

Extant ape dental topography and its implications for reconstructing the emergence of early *Homo*

9 **Abstract**

10 Dental topography has successfully predicted the diets of species in several extant and extinct
11 mammalian clades. However, dental topographic dietary reconstructions have high success rates only
12 when closely related taxa are compared. Given the dietary breadth that exists among extant apes and
13 likely existed among fossil hominins, dental topographic values from many species and subspecies of
14 great apes are necessary for making dietary inferences about the hominin fossil record. Here, we
15 present the results of one metric of dental topography, Dirichlet normal energy (DNE), for seven groups
16 of great apes (*Pongo pygmaeus pygmaeus*, *Pan paniscus*, *Pan troglodytes troglodytes* and
17 *schweinfurthii*, *Gorilla gorilla gorilla*, *Gorilla beringei graueri* and *beringei*). DNE was inadequate at
18 differentiating folivores from frugivores, but was adequate at predicting which groups had more fibrous
19 diets among sympatric African apes. Character displacement analyses confirmed there is substantial
20 dental topographic and relative molar size ($M_1:M_2$ ratio; length, width, and area) divergence in sympatric
21 apes when compared to their allopatric counterparts, but character displacement is only present in
22 relative molar size when DNE is also considered. Presence of character displacement is likely due to
23 indirect competition over similar food resources. Assuming similar ecological conditions in the Plio-
24 Pleistocene, the derived masticatory apparatuses of the robust australopithecines and early *Homo* may
25 be due to indirect competition over dietary resources between the taxa, causing dietary niche
26 partitioning. Our results imply that dental topography cannot be used to predict dietary categories in
27 fossil hominins without consideration of ecological factors such as dietary and geographic overlap. In
28 addition, our results may open new avenues for understanding the community compositions of early
29 hominins and the formation of specific ecological niches among hominin taxa.

30

31 **Introduction**

32 Plio-Pleistocene hominin dietary ecology has been the focus of many studies over the past
33 century (e.g. (Dart, 1934; Jolly, 1970; Teaford and Ungar, 2000; Smith et al., 2005, 2015; Ungar et al.,
34 2006a; Ungar, 2007; Strait et al., 2009, 2013; Berthaume et al., 2010; Grine et al., 2010, 2012; Ungar and
35 Sponheimer, 2011; Daegling et al., 2013)). Dietary ecology is inferred by determining the properties of
36 the foods hominins consumed (e.g. isotopic (Sponheimer et al., 2013), microwear/microwear textural
37 analyses (Ungar et al., 2008; Ungar, 2011; Ungar and Sponheimer, 2011), and dental calculus analysis
38 (Henry et al., 2012)) or from aspects of morphology that suggest what the hominins may have been
39 adapted to consume (e.g. morphological studies of the cranium, mandible, and/or the teeth (Spencer,
40 2003; Ungar, 2004; Smith et al., 2005; Lucas et al., 2008; Berthaume et al., 2010; Constantino et al.,
41 2010; Skinner et al., 2015)). As with many studies dealing with extinct taxa, having an appropriate
42 comparative dataset of extant taxa helps interpret how mechanical properties and morphology might
43 relate to dietary ecology (Wood and Schroer, 2012), but see (Michael A. Berthaume, 2016). In the case
44 of the hominins, a common extant reference is the great apes.

45 One recently developed method that has been successful in correlating dietary ecology to
46 postcanine tooth shape is dental topography. Dental topography is the quantification of occlusal tooth
47 shape using geographic information system (GIS) software (Zuccotti et al., 1998). Since its development,
48 dental topography has broadened to include several other non-GIS specific metrics, such as Dirichlet
49 normal energy (DNE; Bunn et al., 2011; Winchester et al., 2014) and ambient occlusion (portion de
50 ciel visible or “portion of visible sky,” PCV; Berthaume, 2016b; Berthaume and Winchester,
51 unpublished). Several studies have been conducted using dental topography to reconstruct the diets of
52 extinct primates (see Table 1), all of which have compared the extinct taxa to closely related extant taxa.
53 This is important as the same dental topographic score can be correlated to different dietary categories

54 in different extant samples (Winchester et al., 2014), meaning a distantly related extant sample can lead
55 to erroneous results. In the case of the hominins, this means using a sample that does not consist solely
56 or partially of the great apes. What remains consistent across clades, however, is that a higher dental
57 topographic score indicates a more insectivorous/folivorous/fibrous diet, while a lower dental
58 topographic score indicates a more omnivorous/frugivorous/harder diet (Boyer, 2008; Bunn et al., 2011;
59 Godfrey et al., 2012; Winchester et al., 2014; Allen et al., 2015). Two studies have used dental
60 topography to better understand the dietary ecology of the hominins (Ungar, 2004, 2007), relying on the
61 same extant sample (*Gorilla gorilla gorilla* and *Pan troglodytes troglodytes*). These apes are highly
62 frugivorous, and do not capture the dietary or morphological variability that exists across populations of
63 extant apes. Including a sample of apes that cover a larger dietary diversity may alter how we interpret
64 the hominin record.

65 *Dietary Variability in the Great Apes*

66 Great apes are primarily frugivorous, with the exception of two primarily folivorous subspecies
67 of *Gorilla beringei*. *Gorilla beringei beringei* is found in two populations: one in the Bwindi Impenetrable
68 National Park (Uganda) and the other in the Virunga volcanoes (Uganda, Rwanda, and the Democratic
69 Republic of Congo). These high-altitude environments, particularly in the Virunga volcanos, provide
70 little to no fruit (Tutin and Fernandez, 1985; Hladik, 1988; Watts, 1990; Yamagiwa et al., 1992; Rogers et
71 al., 2004), and as a consequence, *G. b. beringei* is highly folivorous (Robbins and McNeillage, 2003;
72 Elgart-Berry, 2004; Ganas et al., 2004; Rothman et al., 2007). *Gorilla beringei graueri* lives in eastern
73 portions of the Democratic of Congo in an environment that provides *G. b. graueri* more fruit than *G. b.*
74 *beringei*. However, *G. b. graueri* still consumes more folivorous than frugivorous matter, and we classify
75 *G. b. graueri* as a folivore (Yamagiwa et al., 1992, 1994, 1996, 2005).

