

## RESEARCH ARTICLE

# Variability in molar crown morphology and cusp wear in two Western chimpanzee populations

Julia Stuhlträger<sup>1,2</sup>  | Ottmar Kullmer<sup>3,4</sup> | Roman M. Wittig<sup>5,6,7</sup> |  
Kornelius Kupczik<sup>1,8</sup> | Ellen Schulz-Kornas<sup>1,9,10</sup>

<sup>1</sup>Former Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

<sup>2</sup>Group Animal Husbandry and Ecology, Group Animal Breeding, Institute of Agricultural and Nutritional Sciences, Martin-Luther University Halle-Wittenberg, Halle (Saale), Germany

<sup>3</sup>Division of Paleoanthropology, Senckenberg Research Institute and Natural History Museum Frankfurt, Frankfurt am Main, Germany

<sup>4</sup>Department of Paleobiology and Environment, Institute of Ecology, Evolution, and Diversity, Goethe University Frankfurt, Frankfurt am Main, Germany

<sup>5</sup>Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

<sup>6</sup>Taï Chimpanzee Project, CSRS, Abidjan, Ivory Coast

<sup>7</sup>Institute for Cognitive Sciences, CNRS UMR5229 University Claude Bernard Lyon 1, Bron, France

<sup>8</sup>Department of Anthropology, Faculty of Social Sciences, University of Chile, Santiago de Chile, Chile

<sup>9</sup>Department of Cariology, Endodontics and Periodontology, University of Leipzig, Leipzig, Germany

<sup>10</sup>Section Mammalogy and Palaeoanthropology, Leibniz Institute for the Analysis of Biodiversity Change and University of Hamburg, Hamburg, Germany

## Correspondence

Julia Stuhlträger, Former Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. Email: [julia.stuhltraeger@landw.uni-halle.de](mailto:julia.stuhltraeger@landw.uni-halle.de)

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## Abstract

**Objectives:** Chimpanzees (*Pan troglodytes*) possess a relatively generalized molar morphology allowing them to access a wide range of foods. Comparisons of crown and cusp morphology among the four subspecies have suggested relatively large intraspecific variability. Here, we compare molar crown traits and cusp wear of two geographically close populations of Western chimpanzees, *P. t. verus*, to provide further information on intraspecific dental variability.

**Materials and Methods:** Micro-CT reconstructions of high-resolution replicas of first and second molars of two Western chimpanzee populations from Ivory Coast (Taï National Park) and Liberia, respectively were used for this study. First, we analyzed projected tooth and cusp 2D areas as well as the occurrence of cusp six (C6) on lower molars. Second, we quantified the molar cusp wear three-dimensionally to infer how the individual cusps alter with advancing wear.

**Results:** Both populations are similar in their molar crown morphology, except for a higher appearance rate of a C6 in Taï chimpanzees. In Taï chimpanzees, lingual cusps of upper molars and buccal cusps of lower molars possess an advanced wear pattern compared to the remaining cusps, while in Liberian chimpanzees this wear gradient is less pronounced.

**Discussion:** The similar crown morphology between both populations fits with previous descriptions for Western chimpanzees and provides additional data on

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dental variation within this subspecies. The wear pattern of the Taï chimpanzees are in concordance with their observed tool rather than tooth use to open nuts/seeds, while the Liberian chimpanzees may have consumed hard food items crushed between their molars.

#### KEYWORDS

cuspid 6, *Pan troglodytes*, Taï National Park, topography

## 1 | INTRODUCTION

Studies of dental morphology and wear have differentiated between primate taxa, inferred dietary ecology and reconstructed masticatory function (e.g., Cuozzo et al., 2012; Hiiemae & Kay, 1973; Janis, 1984; Kay & Hiiemae, 1974; Lucas, 2004; Mills, 1955, 1973). Characteristics that are often used to define tooth crown morphology across taxa are tooth size, cusp shape, number of cusps or number of enamel ridges connecting the cusps (lophs) (e.g., Jernvall et al., 1998; Jernvall et al., 2000; Pilbrow, 2006; Skinner & Gunz, 2010; Uchida, 1996). Chimpanzees (*Pan troglodytes*) possess a relatively generalized tooth morphology. Chimpanzee molar cusps are generally considered to be blunt and more rounded, and therefore are more resistant against fractures compared to more pointed cusps (Berthaume et al., 2010; Berthaume et al., 2014; Godfrey et al., 2012). This generalized tooth morphology enables them to consume a wide range of foods, some of which are mechanically challenging (van Casteren et al., 2018). While comparisons of three of the four chimpanzee subspecies (*P. t. verus*, *P. t. troglodytes*, and *P. t. schweinfurthii*) as well as among geographically distant populations of the same subspecies (*P. t. verus*) have revealed differences in molar (cusp) metrics (Pilbrow, 2006; Uchida, 1996), little is known about dental morphological variability and tooth use/wear within geographically close populations of a single subspecies. Here, we analyze both the molar crown morphology and the molar cusp wear of two geographically close chimpanzee populations of *P. t. verus*, one from the Taï National Park in Ivory Coast (Taï chimpanzees) and one from northeastern Liberia (Liberian chimpanzees). For the Taï chimpanzees detailed behavioral information have been gathered for over 40 years (Boesch & Boesch-Achermann, 2000), while the Liberian chimpanzee population is a historical extinct population with no detailed behavioral or ecological records available. Analyzing specifically these two populations gives us the opportunity to expand our knowledge on molar crown morphology and cusp wear within the subspecies *P. t. verus*. We aim to answer the following two questions: (1) Do both populations share a similar first and second molar crown morphology? (2) Do both populations follow a similar cusp wear pattern?

### 1.1 | Molar crown morphology in chimpanzees

Various studies collecting 2D distance measurements (length and width) of chimpanzee teeth and tooth cusps have been conducted in the past 50 years and they reported a great variety in the intraspecific molar crown morphology. For example, Uchida (1996) analyzed and

compared the dentition of the chimpanzee subspecies *P. t. verus*, *P. t. troglodytes*, *P. t. schweinfurthii* and found that the upper M1 has the largest relative crown size (calculated from mesio-distal and bucco-lingual length of the tooth) among all molars in *P. t. verus* and *P. t. schweinfurthii*, while in *P. t. troglodytes* the upper M2 has the largest relative crown size. Furthermore, in *P. t. verus* the protocone of both upper M1s and M2s has the largest relative cusp size (calculated from mesio-distal and bucco-lingual length of the cusp), followed by the paracone and metacone, while the hypocone has the smallest relative cusp size. For the lower M1s Uchida found the following cusp size gradient: protoconid > metaconid > entoconid > hypoconid > hypoconulid; and for the lower M2: protoconid > metaconid > hypoconid > entoconid > hypoconulid (Uchida, 1996). Similar to these analyses, Pilbrow (2006) investigated the variability of several dental measurements (e.g., mesiodistal length, distance between mesial cusp tips) across and within chimpanzee subspecies. She found some evidence that spatially distant Western chimpanzee groups from the western end of the distribution range of the subspecies (Guinea, Sierra Leone, Liberia) differed from Western chimpanzee groups from the eastern part of the distribution range (Ivory Coast, Ghana, Togo) (Pilbrow, 2006). Both studies suggest that the morphological variation in tooth measurements may be in relation to evolutionary factors such as adaptation or isolation between chimpanzee subspecies (Pilbrow, 2006; Uchida, 1996).

Besides studies on intraspecific dental size variability, studies on sexual dimorphism revealed that male chimpanzees have larger mesio-distal and buccolingual diameters on their molars than those of females (Johanson, 1974; Schuman & Brace, 1954; Swindler et al., 1998). Nevertheless, cusp size gradients between sexes remain the same (protocone > paracone > metacone > hypocone), with the exception of the second molar, where the hypocone of males is slightly larger than the metacone (Uchida, 1996).

