpretations of their results[23]. Future studies could include a larger sample of mountain gorillas, and could also compare the analysis of permanent and deciduous dentition to examine if there are any dietary difference between adult and immature individuals.

In this study we have demonstrated that the OFA approach is able to detect ecomorphological signals and can detect dietary differences in *Gorilla* even at the subspecies level. Specifically, Grauer's and western lowland gorillas are characterised by a macrowear pattern indicating a larger intake of fruit in their diet, while mountain gorilla's macrowear is associated with the consumption of more folivorous foods. Moreover, western lowland gorillas show the most variable wear patterns which is probably associated with their more flexible diet. We also found that the consumption of THV foods is generally associated with an increase in dentine and enamel wear, confirming the results of previous studies. Finally, no differences have been found between males and females of western lowland gorillas, suggesting no sex differences in diet. Future studies could investigate if dietary difference exist at the subspecies level in the other African and Asian apes. Moreover, the integration of OFA with other dental topographic methods could provide more information for a better interpretation of diet and ecology in great apes.

Materials And Methods

Ethical statement. No live animals were handled in this study.

The sample examined consists of 112 gorilla specimens, including 10 *Gorilla beringei beringei*, 25 *Gorilla beringei graueri*, and 77 *Gorilla gorilla gorilla*. We selected only fully erupted M2s (either left or right, but no antimeres) because they provide a good general overview of the development of masticatory function in primates[43]. We included only molars with a slight to moderate degree of wear because in heavily worn teeth occlusal facets tend to coalesce often preventing a clear identification[34]. We qualitatively evaluated the level of wear based on the amount of dentine exposure and cusp removal (wear stages 1-4)[44]. When available we included from museum records[45] information about age (subadult and adult), sex and locality (electronic supplementary material, Table S7).

Occlusal Fingerprint Analysis (OFA)

Three-dimensional (3D) digital models of teeth were post-processed using Polyworks® V12 (InnovMetric Software), a 3D metrology software. OFA consists of four consecutive steps: 1) model orientation, 2) facet identification, 3) facet area, and 4) facet inclination[29]. The polygonal models are oriented using a reference plane that is created along the cervical line of the tooth through the least square best-fit method. Successively, the reference plane is rotated to the *xy* plane obtained from the original coordinate system.

The identification of wear facets follows the numbering system originally created by Maier and Schneck[46] and later modified by Kullmer and colleagues[29]. Facets 1, 1.1, 2, 2.1, 3 and 4 develop along the buccal slopes of protoconid, hypoconid and hypoconulid, while facets 5, 6, 7 and 8 form along the buccal slopes of the metaconid and entoconid (Fig. 3). These facets are created during the initial phase of the rhythmic chewing cycle (phase I), and they can be further divided into buccal (facets 1-4) and lingual (facets 5-8) facets[37]. Facets 9, 10, 11, 12 and 13 are formed during the second phase of the rhythmic chewing cycle (phase II), when the mandibular molars move out of occlusion. These facets develop along the lingual slopes of protoconid, hypoconid and hypoconulid.

During the rhythmic chewing cycle, the food bolus is initially processed by shearing, which is generated by forces parallel to the contact plane (phase I), followed by crushing between basins and cusps of molars, where the occlusal force is perpendicular to the contact plane[37]. After the molars reach centric occlusion (phase II), the food bolus is processed by grinding, which is the resulting action of the combination of perpendicular and parallel forces to the contact plane.

We also identify tip crush areas, which are generally formed during puncture-crushing, when food is initially pulped by a series of masticatory cycle where tooth-to-tooth contacts do not occur[27]. Finally, we identify three additional facets in gorilla molars: facet 5.1, facet 8.1 and facet 10.1. These facets are created by the presence of additional dental traits, which are less common in *Homo*. More specifically, facets 5.1 forms in mandibular molars around the area of cusp 7 (C7), and it occludes with maxillary molars in proximity of the lingual cingulum[47]. Facet 8.1 forms around cusp 6 (C6) and it occludes with the lingual cingulum of the maxillary molars in correspondence of the mesiolingual aspect of the protocone[48]. Facet 10.1 has been previously described in Neanderthal molars, and it is created by the contact between the distolingual slope of the metaconule of the maxillary molar with the mesiolingual slope of the protoconid[49]. Facets 5.1 and 8.1 are grouped with lingual phase I facets, while facet 10.1 is considered a phase II facet.