76 The remaining species of great apes (i.e. *Gorilla gorilla*, *Pan troglodytes*, *Pan paniscus*, *Pongo*
77 *abelii* and *Pongo pygmaeus*) are frugivores, though the pattern and degree of frugivory differs among
78 these species. *Gorilla gorilla* is broken into two subspecies (*G. g. gorilla* and *G. gorilla diehli*) which are
79 both primarily frugivorous, but also consume a significant amount of terrestrial and aquatic herbaceous
80 vegetation. *Gorilla gorilla* predictably consumes more herbaceous vegetation during times when fruit is
81 less available (Rogers et al., 2004) and *G. g. diehli* is somewhat less frugivorous than *G. g. gorilla*,
82 potentially because of reduced fruit availability in its habitat (McFarland, 2007).

83 There are four subspecies of chimpanzees (*P. t. troglodytes*, *P. troglodytes schweinfurthii*, *P.*
84 *troglydytes ellioti*, and *P. troglodytes verus*) and one species of bonobos (*P. paniscus*). Eastern
85 chimpanzees (*P. t. ellioti*, *P. t. troglodytes* and *P. t. schweinfurthii*) are found across central Africa and are
86 broadly sympatric with species of *Gorilla*. *Pan troglodytes troglodytes* is frugivorous, but differs from
87 sympatric *G. g. gorilla* in that *P. t. troglodytes* is a fruit pursuer, consumes fruit year-round and prefers
88 compliant, ripe fruit, only consuming mechanically challenging fruits like figs during fallback episodes
89 (Kuroda et al., 1996). Meanwhile *G. g. gorilla* is an opportunistic frugivore and falls back on more
90 fibrous, folivorous matter (Tutin and Fernandez, 1985, 1993; Tutin et al., 1991; Wrangham et al., 2003;
91 Head et al., 2011). The range of *P. t. schweinfurthii* includes the range of *G. b. graueri* (Yamagiwa and
92 Basabose, 2006; Yamagiwa et al., 2012) and one population of *G. b. beringei* in Bwindi Impenetrable
93 Forest, Rwanda (Stanford and Nkurunungi, 2003) . Unlike the gorillas it is sympatric with, *P. t.*
94 *schweinfurthii* consumes the same amount of fruit year-round, regardless of fruit availability (Nishida
95 and Uehara, 1983; Yamagiwa et al., 1996; Reynolds et al., 1998). *Pan troglodytes schweinfurthii* differs
96 from *P. t. troglodytes* in that it is more folivorous and consumes mechanically challenging figs year-
97 round (Yamagiwa and Basabose, 2006). *Pan troglodytes ellioti* occupies a range north of *P. t. troglodytes*,
98 where it is sympatric with both subspecies of *G. gorilla*. Although dietary data on *P. t. ellioti* is not as
99 common as with the other subspecies of chimpanzees, it appears to have a diet similar to *P. t.*

100 *schweinfurthii*, seasonally consuming non-fruit matter including insects, animal matter, and honey, and
101 consuming large quantities of figs year-round (Dutton and Chapman, 2015).

102 The western savanna chimpanzee, *P. t. verus*, can be found in Senegal, Mali, Guinea-Bissau,
103 Guinea, Sierra Leone, Liberia, Cote D'Ivoire, and Ghana, while the bonobo (also called the pygmy
104 chimpanzee), *P. paniscus*, is endemic to the Democratic Republic of Congo. These are the only two
105 (sub)species of *Pan* that are completely allopatric to *Gorilla*, *P. t. verus* and *P. paniscus*. *Pan troglodytes*
106 *verus* appears to have a more restricted diet compared to *P. t. troglodytes* and *P. t. schweinfurthii*,
107 consuming fewer types of foods, with animal matter making up a larger percentage of its diet (McGrew
108 et al., 1988; Pruett, 2006). Like other chimpanzees, it is primarily frugivorous. *Pan paniscus* is also
109 primarily frugivorous, but consumes a large amount of terrestrial herbaceous vegetation and has been
110 described as having a diet intermediate between gorillas and chimpanzees (Kano and Mulavwa, 1984;
111 Malenky and Stiles, 1991). Although bonobos have been described to consume less vertebrate matter
112 than chimpanzees, they can be vicious hunters, searching out and consuming larger mammals such as
113 duiker, often beginning to consume the animals before they are killed (Fruth and Hohmann, 2002).

114 There are three subspecies of Bornean and one species of Sumatran orangutan which are found
115 in Indonesia and Malaysia. All orangutans are primarily frugivorous, with diets sometimes consisting
116 entirely of ripe fruit, particularly during times of extreme fruit abundance (i.e., masting events, Taylor,
117 2006; Kanamori et al., 2010). However, Sumatran orangutans (*Pongo abelii*) consume more ripe fruit
118 and less mechanically challenging foods than Bornean orangutans (Vogel et al., 2014). There is also
119 dietary variation among the three subspecies of Bornean orangutans (*P. pygmaeus morio*, *P. pygmaeus*
120 *pygmaeus*, and *P. pygmaeus wurmbii*), with *P. p. morio* consuming more leaves and bark than *P. p.*
121 *wurmbii* (Kanamori et al., 2010). Little is known about how the diet of *P. p. pygmaeus* compared to the
122 other subspecies of *P. pygmaeus* (Vogel, personal communication).