Additional to the five primary cups (protoconid, metaconid, entoconid, hypoconid, and hypoconulid) *P. troglodytes* spp. often develop an additional cusp on their lower molars (Ortiz et al., 2017; Skinner & Gunz, 2010; Swindler, 2002). The additional cusp is referred to as cusp 6 (C6) (Swindler, 2002). Skinner and Gunz (2010) showed for chimpanzees and bonobos that larger molars (as defined by centroid size) have a higher frequency of C6 compared to smaller molars. In total they found that in *P. t. verus* 64% of the molars have a C6, while in *P. t. troglodytes* only 25% of the molars have a C6 (Skinner & Gunz, 2010). These authors suggested that C6 occurrence is associated with overall tooth size and morphology of adjacent cusps, yet did not explore the changing cusp variability between tooth positions and

wear (Skinner & Gunz, 2010). In a more recent study on cusp variability in hominoid molars, Ortiz et al. (2017) found that 64.9% of the chimpanzee specimens (pooled subspecies) have a C6 on their lower molars. Unfortunately, both studies pooled all analyzed molars and did not investigate the presence of C6 on first, second and third molars separately. In contrast, two earlier studies on *P. t. verus* from Liberia found less frequent C6 expressions, ranging from 15.4% to 13.6% (Swindler et al., 1998) to 22.1% and 35.6% (Johanson, 1974) on the lower M1s and M2s, respectively. Furthermore, female Western chimpanzees were found to more often develop a C6 than males (Johanson, 1974). Taken together, the above studies indicate a wide range of variation of C6 presence within the subspecies *P. t. verus*.

## 1.2 | Molar cusp wear

During phase I of the power stroke of the primate chewing cycle molar cusps of the upper and lower teeth slide past one another in a shearing action (Kay & Hiiemae, 1974), which result in wear facets on the lingual and buccal surfaces of the upper and lower cusps, respectively (for review of the chewing cycle and wear facet location see Kullmer et al. (2020)). Depending on their role during the chewing cycle, molar cusps can be divided into two groups. During phase II of the power stroke, the lingual surfaces of the lower buccal cusps (protoconid, hypoconid, hypoconulid) move against the buccal surfaces of the upper lingual cusps (protocone, hypocone). Hence, the protocone, hypocone, protoconid, hypoconid, and hypoconulid are important during both phases of the power stroke. In the following we refer to them as “multi-phase-cusps.” In the literature they have also been referred to as, “functional” cusps (Macho & Berner, 1993; Schwartz, 2000). The remaining cusps, that is, the upper buccal (paracone, metacone) and the lower lingual (metaconid, entocoid) cusps play a lesser role during phase II. Therefore, we refer to them as “single-phase-cusps.” In the literature they have also been referred to as, “non-functional” cusps (Macho & Berner, 1993; Schwartz, 2000). Both “multi-phase-cusps” and “single-phase-cusps” decrease in height as they wear, and they become flatter and blunter until dentin is exposed. Even though little attempt has been given to quantify the wear on cusp group level “multi-phase-cusps” tend to wear more rapidly than “single-phase-cusps,” independent of molar morphology. However, the wear proportion between the cusp groups vary between species (Töpfer, 2008; Towle, Loch, et al., 2021).

Tooth wear studies comparing several modern human groups showed that craniodental features, such as dental arch shape and size or crown morphology, contribute to specific wear patterns, for example, wear gradients along the tooth row or position of wear facets on the tooth (Molnar & Molnar, 1990; Richards & Brown, 1986). In addition, teeth wear and change their crown morphology as they interact with biotic (e.g., diet) and abiotic (e.g., dust, grit) factors during dietary and non-dietary related actions (e.g., Janis, 1990; Schulz et al., 2013; Scott et al., 2005; Teaford et al., 2017; Yamashita et al., 2016).

Other studies have focused on macroscopic tooth wear characteristics (e.g., wear facet formation, dentine exposure) and found that dental wear patterns may vary between populations if they differ in

craniodental features and/or if they are exposed to different biotic and/or abiotic factors (e.g., Fiorenza, et al., 2011; Galbany et al., 2014; Molnar & Molnar, 1990; Scott et al., 2005; Stuhlträger et al., 2021; Yamashita et al., 2016). For example, Fiorenza and colleagues investigated whether cusp areas of the four main cusps of upper first molars lead to a variation in the wear pattern of Neanderthals, Paleolithic and modern hunter-gatherer groups (Fiorenza, et al., 2011). They found that Neanderthals have the highest wear pattern variability which also differed from the wear patterns of Paleolithic *Homo sapiens*, but in both species no correlation was found between cusp wear and cusp areas (Fiorenza, et al., 2011). In another study, it was investigated whether three populations of *Lemur catta* from southwest Madagascar differ in their tooth wear patterns (Yamashita et al., 2016). The authors found population-specific tooth wear rates depending on the proportion of hard-shelled fruits in the diet; that is, the greatest dental wear was found in the population with the highest consumption rates of the hard-shelled fruits (Yamashita et al., 2016). Population-specific macroscopic tooth wear patterns were also found between two Western chimpanzee populations (Janocha, 2019; Stuhlträger et al., 2021). The Western chimpanzee population from the Tai National Park in Ivory Coast (Tai chimpanzees) were found to have a less frequent probability of tip-crushing wear facets and no indications of dental chipping compared to the Western chimpanzee population from Nimba County in Liberia (Liberian chimpanzees) (Janocha, 2019). Tip-crushing wear facets and dental chipping are often associated with the consumption of hard food items (e.g., hard-shelled fruits, seeds) and/or the consumption of grit/dust with the food, which additionally lead to accelerate tooth wear (Chai et al., 2011; Constantino et al., 2010; Constantino et al., 2018; Fannin et al., 2020; Karne et al., 2016; Lucas et al., 2008; Towle & Loch, 2021; Towle, Loch, et al., 2021). Another tooth wear study on the same chimpanzee populations revealed similar wear facet areas and inclinations of phase II wear facets of the chewing cycle (Stuhlträger et al., 2021). The results indicate that the chewing behavior during phase II of the power stroke follows a similar pattern in both populations. Nevertheless, the results of Janocha (2019) lead to the suggestion that a certain amount of dietary disparity exists between both populations that might have not been associated to phase II of the power stroke of the chewing cycle. To investigate this further one needs to analyze not only single wear facets or facet categories (e.g., phase II facets). Rather, the wear pattern of all molar cusps should be analyzed because cusps comprise several wear facets including areas that do not necessarily wear during the standard chewing cycle, and could therefore provide additional information on their dietary ecology. In addition, and due to the reported wide range of tooth crown variation within the subspecies *P. t. verus* (e.g., Pilbrow, 2006; Skinner & Gunz, 2010; Swindler, 2002), it should be investigated whether both Tai and Liberian chimpanzees share a similar crown morphology, which may be relevant for interpreting the cusp wear results.

## 1.3 | Aims and predictions

Here, we aim to expand the knowledge on intraspecific population level variation in molar crown morphology and molar cusp wear in

*P. t. verus*, specifically between the relatively geographically closely related Taï and Liberian chimpanzee populations.

The first aim of our study is to quantify the molar crown morphology by analyzing projected tooth and cusp 2D areas (in the following referred to as tooth and cusp area), and by determining the number of cusps per tooth. For lower molars we expect to find molars that have an additional cusp (C6), as previously found by others (Ortiz et al., 2012; Skinner & Gunz, 2010; Uchida, 1996). We predict that both populations have similar molar crown morphologies, that is, tooth and cusp areas and number of cusps, because they belong to the same subspecies. Similar to the findings of Schuman and Brace (1954) and Johanson (1974), we predict that male chimpanzees in our samples possess larger tooth and cusp areas than those of female chimpanzees due to sexual dimorphism. However, we suggest that cusp area proportions within the same tooth are similar between the sexes, as previously found by Uchida (1996) who analyzed the length and width of the cusps.

The second aim is to investigate whether both populations show similar cusp wear patterns, and whether these cusp wear patterns can provide additional clues about the Liberian chimpanzees' dietary ecology. We quantify the cusp wear by using three parameters (cusp height, cusp volume, sphere area). Cusp height and volume are expected to decrease with advancing wear, while sphere area is expected to increase because it is a measure of the radius of a best fit circle placed onto the cusp tip. We predict that Liberian chimpanzees show greater cusp wear (stronger reduction of cusp height and volume as well as an increase in the sphere area) compared to the Taï chimpanzees. This is due to the higher incidences of tip-crushing wear facets in Liberian chimpanzees compared to the Taï chimpanzees (Janocha, 2019), which implies a greater vertical chewing movement (Spears & Crompton, 1996). Independent of the total amount of wear we predict for both populations that the “multi-phase-cusps” (protocone, hypocone, protoconid, hypoconid, hypoconulid) wear more rapidly than the “single-phase-cusps” (paracone, metacone, metaconid, entoconid). Hence, “multi-phase-cusps” are characterized by a stronger reduction of cusp height and volume as well as an increase in the sphere area, compared to the “single-phase-cusps.” If some of the lower molars have an additional cusp; that is, a C6 (as predicted above) we expect that this will have no or only a minor effect on the cusp wear of the remaining cusps as was shown previously for other cusps (cf. Fiorenza, et al., 2011).