Once the facets have been identified, we automatically calculate the surface area using the *area* function available in Polyworks® V12 (InnovMetric Software). To facilitate the analysis of the occlusal contact areas we grouped phase II facets together with tip crush areas, and divided the phase I facets into buccal and lingual facets[34]. However, tip crush areas and phase II facets have been kept separated for the analysis of facet inclination, considering they are characterised by significant different angles[40]. Because larger teeth generally develop larger facets than smaller teeth, we eliminate the size factor by using relative areas only. Relative areas are calculated by dividing the absolute area of a facet with the total wear area (TWA), which is the sum of absolute area of all facets[34]. The facet inclination is calculated by measuring the angle between the reference, or cervical plane, with the facet plane, which is created by selecting all triangles within its perimeter and by applying the best-fir plane function of Polyworks® V12 (InnovMetric Software) (electronic supplementary material, figure S1).

Occlusal relief index (OR)

The occlusal relief index (OR) was calculated by dividing the 3D area by the two-dimensional (2D) area of the occlusal surface[50]. The occlusal plane, parallel to the cervical plane, was translated along the *y* axis until it reached the deepest point of the occlusal surface, known as the central fossa. Next, the digital model was sliced, with respect to the occlusal plane, and the 2D area was calculated. The 3D area was calculated by selecting all triangles of the polygonal models above the occlusal plane (electronic supplementary material, figure S2).

Percentage of dentine exposure (PDE) and enamel wear (PEW)

To calculate the percent of dentine exposure (PDE) is obtained by dividing the sum of total dentinal areas for each tooth by the 3D occlusal area and then multiplied by 100[26]. The percentage of enamel wear (PEW) is obtained by dividing the total wear area (TWA) with the 3D occlusal area and then multiplied by 100.

Statistical analysis

We employed summary statistical analyses (median and standard deviation, SD) for each variable considered in this study. Because we further divided our sample according to wear stages 1 to 4[44] the comparative groups became relatively small. As the presence of a small sample size prevents the assumption of a normal distribution, we used the nonparametric Mann-Whitney pairwise test, to test whether two univariate samples are taken from populations with equal medians[51].

For the analysis of facet areas, we grouped together molars characterised by wear stage 2 and wear stage 3 in order to maximize the sample size. We then tested if we could combine these two groups by comparing molars wear stage 2 with molars wear stage 3 of western lowland gorillas without finding any statistically significant result (Table S8). However, for the inclination we kept the molars separated by their wear stages, because the level of wear strongly influences the values of these variables[40]. OR, PDE and PWE were not separated into different wear stage groups. All statistical analyses have been performed using the software PAST v4.04 (Paleontological Statistics)[52].