123 *Dietary Overlap and Niche Partitioning in Sympatric Apes*

124 Great apes are valuable referents for studies of fossil hominins due to their genetic similarities,
125 similar body size, and similar life histories. The propensity for populations of *Gorilla* and *Pan* to overlap
126 and negotiate broadly overlapping diets also lends itself to the study of dietary ecologies among fossil
127 hominins. Recent fossil discoveries suggest that overlap among hominin taxa is an increasingly likely
128 ecological scenario (Swisher et al., 1996; Spoor et al., 2007; Pickering et al., 2011; Leakey et al., 2012)
129 and that dietary divergence between hominin groups may have occurred near the origin of *Homo*
130 (William M. Schaffer, 1968; Wood and Strait, 2004; Ungar et al., 2008; Cerling et al., 2011, 2013; Ungar,
131 2011; Ungar and Sponheimer, 2011; Schroer and Wood, 2015; Spoor et al., 2015). Dietary overlap is a
132 selective force on many animal populations (Mayr, 1966; Schoener, 1971, 1982; Roughgarden, 1976;
133 Goldberg and Barton, 1992; Webb et al., 2002; Johnson and Stinchcombe, 2007; Emerson and Gillespie,
134 2008; Cavender-Bares et al., 2009), and determining eras of overlap is fundamental for reconstructing
135 the emergence and maintenance of hominin dietary niches. Quantifying dental topography in
136 subspecies of extant apes presents a unique opportunity to test for signals of dietary overlap and
137 competition, and to determine whether similar signals may be recovered in the fossil record.

138 Character displacement is an evolutionary phenomenon by which sympatric taxa (i.e. taxa that
139 overlap geographically and temporally) indirectly or directly compete with each other, causing selective
140 pressures and consequently inducing population-level evolutionary changes. These changes can be
141 detected through comparison with allopatric (i.e. isolated and non-overlapping) populations of the same
142 taxa, which do not experience competition with one another and subsequently have different selection
143 pressures. Character displacement can be assessed at taxonomic levels higher than the species or
144 subspecies level (73, 111, 113, 114), so long as the allopatric taxa share the same phylogenetic distance
145 as the sympatric taxa. Character displacement encompasses a number of different ecological

146 mechanisms, including both direct and indirect competition for dietary resources (Abrams and Cortez,
147 2015). Such a diversity of potential mechanisms can be seen in the living great apes, particularly among
148 populations of *Gorilla* and *Pan* who have similar ecological needs and can have broadly overlapping
149 ranges and diets (Figure 1; Tutin and Fernandez, 1993; Yamagiwa et al., 1996; Stanford and Nkurunungi,
150 2003; Yamagiwa and Basabose, 2006, 2009; Head et al., 2011).

151 Although gorillas and chimpanzees tend to avoid each other (Yamagiwa and Basabose, 2006),
152 particularly during feeding, this is not always possible and can lead to both peaceful interactions such as
153 co-feeding (Suzuki et al., 1995; Tutin, 1996; Stanford and Nkurunungi, 2003; Yamagiwa and Basabose,
154 2006) and aggressive displays by chimpanzees toward gorillas (Kuroda et al., 1996; Yamagiwa et al.,
155 1996; Stanford and Nkurunungi, 2003). Physical altercations have never been reported due to feeding
156 competition between the species. Encounters are also more likely to occur during times of fruit scarcity
157 (i.e. during fallback episodes) (Stanford and Nkurunungi, 2003; Yamagiwa and Basabose, 2006). Though
158 direct competition over resources is relatively sparse between gorillas and chimpanzees, indirect
159 competition is relatively high. Sympatric gorillas and chimpanzees broadly consume the same food
160 resources, each diminishing the availability of food for the other species (Tutin et al., 1991; Tutin and
161 Fernandez, 1993; Kuroda et al., 1996; Tutin, 1996; Yamagiwa et al., 1996; Stanford and Nkurunungi,
162 2003; Yamagiwa and Basabose, 2006). Such indirect resource competition has been hypothesized to act
163 as a selective pressure that leads to adaptations in the masticatory apparatus and digestive system in
164 gorillas (to allow them to have a higher fiber diet) and in the locomotor and social system in
165 chimpanzees (that permits fission-fusion societies and increased home ranges) (Yamagiwa and
166 Basabose, 2009). Behavioral differences do not preclude the possibility that character displacement has
167 occurred in the masticatory apparatuses of both species (Schoener, 1971; Yamagiwa and Basabose,
168 2006). It is possible that sustained dietary overlap has left a morphological signature in the jaws and
169 teeth of both sympatric gorillas and chimpanzees that could manifest itself as character displacement.

170 Character displacement analysis can detect these potential signatures by quantifying the
171 differences in morphology between pairs of sympatric and allopatric taxa. When the difference
172 observed in sympatric taxa is greater than the difference observed in allopatric taxa, competition (direct
173 or indirect) is implicated. Character displacement analysis can use behavioral characters (L. and O.,
174 1956; Husar, 1976; Gerhardt, 1994; Allen et al., 2014) or morphological characters (William M. Schaffer,
175 1968; Malmquist, 1985; Schluter and McPhail, 1992; Dayan and Simberloff, 1994, 2005; Losos, 2000;
176 Schluter, 2000; Simberloff et al., 2000; Collyer and Adams, 2007; Davies et al., 2007; Schroer and Wood,
177 2015), provided these characters are ecologically-informed (Yom-Tov, 1991; Schluter and McPhail, 1992;
178 Jones, 1997; Dayan and Simberloff, 2005; Grant and Grant, 2006; Albert et al., 2007). Gnathic and dental
179 structures correlate with diet (Kay, 1975; Lucas and Luke, 1984; Maier, 1984; Lucas et al., 1986b; Lucas,
180 2004; Berthaume, 2014; Schroer and Wood, 2015) and jaws and teeth are often the source of
181 morphological data for character displacement analyses (Malmquist, 1985; Dayan et al., 1989, 1990;
182 Schluter and McPhail, 1992; Jones, 1997; Adams and Rohlf, 2000; Schroer and Wood, 2015). Character
183 displacement analysis can accommodate any taxonomic level, including different genera (Dayan et al.,
184 1990; Monroe, 2012; Schroer and Wood, 2015) and guild structures (Schluter, 1986), although the
185 degree of evolutionary distance between the sympatric taxa and between the allopatric taxa must be
186 the same. Character displacement has not been widely integrated with dental topography metrics (but
187 see Boyer et al., 2012), and our study provides a test-case of its utility for understanding dental
188 morphological variation among extant apes.