## 2 | MATERIALS AND METHODS

### 2.1 | Dental material

The study sample consisted of upper and lower first (M1) and second molars (M2) ( $N_{\text{upper M1}} = 60$ ,  $N_{\text{upper M2}} = 56$ ,  $N_{\text{lower M1}} = 49$ ,  $N_{\text{lower M2}} = 42$ ) from two Western chimpanzee populations. The dental material of the first population (Taï chimpanzees,  $N = 36$  individuals), from the Taï National Park (Ivory Coast), is part of the Taï osteological collection (MPITC) of the Taï Chimpanzee Project

(Wittig, 2018) housed at Max Planck Institute for Evolutionary Anthropology (MPI-EVA Leipzig, Germany). The material of the second population (Liberian chimpanzees,  $N = 36$  individuals) is part of the mammal collection (SMF-PA-PC) of the Senckenberg Research Institute and Natural History Museum Frankfurt (Germany,  $N = 32$ ) and the Phyletic Museum (Jena, Germany,  $N = 4$ ) (for details on the specimen descriptions see Schulz-Kornas et al., 2019; Stuhlträger et al., 2021).

### 2.2 | Sample preparation, scanning and data processing

For each molar, the number of cusps was determined. The upper molars always possessed four cusps, while the cusp number on the lower molars varied between five and six cusps. For the detection of a sixth cusp (C6) on the lower molars, we followed scoring similar to that outlined by the Arizona State University Dental Anthropology System (Turner et al., 1991). However, here we only distinguished between two grades, because if present the C6 only appeared as the smallest cusp in all specimens: 0 = C6 is absent; 1 = C6 is present and smaller than the hypoconulid.

Each tooth cusp was scored for gross wear using the wear scores described by Scott (1979). The wear scores varied between 0 and 9, where 0 denoted an unworn cusp and 9 denoted a cusp with just a thin strip of enamel preserved (Scott, 1979). To obtain a total wear score for each tooth we summed the cusp wear scores for the tooth and divided this score by the number of cusps, receiving scores ranging between 0.2 and 7. For the cusp wear analysis, wear scores were analyzed separately to generate a wear sequence for each cusp.

High-resolution replicas of M1s and M2s were molded from the original specimens using a high-resolution silicone (Provil novo Light C.D.2 regular set; Type 3; Heraeus Kulzer, Dormagen, Germany) following the replica technique outlined in Hayek et al. (1992). These replicas were then filled with epoxy resin (Injektionsharz EP, Reckli-Chemiewerkstoff Co., Herne, Germany) to generate positive casts of the teeth following the protocol in Schulz et al. (2007). The casts were micro-CT scanned at the MPI-EVA. We decided to use this procedure because micro-CT scans and respective high-resolution tooth surface models of some Taï chimpanzee specimens had been generated previously for other studies. Hence, we used the same method to keep the scanning conditions constant to enable an accurate data analysis. For the micro-CT scanning, we used a Diondo d3 at 100–130 kV and 170–100  $\mu\text{A}$  with an isometric voxel resolution of 0.027  $\mu\text{m}$ . Resultant cross-section image stacks were loaded and segmented in Avizo 9.4.0 (Thermo Fisher Scientific, 2017), and tooth crown surface models were created. Those models were further processed using the tool “remesh surface” using the settings “fix contours,” “best isotropic vertex placement,” “33% size reduction,” and “smoothly” to create the final surface models, which were saved as stl-files. The models were then loaded in Geomagic Studio 2014 (Version 2014.2.0.1781) (3D Systems Incorporated, © 2014 Geomagic) and manually rotated along the z-axis (occlusal pointing toward z, mesial pointing toward x).

A reference plane was calculated by manually fitting a polyline along the cervical line of each tooth generating a best-fit plane through all surface model data points marked within a user-defined threshold distance (see description in Kullmer et al. (2020)). The reference plane was aligned to the xy-plane of a Cartesian coordinates system. The model of the tooth crown was cropped at this plane and only the standardized tooth crown model (including the projected cervical line onto the reference plane) was kept and saved as in a stl-file format for further morphometric analyses.

## 2.3 | Tooth/cusp area and cusp wear analysis

The tooth models were analyzed in the  $\mu$ soft analysis premium software version 7.4.8076 (NanoFocus AG, Oberhausen, Germany; a derivative of Mountains<sup>®</sup> Analysis software by Digital Surf, Besançon, France). We applied the motif analysis that uses a watershed segmentation algorithm to detect hills (tooth cusps) using the combination of peak detection for grains, open and closed motifs, and spherical caps. With the motif analysis, we used a new approach to quantify tooth cusps three-dimensionally in an automated routine. Within this analysis, we used the following variables: tooth area, cusp area, cusp height, cusp volume, and sphere area (Figure 1). Tooth and cusp area were measured in 2D as the projected area enclosed in the crown and cusp outlines on the cross-sectional reference plane (Figure 1a). For the lower molars, we analyzed tooth areas of the full data set and of a reduced data set (see Supporting information 1 Table S1). The reduced data set consisted of lower molars that exclusively have five cusps; that is, lower molars that have a C6 were excluded, to test the effect of an additional cusp on tooth areas.

Cusp height, cusp volume, and sphere area were used to quantify the cusp wear pattern relative to the tooth wear stages. The cusp height

is the perpendicular height from the cervical plane to the cusp tip (Figure 1b). The cusp volume was calculated as the volume of the upper part of the cusp. More precisely, within the analysis the highest point along the course line (highest saddle point) of a cusp was identified using the automated routine in the  $\mu$ soft analysis software (Figure 1c) and used to create another reference plane that is parallel to the cervical plane. The cusp volume was then calculated from this reference plane to the cusp tip. The sphere area was calculated from the sphere radius, which is a measure of the radius of the best fit circle onto the cusp tip (Figure 1d), similar to the radius of curvature described by Yamashita (1998).

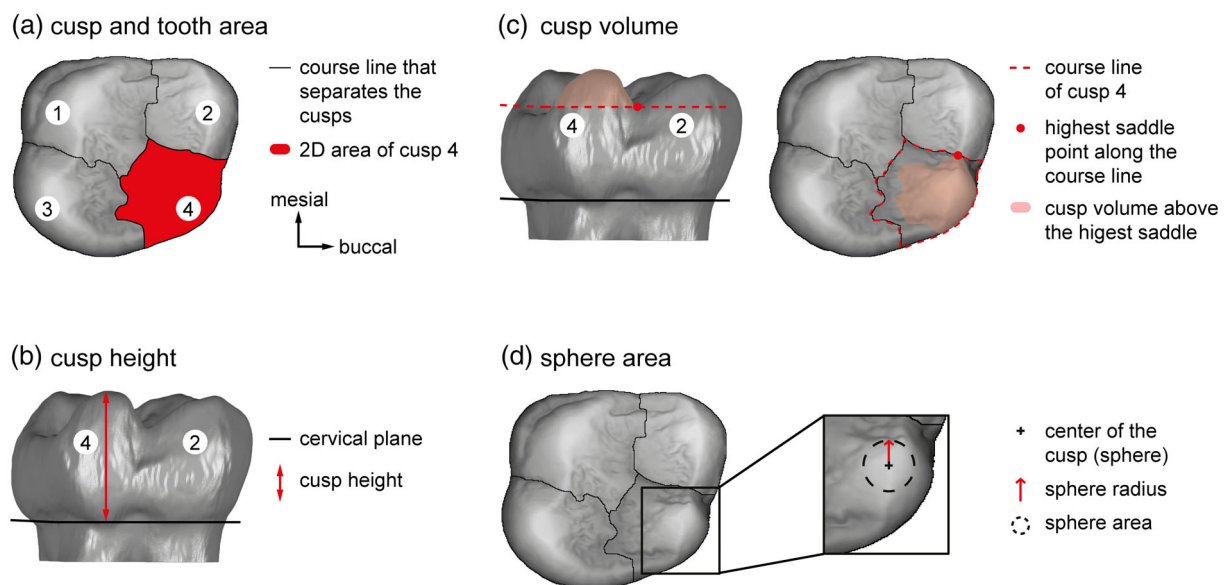
## 2.4 | Statistics

For the group-wise comparisons, we analyzed upper and lower M1s and M2s separately; datasets are used as indicated in Supporting information 1. All statistical analyses were computed using the software R 4.0.3 (R Development Core Team, 2020). R-Scripts are supplied as supplementary information (Supporting information 2). All obtained p-values were corrected with Bonferroni adjustments.