Declarations

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Figures

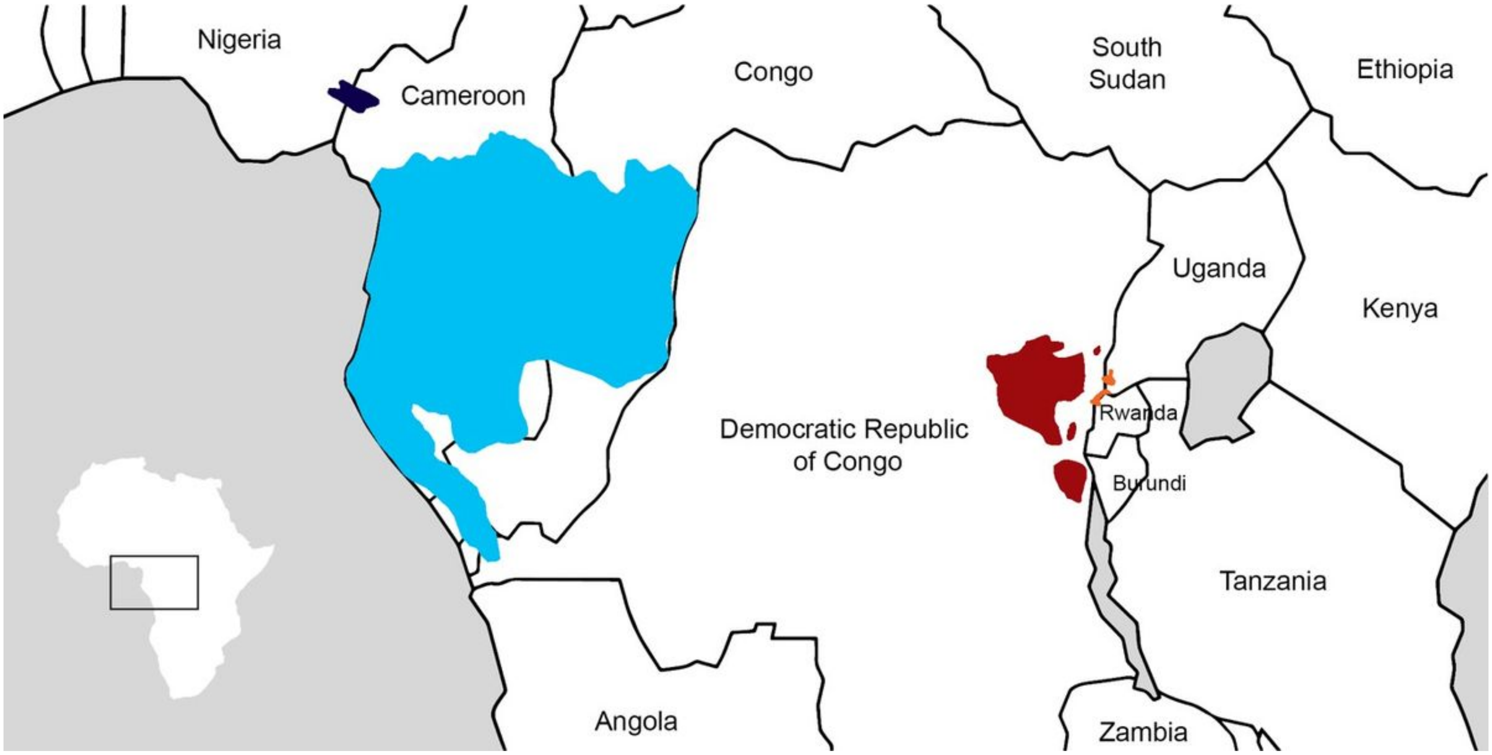

Figure 1

Map of Sub-Saharan Africa showing the distribution of western lowland gorillas (*Gorilla gorilla gorilla*, in light blue), cross river gorillas (*Gorilla gorilla diehli*, in dark blue), Grauer's gorillas (*Gorilla beringei graueri*, in dark red), and mountain gorillas (*Gorilla beringei beringei, in orange*). Adapted from Xue et al.[5].