189 In this study, we conduct two related analyses: a comparison of one metric of dental topography
190 (DNE) among seven species and subspecies of great apes with varying diets, and a character
191 displacement analysis of the resulting DNE scores. In our dental topographic comparison, we test two
192 hypotheses. First, that more folivorous apes with more fibrous diets (*G. b. beringei* and *G. b. graueri*)
193 will have higher DNE scores than the more frugivorous apes with less fibrous diets (*P. t. schweinfurthii*,

194 *P. t. troglodytes*, *P. paniscus*, *G. g. gorilla*, and *Pongo pygmaeus*). Second, the apes that consume the
195 “hardest” foods (*P. t. schweinfurthii* and *P. pygmaeus*) will have the lowest DNE scores. In the character
196 displacement analysis, we test whether the overlapping subspecies of *Gorilla* and *Pan* have greater
197 divergence in dental topographic scores. If competition over food resources, indirect or otherwise, is
198 occurring in populations of apes and affecting dental morphology, then character displacement analysis
199 should uncover greater divergence in DNE scores among sympatric, but not allopatric, taxa.

200 As previous character displacement analyses on the masticatory apparatus have frequently
201 relied on linear and size measurements, data on M_1 and M_2 tooth size (width, length, and size) was
202 gathered on the same specimens and submitted to a character displacement analysis. Tooth size is
203 roughly correlated with diet in primates, with more folivorous primates having larger teeth (e.g. (Lucas,
204 2004; Boyer, 2008; Winchester et al., 2014)). Given the high level of sexual dimorphism in great ape
205 tooth size (Swindler, 2002), either sex must be kept constant or relative tooth size must be used. There
206 is some evidence suggesting a distally expanding tooth row may be correlated to the degree of folivory
207 in some primates (e.g. (Lucas et al., 1986a; Teaford and Ungar, 2000)), but this is largely confined to
208 $M_1:M_3$ ratio. Given the difficulties in obtaining a single sex or a balanced mixed sex sample with minimal
209 wear and well preserved, erupted M_3 's, we used an unbalanced mixed sample and excluded the
210 confounding effects of body by investigating relative molar size, which was quantified using $M_1:M_2$ ratio.
211 Should the relative molar size analyses yield the same results, it would suggest that relative molar size
212 can be reliably used in lieu of DNE in future studies. This would be useful to researchers, as relative
213 molar size is preserved in the fossil record and in museum specimens more frequently than tooth shape,
214 quantified by DNE.

215

216 **Materials and Methods**

217 A mixed sex sample of 44 frugivorous and 17 folivorous ape M₂'s were chosen for analysis.
218 Teeth with minimal wear were chosen (i.e. no or low levels of dentin exposure), as dental topographic
219 measurements are known to be highly sensitive to tooth wear (Ungar and Williamson, 2000; M'Kirera
220 and Ungar, 2003; Ungar and M'Kirera, 2003; Ungar, 2004; Klukkert et al., 2012; Venkataraman et al.,
221 2014). This resulted in a mixed sample of left and right molars, but no antimeres from the same
222 individual were used in the study. As the potential effects of sex or bilateral asymmetry on dental
223 topographic measurements have yet not been investigated, we cannot say whether or not these
224 assumptions will have an effect on our results. In *Pan troglodytes verus*, small sex based differences
225 have been observed hypocone sharpness (Stuhltraeger et al., 2016), but this could be due to allometry,
226 as males tend to have larger teeth (Swindler, 2002) and cusp size is positively correlated with cusp
227 sharpness (Berthaume, 2014). While some studies have found small sexual differences in ape diet (e.g.
228 differences in nut and meat consumption in *Pan* (Boesch and Boesch-Achermann, 2000)), other studies
229 have found no systematic differences between male and female diet (e.g. (Doran et al., 2002)). There is
230 also the possibility that, even if there are sex-based differences in diet, they will not manifest in dental
231 morphology due to genetic similarities between males and females of the same species. Here, our
232 sample is too small to meaningfully analyze male and female data separately, and we thus pool sexes.

233 Second molars were chosen because their structure is usually representative of the postcanine
234 mandibular tooth row (Kay, 1975; Sheine and Kay, 1977), and they have been shown to contain a dietary
235 signature in dental topographic studies on platyrrhines and prosimians (Godfrey et al., 2012; Ledogar et
236 al., 2013; Winchester et al., 2014; Boyer et al., 2015). This does not preclude other postcanine teeth
237 from also carrying dietary signatures (Kay, 1975, 1981, Sheine and Kay, 1977, 1982; Berthaume, 2014;
238 Allen et al., 2015; Boyer et al., 2015).

239 Character displacement analysis is improved by an understanding of how long populations have
240 been sympatric. Hypothetically, populations sympatric for a longer time will have a higher level of
241 specialization than populations sympatric for a shorter time. However, length of sympatry is often
242 unknown or poorly understood, and character displacement can be detected even in species
243 phylogenetically close enough to hybridize (90). The effects of the so-called “ghost of competition past”
244 imply that while the timing and duration of character displacement cannot easily be pinpointed, the
245 contribution (or not) of sympatric pressures on morphological evolution can (Pritchard and Schluter,
246 2001). It is therefore possible to detect character displacement (in morphological characters) in taxa
247 that have both sympatric and allopatric populations if gene flow has occurred from the sympatric to the
248 allopatric populations. This would make the exact location of the individuals used in the character
249 displacement analysis irrelevant. Exact location of individuals from the allopatric taxa is always
250 irrelevant in the character displacement analysis. Due to the difficulties in obtaining an ideal sample
251 (due to variation in tooth wear, and year and site at which specimens were collected), we are assuming
252 that, due to gene flow, tooth shape and size is relatively homogeneous within each subspecies.

253 The frugivorous apes included in this study were *G. g. gorilla*, *P. t. troglodytes*, *P. t.*
254 *schweinfurthii*, *P. paniscus*, and *P. p. pygmaeus*, and the folivorous apes were *G. b. beringei* and *G. b.*
255 *graueri* (Table 2). Two pairs of sympatric apes (*G. g. gorilla* and *P. t. troglodytes*, and *G. b. graueri* and *P.*
256 *t. schweinfurthii*), and one pair of allopatric apes (*P. paniscus* and *G. b. beringei*) were chosen for the
257 character displacement analysis. While *P. p. pygmaeus* was included in the dental topographic analysis,
258 it was excluded from the character displacement analysis because the genetic distance between *Pongo*
259 and the African apes exceeds the genetic distance between *Gorilla* and *Pan*. Exact locations and sexes
260 for each specimen can be found in the supplementary material.