### 2.4.1 | Molar crown morphology

We analyzed whether there was a significant difference between tooth areas of lower molars with and without a C6 by using the two-sampled Wilcoxon test (data set given in Supporting information 1 Table S1). For that, we analyzed Tai and Liberian chimpanzees separately.

For the comparison of tooth areas between populations, we used the Welch's Two Sample t-test, because the data were normally distributed (test for normal distribution is given in the R scripts in the



**FIGURE 1** Scheme of the analyzed parameters shown on the upper left molar of the specimen MPITC-15005. The cusp and tooth areas (a) are wear independent and were analyzed as part of the molar crown morphology description, while cusp height (b), cusp volume (c), and sphere area (d) are wear dependent. The calculations were conducted for each cusp separately and shown here in red for cusp 4, as an example. The numbers refer to the individual cusp of the tooth: protocone (1), paracone (2), hypocone (3), and metacone (4).

Supporting information 2). For the comparison of single cusp areas between populations, we used the two-sampled Wilcoxon test, because the data were not normally distributed. For tooth area comparisons between sexes within and between populations, as well as lower molars with and without a C6 we used a one-way ANOVA (data were normally distributed), while we used the Kruskal-Wallis test (reveals if there is any significant difference) and the pairwise Wilcoxon test (revealing the source of difference) for comparing cusp areas between the sexes (data were not normally distributed).

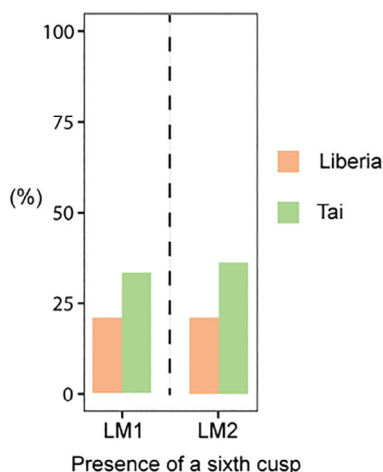
## 2.4.2 | Molar cusp wear

Correlation between the three wear parameters (cusp height, cusp volume, sphere area) and tooth wear stages as well as crown morphology (presence/absence of C6 on lower molars) were explored within each chimpanzee population. We tested each population and tooth position separately to assess the changes in the wear parameters with advancing tooth wear.

## 3 | RESULTS

### 3.1 | Molar crown morphology

In both Tai and Liberian chimpanzees, the presence of a C6 on the lower molars is independent of the tooth position. In the Tai



**FIGURE 2** Occurrence rates of cusp 6 (C6) on lower molars.

Tooth	Tai chimpanzees		Liberian chimpanzees		Test statistics*	
	N	Mean ± SD	N	Mean ± SD	Df	p value
UM1	30	110.55 ± 7.8	29	109.24 ± 10.7	50.99	0.595
UM2	27	105.22 ± 8.9	28	102.89 ± 15.1	44.08	0.487
LM1	24	104.15 ± 6.9	24	101.43 ± 7.6	45.59	0.203
LM2	23	112.59 ± 10.0	19	104.57 ± 13.2	33.02	<b>0.037</b>

Note: The analysis for the lower molars (LM1, LM2) was conducted on all teeth, that is, the one's with and without a C6. N = specimen number, mean values are given in mm<sup>2</sup>, SD = standard deviation,

\*Welch's two sample t-test, p value = level of significance.

population, 33.3% and 36.4% of the specimens have a C6 on their lower M1s and M2s, respectively. In the Liberian population, the occurrence rate is lower with 20.8% for the M1s and 21.1% for the M2s, respectively (Figure 2).

The comparison of tooth areas between populations shows that both populations have similar tooth areas on their upper molars, and in both populations the tooth areas of upper M1s are slightly larger than on M2s (Table 1). Similarly, the tooth areas of the lower M1s do not vary between Tai and Liberian chimpanzees. However, on the lower M2s Tai chimpanzees have significantly larger tooth areas ( $p = 0.037$ ) compared to the Liberian population (Table 1). To exclude the possibility that those tooth area differences are due to the presence/absence of a C6 we additionally used a reduced data set for the lower molars, where teeth with a C6 were excluded from the analysis (see Supporting information 1 Table S1). Although lower M1s that possess a C6 are slightly larger than lower M1s without a C6 (Table 2), none of these findings are significant. Similarly, the presence of a C6 on lower M2s does not result in significantly larger tooth areas.

The cusp areas within Tai chimpanzees' upper M1s (females and males) follow the pattern protocone > metacone > hypocone > paracone while in the Liberian chimpanzees the hypocone has a smaller cusp area than the paracone (protocone > metacone > paracone > hypocone). On upper M2s, we see a shift in the cusp areas toward a reduction of the metacone area and an enlargement of the paracone area (Table 3). This results in the following cusp area proportions: protocone > paracone > metacone > hypocone for Tai chimpanzees and protocone > paracone > hypocone > metacone for Liberian chimpanzees. The common pattern found on the lower molars in both populations is protoconid > metaconid > hypoconid > entoconid > hypoconulid (> C6) (Table 3). Furthermore, the hypoconid area on lower M1s and the protoconid area on lower M2s is significantly larger in the Tai chimpanzees (Table 3). For lower M1s that possess a C6, we see a slight increase in cusp areas of the mesial cusps (protoconid, metaconid). However, this is only significant for the protoconid of the Tai chimpanzees (Supporting information 3 Table S1).

The comparison between the sexes shows that females and males of the Tai chimpanzees have similar tooth areas, even though there is a slight tendency for smaller areas in females (Table 4, Supporting information 3 Table S2). In the Liberian chimpanzee population, females have significantly smaller tooth areas on the upper M2s compared to males ( $p = 0.0003$ ; see Supporting information 3 Table S2). These sex

**TABLE 1** Descriptive and test statistics for the tooth areas compared between populations

**TABLE 2** Descriptive and test statistics for tooth areas of lower molars compared between populations 7 and between teeth

Tooth	Data set <sup>a</sup>	Tāi chimpanzees		Liberian chimpanzees		
		N	Mean ± SD	N	Mean ± SD	
LM1	Without C6	16	101.86 ± 5.8	19	99.63 ± 6.7	0.756*
	With C6	7	109.32 ± 7.5	5	108.24 ± 7.9	0.992*
			0.077*		0.061*	
LM2	Without C6	14	113.21 ± 11.2	14	105.81 ± 16.0	0.347*
	With C6	8	109.75 ± 6.6	5	101.10 ± 16.0	0.566*
			0.908*		0.864*	

Note: The test statistics used here was a one-way ANOVA with a Tukey post-hoc test (\*). LM1 = lower first molars, LM2 = lower second molars, *p*-values = level of significance.

<sup>a</sup>Reduced data set = without C6, full data set = with C6.