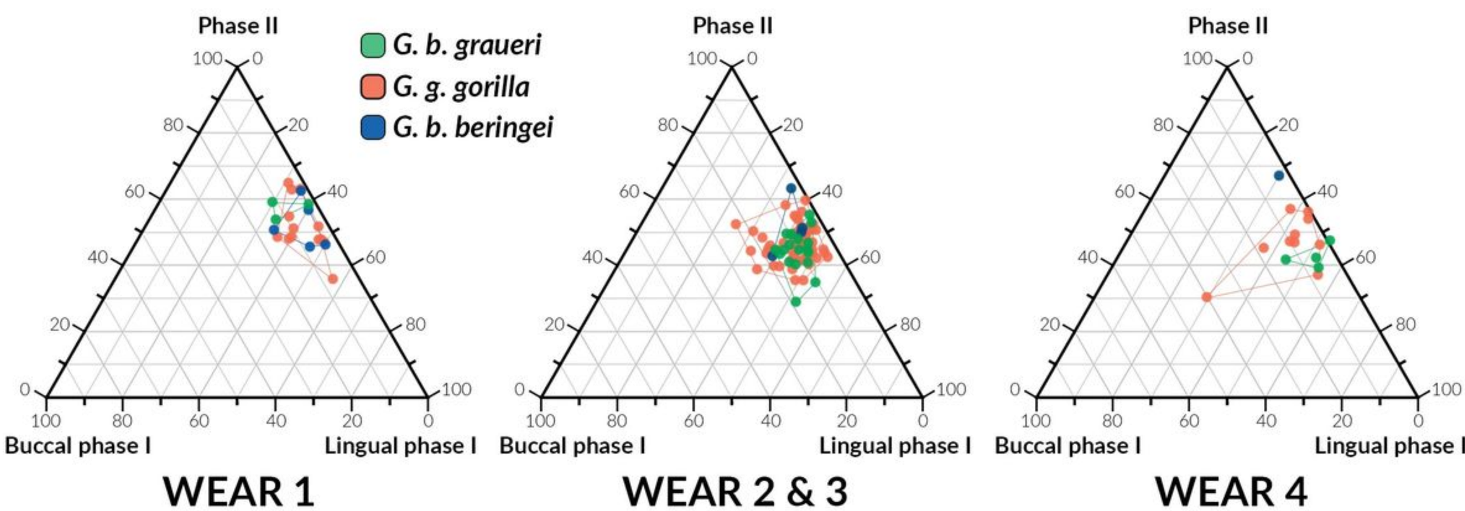

Figure 2

Ternary diagrams showing the proportions (in %) of relative wear areas of buccal phase I facets, lingual phase I facets, and phase II facets, which are positioned in an equilateral triangle. Each base of the triangle represents a ratio of 0% while the vertices correspond to a percentage of 100%. Tip crush areas were included in phase II facets. *Gorilla beringei graueri* in green, *Gorilla gorilla gorilla* in orange, and *Gorilla beringei beringei* in blue.

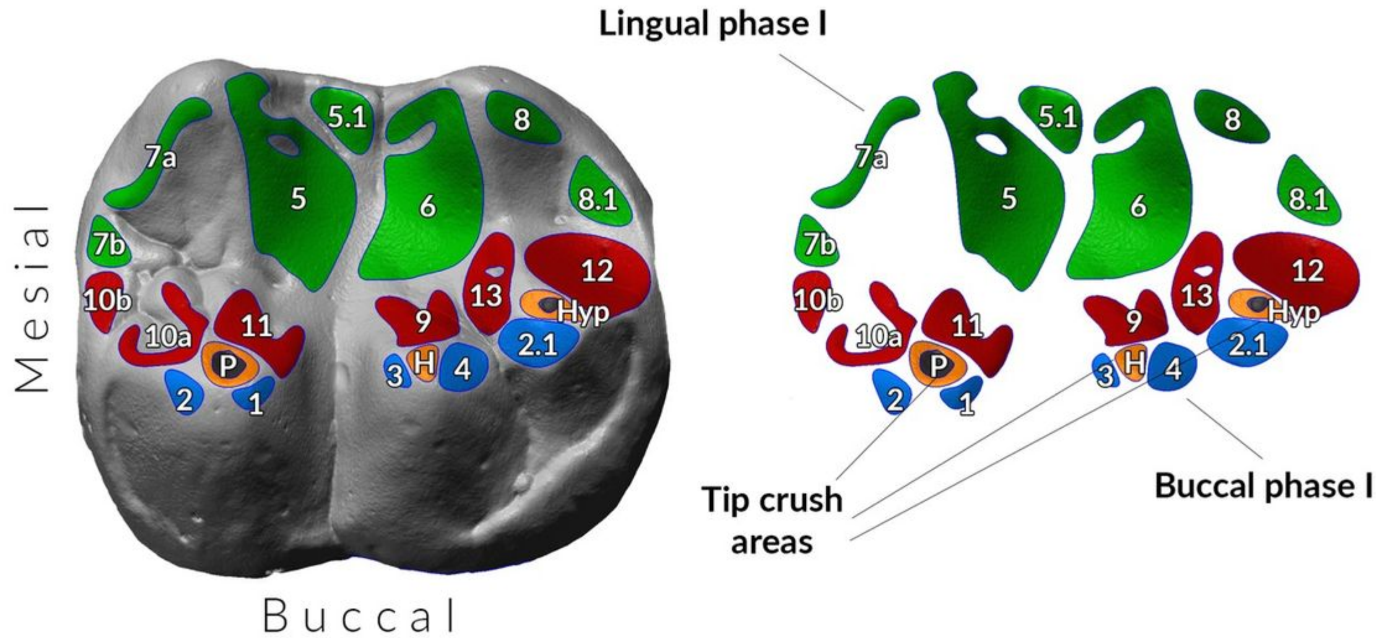

Figure 3

Second right lower molar of a western lowland gorilla adult male (90194) showing the macrowear pattern. Facets are numbered according to the Maier and Schneck's labelling system[46]. Buccal phase I (facets 1, 2, 2.1, 3 and 4; in blue), lingual phase I (facets 5, 5.1, 6, 7, 8 and 8.1; in green) and phase II (facets 9, 10, 11, 12 and 13; in red). We also identified tip crush areas (in orange) and dentine exposures (in dark grey). P = protoconid, H = hypoconid, Hyp = hypoconulid.

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