261 Digital representations of the teeth were produced by taking laser scans of casts of the teeth,
262 which are housed at the Paleoanthropology Laboratory at the University of Arkansas and were supplied

263 courtesy of Peter Ungar (Figure 2). Casts were produced by pouring translucent epoxy mixed with a pale
264 pink pigment into high resolution negative molds of tooth rows of museum specimens (M'Kirera and
265 Ungar, 2003; Ungar and M'Kirera, 2003; Klukkert et al., 2012). Casts were coated with a thin layer of
266 Magnaflux Spotcheck SKD-S2 Developer to aid the XSM multisensory scanner (Xystrum Corp., Turino,
267 Italy) in picking up the surface of the tooth (Ungar, 2004; Berthaume, 2014). 2.5D scans of the teeth
268 were taken, with teeth in anatomically correct position such that the y-axis ran in the mesiodistal
269 direction, the x-axis ran in the buccolingual direction, and the z-axis ran in the superior-inferior
270 direction, with the most distal molar closest to the origin of the scan. (2.5D scans are scans where a
271 surface is a projection of a plane into the 3rd dimension. In this case, this means there is one height
272 coordinate for each pair of length and width coordinates.) Scans were taken at a resolution of 50 μm ,
273 resulting in point cloud representations of the teeth that had a resolution of 400 data points per square
274 millimeter.

275 Dental topographic analyses can be performed with the entire enamel crown (Boyer, 2008) or
276 the superior portion of the occlusal surface (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003). DNE
277 is relatively insensitive to the cropping method (Bunn et al., 2011). As it is not possible to capture the
278 entire tooth crown with this laser scanner, we chose the latter cropping method, using just the superior
279 portion of the occlusal surface.

280 DNE is a summative metric that measures the curviness of a 2.5D or 3D surface constructed by
281 triangles, meaning it is sensitive to the number of triangles in a mesh. Teeth meshed with more
282 triangles have higher DNE scores than the same teeth meshed with fewer triangles, making it important
283 to keep the number of triangles constant across all teeth. Triangular surface meshes of the tooth rows
284 were constructed from the point clouds using the Delaunay Triangulation command in AVIZO 6.1 and
285 saved as *.ply files. The 2.5D surfaces were imported into CloudCompare, where M_2s were isolated and

286 all triangles inferior to the lowest point on the occlusal surface were deleted. Surfaces were again
287 exported as *.ply files and reimported into AVIZO 6.1, where M₂s were simplified down to 19,990-
288 20,000 triangles and smoothed using the Smooth Surface command (lambda=3, 100 iterations). This
289 protocol is similar to that set forth in Bunn et al. (2011) with one distinct change: the molars in Bunn et
290 al. (2011) were simplified down to 9,990-10,000 instead of 19,990-20,000 triangles. We chose to
291 simplify our teeth to a larger number of triangles because we felt too much of the occlusal topography
292 was lost at the lower resolution (i.e. crenulated teeth began to look like flat surfaces). While a
293 significant amount of detail was still lost at the resolution used in this study, we felt it was a high enough
294 to capture the general shape of the tooth (see Figure 3). This loss in resolution was not observed in
295 crenulated platyrrhine teeth (i.e. the *Pithecia* teeth used in Winchester et al., 2014) and implies there
296 may be a size effect that needs to be taken into account when performing DNE (Winchester, personal
297 communication). Furthermore, as two of the most commonly used dental topographic measurements
298 (DNE and orientation patch count, OPC) are summative, measurements taken at different resolutions
299 cannot be directly compared. The numerical results from this study are therefore not comparable to
300 previous DNE studies; the patterns of results, however, are. To foster additional comparisons between
301 studies, we have reported our results from lower resolution M₂s in the electronic supplementary
302 material (ESM 1).

303 DNE was calculated in a beta version of MorphoTester, which is now available for download at
304 <http://morphotester.apotropa.com/> (Winchester, 2016), with 1% energy*area outlier removal. It is also
305 possible to calculate DNE using a recently released R package named molaR (Pampush et al., 2016).
306 Some teeth encountered the *CHOL error*, which prevents DNE from being calculated. For surfaces
307 encountering this problem, it is recommended a 1 or 2-iteration Laplacian smooth be applied in Meshlab
308 (Cignoni et al., 2008). As this can decrease DNE scores by around 20-30%, all teeth were imported into
309 Meshlab and had 2 iterations of Laplacian smooth applied to them.

310 *Determining the Presence of a Dietary Signature*

311 The importance of controlling for phylogeny when deriving dietary signatures from tooth shape
312 is well documented (Kay and Ungar, 1997; Ungar, 2004; Winchester et al., 2014; Allen et al., 2015). In
313 order to control for phylogeny in our study, we used phylogenetically-corrected ANOVA with a
314 Bonferroni correction to determine if DNE was correlated to diet. This was done using the Geiger
315 package (Harmon et al., 2008) in R (R Development Core Team and Team, 2015), and a published
316 primate phylogeny created using a supermatrix (Springer et al., 2012).

317 As there is no published phylogeny that differentiates apes at the subspecies level, we ran our
318 phylogenetically corrected ANOVAs using the same protocol as in Berthaume (2014). Briefly, we created
319 four trees, with each of the pair of subspecies splitting either 10,000 years after speciation (i.e. *G. b.*
320 *beringei* and *G. b. graueri* split only 10,000 years after *G. beringei* and *G. gorilla* split) or only 10,000
321 years ago (Figure 4). This encompasses the full range of times in which subspecies may have divided.
322 We then ran four phylogenetically-corrected ANOVAs, one with each tree. If the P-values were
323 significant ($p < 0.05$) for all trees, this implied that our results were significant and robust. If the P-values
324 were not significant ($p > 0.05$) for all trees, this implied that our results were robust but not significant.
325 If the P-values were a mix of significant and not significant, we considered our results not robust. All P-
326 values were adjusted using a Bonferroni correction for multiple comparisons.