**TABLE 3** Descriptive and test statistics for cusp areas compared between populations

Tooth	Cusp	Tāi chimpanzees		Liberian chimpanzees		Test statistics <sup>a</sup> <i>p</i> value
		N	Mean ± SD	N	Mean ± SD	
UM1	Paracone	29	24.32 ± 1.9	24	25.34 ± 2.6	0.132
	Metacone	29	25.87 ± 2.4	27	25.54 ± 2.9	0.591
	Protocone	28	35.61 ± 3.9	23	35.34 ± 3.4	0.786
	Hypocone	28	24.90 ± 3.2	25	23.38 ± 3.6	0.089
UM2	Paracone	25	25.46 ± 2.9	28	25.60 ± 4.7	0.627
	Metacone	26	21.19 ± 2.9	28	20.48 ± 4.3	0.553
	Protocone	24	39.20 ± 4.3	25	36.11 ± 6.3	0.067
	Hypocone	24	20.42 ± 3.0	25	20.75 ± 4.8	0.913
LM1	Metaconid	24	22.18 ± 1.9	22	22.60 ± 2.4	0.289
	Entoconid	23	19.00 ± 2.2	21	18.72 ± 1.5	0.762
	Protoconid	23	27.15 ± 2.2	20	26.19 ± 1.8	0.163
	Hypoconid	22	21.32 ± 2.0	18	19.96 ± 1.7	<b>0.032</b>
	Hypoconulid	15	13.65 ± 3.4	16	13.73 ± 2.3	0.861
	C6	1	6.81	2	5.74 ± 1.7	/
LM2	Metaconid	21	25.77 ± 2.8	17	24.17 ± 3.5	0.17
	Entoconid	18	18.22 ± 3.1	19	16.77 ± 3.4	0.086
	Protoconid	21	31.39 ± 3.8	17	28.78 ± 4.1	<b>0.048</b>
	Hypoconid	15	21.73 ± 3.4	18	20.24 ± 2.4	0.307
	Hypoconulid	12	13.88 ± 3.2	18	13.11 ± 3.6	0.983
	C6	4	5.17 ± 2.4	6	3.19 ± 0.7	0.111

Note: *N* = specimen number, mean values are given in mm<sup>2</sup>, SD = standard deviation, *p* value = level of significance.

<sup>a</sup>Two-sampled Wilcoxon test.

differences are mainly driven by the cusp areas of the paracone and protocone (Supporting information 3 Table S3). Interestingly, Liberian females tend to have the smallest tooth areas of the whole data set (Table 4), which are significantly smaller on their lower M1s compared to Tāi females ( $p_{\text{whole data set}} = 0.034$ ,  $p_{\text{reduced data set}} = 0.042$ ; Supporting information 3 Table S2). Cusp areas are similar between the sexes of both populations (Supporting information 3 Tables S3–S5), except for the paracone and protocone of upper M2s in Liberian chimpanzees (see above).

### 3.2 | Molar cusp wear

On the protocone and hypocone of both upper M1s and M2s cusp height and volume decrease significantly with increasing tooth wear in both populations (Figure 3a and Supporting information 3 Figure S1A). Furthermore, Tāi chimpanzees show a significant reduction of the cusp volume, but not of cusp height, on the “single-phase-cusps” of the upper molars with increasing tooth wear (Figure 3b and Supporting information 3 Figure S1B). In contrast, Liberian chimpanzees show a significant

Tooth	Data set	N	Tooth area (full data set)		Tooth area (reduced data set)	
			Mean ± SD	N	Mean ± SD	N
UM1	Tai females	17	108.30 ± 6.8	/	/	/
	Tai males	13	113.49 ± 8.2	/	/	/
	Liberian females	10	107.26 ± 12.6	/	/	/
	Liberian males	8	115.01 ± 8.1	/	/	/
UM2	Tai females	15	101.94 ± 7.9	/	/	/
	Tai males	12	109.32 ± 8.7	/	/	/
	Liberian females	12	95.05 ± 8.8	/	/	/
	Liberian males	9	115.23 ± 16.1	/	/	/
LM1	Tai females	11	102.75 ± 5.6	9	102.92 ± 6.1	
	Tai males	12	106.68 ± 6.5	6	102.39 ± 2.3	
	Liberian females	7	93.91 ± 7.6	6	93.79 ± 8.3	
	Liberian males	4	109.06 ± 4.7	2	105.54 ± 2.2	
LM2	Tai females	11	109.61 ± 8.5	5	110.48 ± 9.0	
	Tai males	12	115.33 ± 10.9	9	114.73 ± 12.5	
	Liberian females	7	97.25 ± 8.7	6	100.31 ± 3.4	
	Liberian males	4	113.25 ± 16.7	2	111.87 ± 28.5	

Note: Full data set = teeth with and without C6 (accounts only for LM1 and LM2), reduced data set = teeth without C6, N = specimen number, mean values are given in mm<sup>2</sup>, SD = standard deviation.

reduction of both cusp height and volume on the “single-phase-cusps” (Figure 3), with an exception of the metacone on the upper M2s (Supporting information 3 Figure S1B).

For the lower molars, we used two data sets to test whether the occurrence of a C6 on lower molars influences the wear patterns. The full data set includes all teeth and a reduced data set includes only teeth that lack a C6. The analysis of the full data set reveal that on the lower M1s, there is only a trend for height and volume reduction in the Tai chimpanzees (Figure 4). However, it is important to note that there are no data available for early and late tooth wear stages for this tooth position. Liberian chimpanzees show a significant height reduction on both “multi-phase-cusps” (protoconid, hypoconid, hypoconulid) and “single-phase-cusps” (metaconid, entoconid), while the volume reduction is significant for the hypoconid and the entoconid (see Figure 4). Similar results were found when teeth that possess a C6 were excluded (Supporting information 3 Table S6). Only volume reduction on the hypoconid and hypoconulid changed slightly in the Liberian chimpanzees. When lower M1s that possess a C6 were excluded from the analysis, the volume reduction was less on the hypoconid and a greater on the hypoconulid. No such observation was found in the Tai chimpanzees.

The analysis of the full data set on the lower M2s of the Tai chimpanzees reveal that the height reduction is significant on two of the three “multi-phase-cusps”; the protoconid and the hypoconid, while the volume reduction is only significant on the protoconid (Supporting information 3 Figure S2A). Liberian chimpanzees' cusp height on the lower M2s decreases significantly throughout the tooth wear process on the two mesial cusps; the protoconid and the metaconid, while the volume decreases on the protoconid, hypoconid as well as the

entoconid. When teeth with a C6 were excluded from the analysis, only slight changes were found. In the Liberian chimpanzees, the height reduction was stronger on the hypoconid, while in the Tai chimpanzees the opposite was found on the protoconid and metaconid (Supporting information 3 Table S6).

The sphere area is less linked to cusp wear (Supporting information 3 Figures S3 and S4). In the Tai population there is only a significant increase of the sphere area on the paracone and hypocone of M1s (Supporting information 3 Figure S3B), while in the Liberian population, the sphere area remains stable during the tooth wear process.

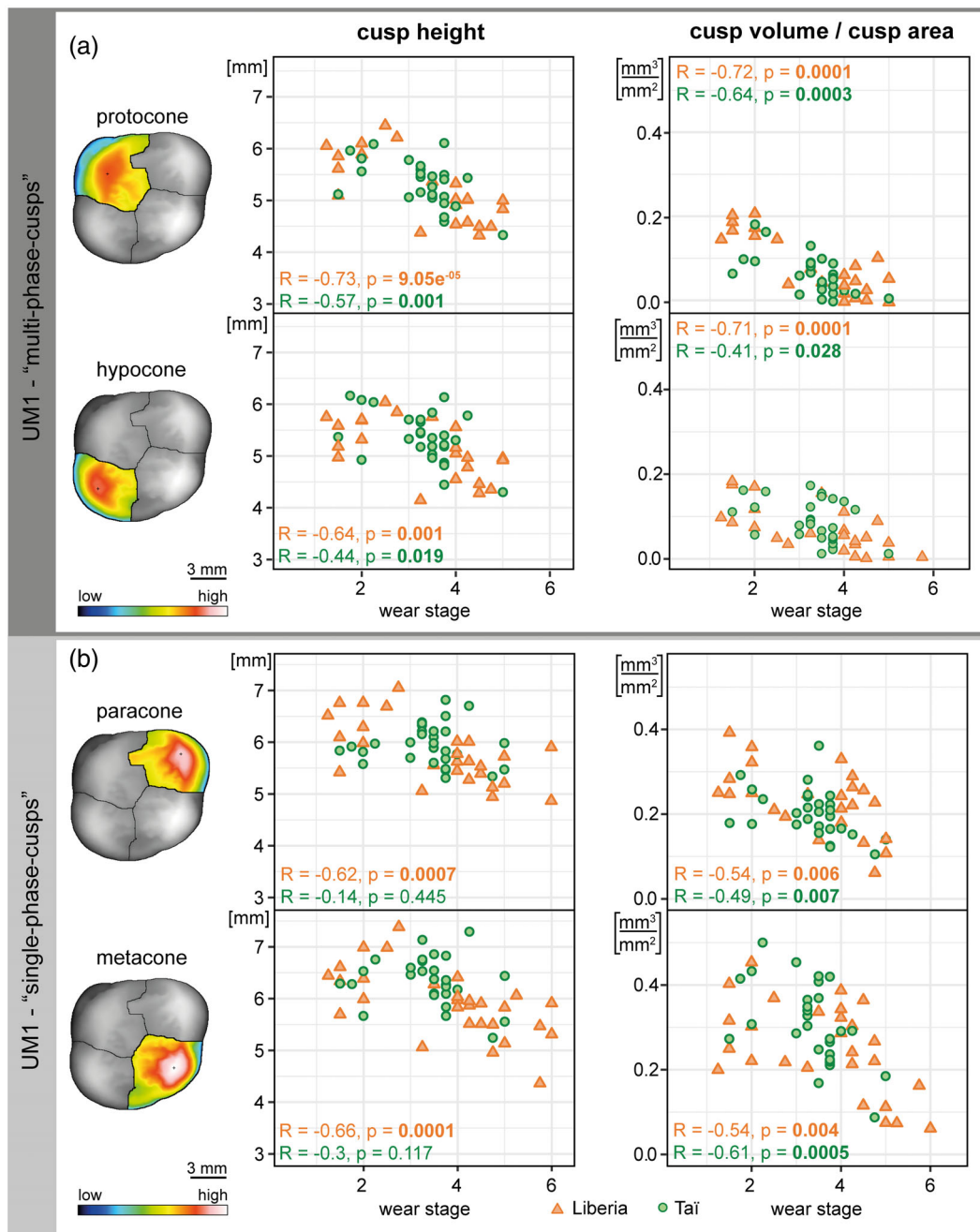
## 4 | DISCUSSION

### 4.1 | Molar crown morphology

The results support our prediction that tooth areas are similar between Tai and Liberian chimpanzees, and they are further concordant with previous findings that revealed that upper M1s are larger than upper M2s (Uchida, 1996). However, when comparing our findings for projected 2D tooth areas of M1s and M2s, respectively, our results partly contradict those previously described for this subspecies. The tooth areas of the Tai chimpanzees (both females and males) exceed those measured by Uchida (1996), while the Liberian chimpanzees analyzed here are at the upper range of Uchida's measurements. When the sexes are compared separately, we found that the Liberian females have the smallest tooth areas of the whole data set, and they fall within the range of the female Western chimpanzees collected by Uchida (1996). In contrast, Liberian males are similar to Tai males in

**TABLE 4** Descriptive statistics for the tooth areas compared between sexes



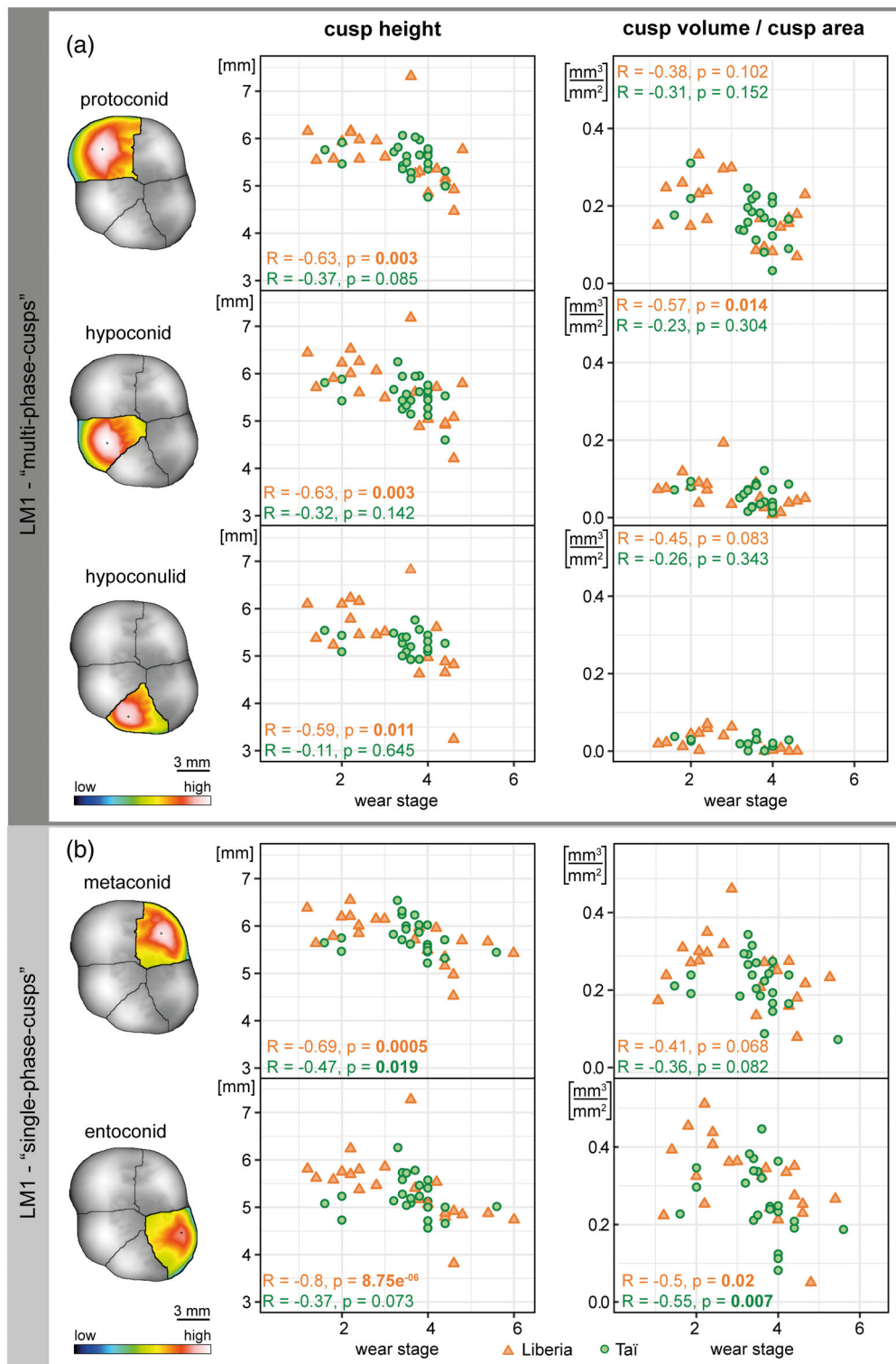


**FIGURE 3** Relationship between the wear parameters (cusp height and cusp volume) and tooth wear on the “multi-phase-cusps” (a) and the “single-phase-cusps” (b) of the upper M1 shown for Liberian and Taï chimpanzees. The tooth model (example shown is the upper left first molar of specimen MPITC-14995) was extracted from Mountains<sup>®</sup> Analysis software to illustrate the elevation of the individual cusps. The tooth model is shown in occlusal view and the top points mesial while the right side points buccal. + tip of the cusp.

their tooth area and both have slightly larger values than the ones collected by Uchida (1996) (for a comparison see Appendix 2-1, 2-2, 4-1, 4-2 in Uchida (1996)).

When molar cusps are compared, previous studies of Western chimpanzees from the region around Ganta in Liberia (Uchida, 1996) and contemporary modern humans (Bailey, 2004), revealed similar results for relative cusp size proportions (calculated from mesio-distal and bucco-lingual length of the cusp) (Uchida, 1996) and projected 2D

cusp area proportions (Bailey, 2004): protocone > paracone > metacone > hypocone. When these findings are compared to our results it seems that on the upper M1s there is an enlargement of the metacone area and a reduction of the paracone area in both populations (see Table 3). For the upper M2s, the Taï chimpanzees' cusp areas follow the pattern described by Uchida (1996). In the Liberian population, there is an enlargement of the hypocone area on upper M2s. Our findings for the lower M1s, where the hypoconid has a larger area



**FIGURE 4** Relationship between the wear parameters (cusp height and cusp volume) and tooth wear on the “multi-phase-cusps” (a) and the “single-phase-cusps” (b) of the lower M1 shown for Liberian and Tai chimpanzees. The tooth model (example shown is the lower left first molar of specimen MPITC-14995) was extracted from Mountains<sup>®</sup> Analysis software to illustrate the elevation of the individual cusps. The tooth model is shown in occlusal view and the top points mesial while the right side points lingual. + tip of the cusp.

than the entoconid contradicts the findings of relative cusp sizes by Uchida (1996) where the entoconid was found to be larger than the hypoconid. However, consistent with our findings on cusp

proportions for the lower molars, Uchida (1996) also found the following pattern on the lower M2s: protoconid > metaconid > hypoconid > entoconid > hypoconid.