327 *Character Displacement*

328 Character displacement analysis was used to test for significant differences between the DNE
329 scores of sympatric and allopatric apes. Previous character displacement analyses on gnathic and dental
330 morphologies have relied on linear and relative molar size measurements. Our study is among the first
331 to use topographic measurements as input variables for character displacement analysis. In order to test
332 the validity of our model and compare the results of our DNE analysis with previous character

333 displacement analyses, we ran three versions of the analysis: one with only relative molar size variables,
334 one with only DNE scores, and a combined analysis of relative molar size variables and DNE scores. We
335 obtained three relative molar size variables from the M_1 s and M_2 s of our specimens: the mesiodistal
336 (MD) diameter, the buccolingual (BL) diameter, and the occlusal area. To obtain these measurements,
337 we rotated surface reconstructions of our xyz coordinates to obtain maximum occlusal area and
338 imported a screenshot of the scaled tooth into TPSdig (Rohlf, 2009). Tooth diameters were maximum
339 linear measurements and occlusal area was calculated from 20 semilandmarks equidistantly fitted
340 around the occlusal margin. All measurements were log-transformed and, in order to reduce the
341 number of variables in our model, we indexed our measurements by dividing the M_1 measurement with
342 the corresponding M_2 measurement.

343 Three pairs of sympatric populations were included in our character displacement analysis: *P. t.*
344 *troglydytes* and *G. g. gorilla*, *P. t. schweinfurthii* and *G. b. graueri*, and a combined sample of all
345 sympatric *Pan* and all sympatric *Gorilla*. Our allopatric comparison for all three comparisons was *P.*
346 *paniscus* and a sample of *G. b. beringei* from the Virunga Mountains, where gorillas do not overlap with
347 chimpanzees.

348 *General linear model*

349 Character displacement is quantified as the displacement statistic $D_S - D_A$, where D_S indicates
350 divergence between sympatric taxa that may compete for resources and D_A indicates divergence
351 between allopatric taxa (Schluter and McPhail, 1992; Figure 5). When $D_S - D_A > 0$, competition is
352 implicated, and significance can be determined by resampling the populations. To quantify divergence
353 and perform resampling, we apply a general linear model derived from Collyer and Adams (2007).

354 A general liner model follows the form $Y = BX + U$. In our model, Y is the morphological matrix of
355 relative molar size or dental topography variables, X is a matrix of general ecological conditions, and U is

356 the residual error, which is assumed at zero. By dividing each side by X, we can solve for B, a matrix that
357 translates the two matrices. The model is described in more detail in Schroer and Wood (2015), which
358 includes examples of the matrices and an R-based script for conducting the analysis. Here, we
359 summarize the most important elements of the analysis. Our raw data is provided in the supplementary
360 material accompanying this manuscript (ESM 2) and at [DOI @ PUBLICATION].

361 The X matrix uses dummy variables (i.e. Boolean indicators) to encode the ecological situation of
362 individual specimens and reduce them to binary conditions. Each specimen belongs to one of four
363 categories: a sympatric population of the first taxon, an allopatric population of the first taxon, a
364 sympatric population of the second taxon, or an allopatric population of the second taxon. We
365 subsequently assign each specimen a series of dummy variables. For taxonomic designations, each
366 specimen in the first taxon is encoded as 1 and each specimen in the second taxon is encoded as -1. For
367 the presence or absence of overlap, sympatric taxa are encoded as 1 and allopatric taxa are encoded as -
368 1. The two values now given for each specimen are multiplied to give a third variable—the interaction of
369 taxon and overlap.

370 Using the X and Y matrices, B is solved. B is a matrix of partial regression coefficients and
371 effectively translates between the ecological conditions and morphological outputs. We can apply this
372 matrix to the least squares mean of each of our four ecological groups (i.e. the two taxa in sympatry and
373 the two taxa in allopatry). This results in four phenotypic change vectors, one for each population. The
374 difference between vectors of the sympatric taxa is D_S , and the difference between vectors of the
375 allopatric taxa is D_A . Subtracting these vectors from one another yields $D_S - D_A$, the character
376 displacement statistic.

377 Using a probability distribution, we can determine whether the observed $D_S - D_A$ value is
378 significant. To generate this probability distribution, we remove the interaction variable from the design
379 matrix so that individuals remain encoded by their taxon and the presence/absence of overlap, but the

380 interaction between these variables no longer creates an effect in the model. We solve again for the B
381 matrix and randomly assign the residual effects to the least squares means of our four populations. This
382 results in four different phenotypic change vectors, and from these vectors we derive a new D_S-D_A value.
383 We encode this value as 1 (greater than or equal to the observed D_S-D_A) or 0 (less than the observed D_S-
384 D_A). We iterate this procedure 999 times to obtain a distribution of possible D_S-D_A values from our
385 randomized study sample and assume significance for our original, observed D_S-D_A if it appears less than
386 5% of the time.

387

388 **Results**

389 DNE scores broadly overlapped between frugivorous and folivorous apes, with *P. p. pygmaeus*
390 having a range of DNE scores that encompassed nearly all other apes (Figure 6). Phylogenetically-
391 corrected ANOVAs revealed that DNE scores could not group apes based on their dietary categories
392 (Tree1 $P=0.304$, Tree2 $P=0.381$, Tree3 $P=0.418$, Tree4 $P=0.319$). Non-phylogenetically corrected Mann-
393 Whitney U-tests indicated statistically significant differences existed between sympatric gorillas and
394 chimpanzees, with sympatric gorillas having higher DNE scores than sympatric chimpanzees (Table 3,
395 significance at $P<0.0083$). Among *Gorilla* and *Pan*, *G. b. graueri* and *P. t. troglodytes* were found to have
396 the highest and lowest DNE scores, respectively, suggesting that *G. b. graueri* has the most fibrous diet
397 and *P. t. troglodytes* had the least fibrous diet among African apes. *Pan troglodytes troglodytes* had
398 significantly lower DNE scores than all other apes, and *G. b. graueri* had significantly higher DNE scores
399 than all other apes save *P. p. pygmaeus*. No other significant differences existed among the apes (Table
400 3).