There are two possible explanations for the tooth and cusp area variations within the above compared data sets. First, Uchida (1996) calculated the relative crown and cusp size measuring the bucco-lingual and mesio-distal lengths and assumed a rectangular shape of the teeth/cusps that were used for an approximation of the areas, while we measured the tooth and cusp areas as the projected areas enclosed in the crown and cusp outlines. This resulted only in an estimate of Uchida's values for tooth and cusp sizes/areas. Second, inter-population variation might account for the differences. This suggestion was proposed by Pilbrow (2006) who found variation in dental measurements within chimpanzee subspecies. Dental measurements of Western chimpanzees from the western end of the distribution range of the subspecies (Guinea, Sierra Leone, Liberia) differed from Western chimpanzee groups from the eastern end of the distribution range (Ivory Coast, Ghana, Togo) (Pilbrow, 2006), suggesting that a certain geographical distance between chimpanzee groups may account for the variation in tooth morphology. Unfortunately, Pilbrow (2006) did not compare biological populations, rather she grouped populations that were geographically close and compared them to other groups of populations that were geographically more distant to the first group of populations. Additionally, it would have been interesting to investigate whether chimpanzee populations of one subspecies that are geographically closer show the same variation in dental measurements.

The Liberian chimpanzees studied here and the specimens analyzed by Uchida (1996) (Ganta chimpanzees) both originate from Liberia, and they were geographically close, or even overlapping (Himmelheber & Himmelheber, 1958; Protsch von Zieten & Eckhardt, 1988; Smith et al., 2010). However, the Ganta chimpanzee specimens analyzed by Uchida were collected before the 1930s, and they stem from a larger geographic area, while the Liberian chimpanzees of the current study were collected approximately 20 years later (Himmelheber & Himmelheber, 1958; Protsch von Zieten & Eckhardt, 1988; Smith et al., 2010). The Liberian and Ganta chimpanzees, which are geographically closer to each other than to the Taï chimpanzees, are also more similar to each other in their tooth and cusp measurements than they are to the Taï chimpanzees from neighboring Ivory Coast. Alternatively, the variation in cusp measurements that primarily affected the distal cusps in our data set (metacone, hypocone, entoconid, hypoconid) may instead be a result of developmental processes. The patterning cascade mode of cusp development suggests that later developing molar cusps display larger area variation, which was found to be true for humans (Kondo & Townsend, 2006). If the same accounts for non-human primates the disto-buccal (metacone and hypoconid) and disto-lingual cusps (hypocone and entoconid) (Reid et al., 1998; Swindler, 2002) should show the greatest variation cusp areas (Hillson, 1996; Swindler, 2002), which is only partly in agreement with our results. In addition, the patterning cascade mode of cusp development also suggests that the probability of developing additional cusps is positively associated with tooth size and negatively associated with cusp spacing (e.g., Jernvall & Jung, 2000). This was already confirmed for humans (Hunter et al., 2010), chimpanzees and bonobos (Skinner & Gunz, 2010). In our data set, there is a trend for Liberian chimpanzees showing slightly smaller tooth areas (significant on lower M2s) than the Taï chimpanzees. Additionally, we

found that Liberian chimpanzees also exhibit less frequently a C6 on their lower molars than Taï chimpanzees (see Figure 2), but the occurrence rate remains stable between M1s and M2s.

However, when tooth areas of molars with and without a C6 are compared, we found that lower M1s that possess a C6 are slightly larger than M1s without a C6, while the opposite was found for lower M2s. This was independent of the populations. Hence, the suggestion of Jernvall and Jung (2000) that the probability of developing additional cusps is positively associated with tooth size and negatively associated with cusp spacing does not fully apply here. Yet, no data are available for cusp spacing of the Liberian and Taï chimpanzees.

These results indicate that at least the occurrence of the C6 may be population-specific. It remains to be tested whether this phenomenon can be explained by the patterning cascade mode of cusp development and whether this can be applied to multiple populations of the same subspecies.

## 4.2 | Molar cusp wear

Here, we tested for a correlation between three wear parameters (cusp height, cusp volume, sphere area) and tooth wear stages within two chimpanzee populations to infer how their specific tooth cusps wear. While cusp height and volume generally decreased with advanced tooth wear, sphere area was independent of tooth wear stages. The height and volume reduction was stronger in upper teeth compared to the lower ones. However, the relatively small sample size for specific tooth wear stages on lower molars may have affected these results and therefore should be considered with caution.

The comparison of the full (all lower M1s and M2s) and reduced data set (lower M1s and M2s with a C6 were excluded) reveal only slight changes in height and volume reduction, which additionally seem to occur randomly between the populations and among single cusps. For example, height reduction on lower M1s was not affected by the presence/absence of a C6. When teeth with a C6 were excluded from the analysis, lower M2s show less height reduction on the metaconid; this accounts for both populations. In contrast, the hypoconid on M2s of Liberian chimpanzees shows a greater height reduction, while the results of the Taï chimpanzees did not change. One possible explanation for this may be that the presence of a C6 lead to an increase in wear on the mesial cusps and a reduction in wear on the more distal cusps. However, at this point this is highly speculative because these changes are only present on lower M2s, they vary between populations, and the entoconid and hypoconid seem to be unaffected by a C6 presence/absence.

In a study of Neanderthals and Paleolithic and modern *Homo sapiens* it was shown that wear facet formations are not correlated with their tooth morphology (Fiorenza, Benazzi, Viola, et al., 2011c), but with dietary, environmental and other behavioral habits (Fiorenza, 2015; Fiorenza, 2011; Fiorenza, et al., 2011; Fiorenza & Kullmer, 2013). More recently, macrowear analysis of *Pan*, *Pongo* and *Gorilla*, which all differ in their primary molar morphology, revealed that *Pongo* and *Gorilla* have similar macrowear patterns, while both differ significantly from *Pan*

(Fiorenza et al., 2022). The authors of this study interpreted the divergence of *Pan* from *Pongo* and *Gorilla*, respectively, as a result of their highly diverse diet (Fiorenza et al., 2022). Even though, *Pongo* and *Gorilla* exploit different foods as well, both species rely on mechanically challenging foods, which probably have a stronger effect on the formation of occlusal wear facets (Fiorenza et al., 2022). These studies do not fully exclude the possibility that variation in molar crown morphology has an effect on the wear pattern, but they all show that other factors such as dietary or environmental factors most probably have a larger effect on tooth wear patterns. Likewise, we do not think that the minor wear changes we found between lower molars with and without a C6 are related to morphological variations between those teeth.

Previously, it was shown for humans and several non-human primate groups that “multi-phase-cusps” of upper (protocone, hypocone) and lower molars (protoconid, hypoconid, hypoconulid) wear more rapidly than “single-phase-cusps” (paracone, metacone, metaconid, entocoid) (Macho & Berner, 1993; Schwartz, 2000; Töpfer, 2008; Towle, Loch, et al., 2021). Similarly, we found for the Tai chimpanzees that “multi-phase-cusps” wear faster than “single-phase-cusps.” These cusp wear patterns are in concordance with the known feeding ecology of the Tai chimpanzees. They regularly feed on nuts/seeds that are opened with tools before consumption (Boesch & Boesch-Achermann, 2000; Wittig, 2018), preventing both an accelerated cusp wear and a high occurrence rate of tip-crushing facets (Janocha, 2019), because only the softer endosperm is consumed.