401 The results of character displacement analyses broadly indicate that sympatric populations of
402 *Gorilla* and *Pan* diverge in their macromorphology and DNE scores compared to allopatric *Gorilla* and

403 *Pan* (Table 4). The two analyses that included DNE scores had significant results in all three sympatric
404 populations of *Gorilla* and *Pan* (i.e. *G. g. gorilla-P. t. troglodytes*, *G. b. graueri-P. t. schweinfurthii*, and
405 the combined *Gorilla-Pan* samples). When relative molar size variables are included in the analysis,
406 results are more significant than when DNE scores are used alone ($P < 0.03$ compared to $P < 0.05$). In the
407 analysis that included only relative molar size variables, results were not significant in the comparisons
408 containing *P. t. troglodytes* ($P > 0.05$), and were only significant in the comparison between *G. b. graueri*
409 and *P. t. schweinfurthii* ($P < 0.05$). Additional character displacement analyses, analyzing each relative
410 molar size index independently, relative molar size variables, can be found in the ESM and generally
411 upholds this result.

412 **Discussion**

413 Dental topography, measured by DNE, was unsuccessful at predicting dietary categories for
414 apes, yielding similar scores for folivores and frugivores (Figure 6). *G. b. beringei*, an obligate folivore in
415 the Virunga Mountains, had lower DNE scores than the more frugivorous *G. b. graueri* ($p = 0.0079$), even
416 though both are primarily folivorous. Statistically significant differences between folivores and
417 frugivores existed only between *G. b. beringei* and *P. t. troglodytes*, and *G. b. graueri* and all frugivores
418 save *P. p. pygmaeus* (Table 3). In previous DNE studies, primates with higher fiber diets tended to have
419 higher DNE scores compared to primates with lower fiber diets (Bunn et al., 2011; Godfrey et al., 2012;
420 Winchester et al., 2014). In the apes, this distinction was significant in comparisons of sympatric apes
421 (*G. b. graueri* and *P. t. schweinfurthii*, $P = 0.0030$, *G. g. gorilla* and *P. t. troglodytes*, $P = 0.0003$) but not
422 allopatric apes (Table 3).

423 Teeth with higher DNE scores have curvier surfaces, which are hypothesized to be more efficient
424 at cutting and breaking down foods with low digestibility and high cell wall content, such as chitinous
425 and fibrous foods (Sheine and Kay, 1977). Breaking down these foods increases digestibility by

426 increasing the surface area to volume ratio, which in turn increases the caloric intake for the animal (Kay
427 and Sheine, 1979). Conversely, foods high in digestibility and low in cell wall content do not need to be
428 broken down as thoroughly—breaking down these foods too efficiently is a waste of energy and can
429 have adverse effects of bolus formation (Sheine and Kay, 1982; Lucas, 2004). Within sympatric apes,
430 gorillas consistently have a higher DNE scores. As chitinous foods make up a small percentage of their
431 diet, it is reasonable to assume the curvier teeth in gorillas is an adaptation to a higher fiber diet.

432 These conclusions are consistent with the literature gathered on diet, where *G. b. graueri* has
433 been observed eating leaves when fruit was readily available (Yamagiwa and Basabose, 2006), and *P. t.*
434 *trogodytes* has been described as being a ripe fruit specialist, avoiding fibrous foods whenever possible
435 (Tutin et al., 1991; Tutin and Fernandez, 1993; Kuroda et al., 1996). The increase in fiber consumption in
436 gorillas has been quantified in many studies. For example, Yamagiwa and Basabose (2006) provided
437 results following an 8 year study of sympatric populations of *G. b. graueri*'s and *P. t. schweinfurthii*.
438 Based the analysis of 14,367 gorilla and 8,070 chimpanzee fecal samples, sieved using a 1 mm mesh,
439 they found that the range for mean proportion of fibrous food remains per fecal sample was 42-100%
440 for *G. b. graueri*'s diet and 7-78% for *P. t. schweinfurthii*'s diet. This demonstrated that, while eastern
441 chimpanzees can have seasonally high fiber diets, gorillas tend to, on average, have high fiber diets
442 throughout the year. Similar results have been found in western gorillas and chimpanzees (Tutin and
443 Fernandez, 1985, 1993; Kuroda et al., 1996). This supports the hypothesis that the curvier teeth in
444 gorillas may be an adaptation in this genus to a higher fiber diet (Berthaume, 2014).

445 It was previously found that dental topography is sensitive to phylogeny (Winchester et al.,
446 2014), but was concluded that, when comparing closely related taxa, dental topography can still be used
447 to predict dietary categories within primates. The results from this study suggest that, while diet can be
448 predicted with dental topographic measures in some groups of closely related primates, such as

449 platyrrhines and strepsirrhines, it is not true for all primates, such as apes and possibly other
450 catarrhines. Additional studies are needed to determine when dental topography is a reliable indicator
451 of dietary categories in fossil hominins.

452 However, dental topography combined with character displacement analysis may provide useful
453 interpretations for dietary distinctions between potentially overlapping populations. Results from the
454 character displacement analysis indicate that the difference in DNE scores between the sympatric apes
455 of two genera was significantly greater than the difference in scores between allopatric apes of the
456 same genera (Table 4). This suggests that sympatry in closely related taxa such as *Gorilla and Pan* may
457 relate to divergence in postcanine tooth morphology and occlusal complexity, probably through dietary
458 partitioning. These results are likely generalizable to more aspects of the masticatory apparatus, not
459 just tooth shape, although additional research is needed. While sympatric taxa form natural testing
460 grounds for hypotheses dealing with interactions between morphological and ecological variables (see
461 also Janson, 2000), caution should be taken when using allopatric taxa to test these hypotheses, as
462 allopatric taxa exist in different locations and will likely face different selection pressures.