Based on recent findings on tip-crushing wear facets in Liberian chimpanzees, which develop mainly during puncture-crushing movements when pulping food items (Lucas & Luke, 1984), we predicted that the Liberian chimpanzees would show more rapid cusp wear than the Tai chimpanzees. This prediction is only partly confirmed. Our results indicate that the “multi-phase-cusps” wear similarly in both populations, while the “single-phase-cusps” wear faster in the Liberian population (see Figures 3 and 4). Hence, all tooth cusps of the Liberian population show rapid wear, leading to a similar degree of height and volume loss among the cusps, at least on the upper molars. On the lower molars, the results are less clear. While the height reduction is the same as predicted for Liberian chimpanzees, there is only a trend for height reduction on the lower M1s in Tai chimpanzees. This might be due to a small sample size for some wear stages on the lower molars.

The fact that the Liberian chimpanzees show accelerated cusp wear in all cusps, while in the Tai population the “single-phase-cusps” show reduced wear, may relate to differences in the dietary ecology between both populations. Accelerated tooth wear patterns have been related to hard object feeding and/or to an elevated consumption of external abrasives (e.g., grit or dust) (e.g., Lucas, 2004; Lucas et al., 2008; Towle et al., 2017; Yamashita et al., 2016). Hard object feeding requires a repeated vertical crushing movement, which tend to result in intensified tooth wear and flatter (blunter) cusps with reduced tooth wear angles (Fiorenza et al., 2015; Fiorenza, et al., 2011; Janis, 1990). In contrast, the periodical consumption of much smaller dust/grit, which is often adhered to food, can cause vertical or more horizontal chewing movements, with a characteristic wear pattern at  $\mu\text{m}$ -scale (Schulz-Kornas et al., 2019).

Similar to the Liberian chimpanzees, the South African *P. robustus* exhibit high cusp wear scores that are similar between “multi-phase-cusps” and “single-phase-cusps,” while other extant and extinct primate species have a larger wear gradient between the cusp groups (Towle, Loch, et al., 2021). Microwear studies of *P. robustus* have found indications for the consumption of hard food items (Constantino et al., 2018; Ungar et al., 2008) while others have related these patterns to an increased consumption of dust/grit as a result of increased aridity in the environment (Lee-Thorp et al., 2007; Reed, 1997). Recent analyses of tooth chipping patterns revealed that *P. robustus* had fewer chips than primate species that regularly masticate hard objects (Towle, Irish, & Loch, 2021). Due to these findings the authors argued that *P. robustus* most probably did not consume a high amount of hard objects, even though it is possible that *P. robustus* did occasionally use their teeth for breaking seeds or nuts by placing these objects between upper and lower teeth for the initial phase of mastication (Towle, Irish, & Loch, 2021). These studies on dietary reconstructions on *P. robustus* demonstrate that using one method alone limits the interpretations of the dietary ecology and in particular reflects the diet of a certain time duration. Thus, we highly recommend combining methods reflecting short- ( $\mu\text{m}$ -scale) as well as long-term (mm-scale) changes to cover a broader period of an individual as well as species dietary signature.

Recent findings on microscopic wear patterns of the Liberian chimpanzees showed that they resemble those of the Tai chimpanzees that are known to have died during a dust-rich dry period, while differing from those Tai chimpanzees that died during a rainy period (Stuhlträger et al., 2021). However, as for the cusp wear patterns of Liberian chimpanzees, we do not think that dust was the major agent causing the specific cusp wear pattern, even though dust and grit has been proven to cause dental wear (e.g., Karme et al., 2016; Lucas et al., 2013). This is due to the various reasons: First, both the Tai and Liberian chimpanzees might have been exposed to the same seasonally occurring dust deposition in the environment (Adhvaryu et al., 2016; Stoorvogel et al., 1997; Stuhlträger et al., 2021), but the Tai chimpanzees do not show such an accelerated wear pattern on their “single-phase-cusps.” Second, there is no evidence from previous tooth wear data (Stuhlträger et al., 2021) that Liberian chimpanzees intendedly consumed grit together with soils, as observed for example in *P. t. schweinfurthii* from Gombe National Park (Tanzania) (Ketch et al., 2001). Third, Liberian and Tai chimpanzees have similar wear facet areas and inclinations, suggesting similar dietary behaviors during phase II of the chewing cycle (Stuhlträger et al., 2021). Hence, it seems unlikely that the Liberian chimpanzee’ cusp wear pattern is a result of dietary comminution during the masticatory power stroke. We rather think that it is most probably a result of specific dietary behaviors that occur during the initial phase of the chewing cycle. We suggest that the cusp wear patterns of Liberian chimpanzees reflect the consumption of more abrasive hard object food items (e.g., seeds or nuts) that were cracked between upper and lower molars. Whether dust or grit were adhered to those hard objects, which would most probably increase the wear probability, can only be speculated.

This proposed hard object cracking with teeth was recently observed in Western lowland gorillas, who seasonally consume the soft endosperm of *Coula edulis* nuts, which is accessed by opening the hard nut shell with their postcanine dentition (van Casteren et al., 2019). Unfortunately, there are no cusp wear data available for this gorilla population. However, dental wear and topographic analyses among gorilla subspecies revealed that their dietary variations are visible in the wear patterns (Berthaume & Schroer, 2017; Galbany et al., 2016; Harty et al., 2022). Other studies also showed that the consumption of hard-shelled fruits is positively correlated with macroscopic tooth wear rates (Galbany et al., 2014; Yamashita et al., 2016). For example, Yamashita et al. (2016) showed that populations of *Lemur catta* from Madagascar reveal different tooth wear rates depending on the proportion of hard-shelled fruits in the diet; that is, the greatest dental wear was found in the population with the highest consumption rates of the hard-shelled fruits (Yamashita et al., 2016).

Nut (hard object) cracking using tools is less common in chimpanzee populations across Liberia and reports are ambiguous across sites (Boesch et al., 1994; Koops et al., 2022; Ohashi, 2015; Vaidyanathan, 2011). For example, Western chimpanzees from the Nimba Mountains rarely crack nuts with tools (Boesch et al., 1994; Koops et al., 2022). The Nimba Mountains are even closer to the previous distribution area of the Liberian chimpanzees studied here than the Taï National Park. Hence, it is probable that the investigated Liberian population used tools less often when eating nuts than the population in the Tai National Park, where tool use is predominant when eating nuts. Therefore, the following scenario for the investigated population of Liberian chimpanzees is conceivable. Food items that needed to be cracked and opened were placed between the teeth from the buccal side (probably still held with one hand), and vertically applied crushing forces led to higher wear on the respective cusps. The more vertical applied crushing action is supported by recent findings on tip-crushing wear facets, as well as the presence of dental chipping in the Liberian chimpanzees (Janocha, 2019). To verify whether the cusp wear analysis really captured hard object consumption in Liberian chimpanzees, studies on individuals with a documented behavior on nut/seed cracking with teeth that are combined with analyses of their cusp wear are needed. Such a study should specifically include a large number of upper as well as lower molars to capture both wear on maxillary and mandibular teeth.

This notwithstanding, our approach demonstrates that cusp wear analysis is a useful tool for characterizing and comparing tooth wear patterns between two populations of Western chimpanzees, but may be also useful for comparing tooth wear patterns within and between other primate groups. However, we suggest that cusp wear analyses should be coupled with other methods, such as microscopic tooth wear analyses as well as other macroscopic tooth wear analyses to answer questions about intraspecific dietary ecologies.

#### AUTHOR CONTRIBUTIONS

**Julia Stuhlträger:** Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (lead); methodology (equal); validation

(equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Ottmar Kullmer:** Conceptualization (supporting); resources (equal); validation (supporting); writing – review and editing (equal). **Roman M. Wittig:** Resources (equal); validation (supporting); writing – review and editing (equal). **Kornelius Kupczik:** Conceptualization (equal); data curation (supporting); funding acquisition (lead); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal). **Ellen Schulz-Kornas:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); investigation (supporting); methodology (equal); project administration (equal); supervision (equal); validation (equal); writing – review and editing (equal).

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

All tooth crown morphology and cusp wear measurements as well as scripts for statistical analyses are available in the Supplementary Information.

#### ORCID

Julia Stuhlträger  <https://orcid.org/0000-0001-9340-3578>

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## SUPPORTING INFORMATION

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