463 If character displacement has occurred between in the postcanine of gorillas and chimpanzees,
464 it is more likely to relate to indirect competition between these two groups rather than direct
465 competition. Gorillas and chimpanzees generally avoid each other during feeding, and any sustained
466 direct competition between them over food resources is likely due to scramble competition. However,
467 ecological competition often occurs indirectly, such as when one taxon affects another taxon by
468 consuming its dietary resources and limiting the amount of available food in its range. Dietary
469 partitioning through adaptations of the masticatory apparatus is one way in which mammalian taxa can
470 reduce indirect competition. Differences in foraging strategies, social systems, and modes of
471 locomotion may also lead to reduced competition. Evidence of such behavioral differences exists in

472 gorillas and chimpanzees. For example, when chimpanzees find a tree full of ripe fruit, they spend a
473 long time in the tree and consume large quantities of fruit (Kuroda et al., 1996). Conversely, gorillas will
474 only forage for a short period of time before moving on, leaving large quantities of ripe fruit behind
475 (Kuroda et al., 1996). Chimpanzees are more likely to deplete most of the resources in a small location,
476 while gorillas are more likely to deplete resources to a lesser extent, but over a larger range. In addition,
477 during fallback episodes, chimpanzees tend to forage further and in smaller groups, while gorillas tend
478 to consume more herbaceous vegetation and bark. This could lead to unequal pressures on the
479 masticatory apparatuses, locomotor systems, and social systems of gorillas and chimpanzees diet
480 (Yamagiwa and Basabose, 2006, 2009), which could result in changes in the general morphology and
481 behavior of a population overtime. While character displacement analysis cannot necessarily pinpoint
482 the time of the origin of competition between sympatric *Gorilla* and *Pan*, nor separate the effects of
483 direct and indirect competition between these taxa, it suggests that sustained and substantial resource
484 competition has affected the masticatory features of these taxa.

485 *Implications for the Hominin Record and the Evolution of Early Homo*

486 During the Plio-Pleistocene, hominin taxa existed sympatrically and allopatrically throughout
487 Africa (e.g. (Schroer and Wood, 2015)). When sympatric, competition between taxa would have led to
488 population extinction, reinforced and maintained allopatry, or sufficient niche separation to allow for
489 continued sympatry (Swedlund, 1974). The idea that character displacement was occurring in the
490 hominins was first introduced in Brown, 1958. Schaffer, 1968 built on this and tested for character
491 displacement in the hominins using postcanine tooth size measurements. They found evidence for
492 character displacement in postcanine tooth area when comparing the robust australopithecines to early
493 *Homo*; differences were exaggerated where the taxa were likely sympatric (Olduvai Gorge and
494 Swartkrans) compared to where they were likely allopatric (Kromdraai, Sterkfontein, and Makapansgat)

495 (Brown, 1958; William M. Schaffer, 1968). Differences in tooth size were hypothesized to have occurred
496 due to different dietary specializations in taxa. Recent dietary reconstructions have confirmed large
497 levels of overlap and specialization in sympatric Plio-Pleistocene hominins (e.g. (Grine et al., 2012;
498 Sponheimer et al., 2013)), suggesting that character displacement may have occurred where taxa were
499 sympatric. More recent work on character displacement by Schroer and Wood (2015) has supported
500 this idea by showing that character displacement likely occurred in hominin premolar tooth size (Schroer
501 and Wood, 2015).

502 As new sites are discovered and old sites are expanded, it has become increasingly apparent
503 that there were several species of hominins living sympatrically or allopatrically around the time of
504 emergence of early *Homo*. Table 5 shows a pairwise comparison between the Plio-Pleistocene African
505 hominins depicting which hominin taxa may have been sympatric or allopatric. Species can be classified
506 as likely sympatric (taxa likely have definite overlapping temporal and geographic ranges), probably
507 sympatric (taxa have potentially overlapping temporal and geographic ranges), geographically separated
508 (temporal, but not geographic, overlap), temporally separated (geographic, but not temporal, overlap)
509 or none-of-the-above (neither temporal nor geographical overlap). Dates were taken from Wood and
510 Boyle (2016) and are inclusive of dating error (Wood and K Boyle, 2016). Early *Homo* is inclusive of
511 *Homo erectus*, *H. ergaster*, *H. georgicus*, *H. habilis*, *H. rudolfensis*, and the Ledi Geraru mandible. *H.*
512 *naledi* was excluded from this grouping due to lack of confirmed dates and because the Rising Star cave
513 system is within the geographic range of early *Homo*.

514 In East Africa, there were at least three species of hominins that were likely or probably
515 sympatric with early *Homo*: *Paranthropus boisei*, *Paranthropus aethiopicus*, and *Australopithecus garhi*
516 (Wood and Lonergan, 2008; Villmoare et al., 2015). Numerous fossils from both genera have been found
517 in the same sites and date to similar periods, and the remains of these genera are more closely

518 associated with one another than to other primate taxa at these sites (e.g. Shungura Formation, Lake
519 Malawi, Olduvai, and Koobi Fora all have *P. boisei* and/or *P. aethiopicus* in the same layers as early
520 *Homo*) (Bobe and Behrensmeyer, 2004). Additionally, there is mounting evidence that multiple taxa of
521 early *Homo* occupied these sites, potentially at the same time (Spoor et al., 2007; Leakey et al., 2012).
522 Dietary overlap and resource competition – which occurs commonly in living primates such as the great
523 apes – must be considered as a potential selection pressure on these fossil taxa. Such selection
524 pressures may have also led to niche specialization in the east African hominins, led to the derived
525 morphologies observed in the masticatory features of *Paranthropus* (Wood and Strait, 2004;
526 Constantino and Wood, 2007; Wood and Constantino, 2007; Berthaume et al., 2010; Dzialo et al., 2013;
527 Schroer and Wood, 2013; Smith et al., 2015) and the dietary shifts observed in *P. boisei* (high C₄
528 consumption). Likewise, dietary overlap and resource competition may have caused a selective
529 pressure that influenced the development of the gnathic and dental diversity observed in early *Homo*
530 (Spoor et al., 2015).

531 In South Africa, there is growing evidence that several species of australopithecines were living
532 sympatrically with each other and early *Homo* (e.g. (Berger et al., 2010; Pickering et al., 2011)) with
533 varying levels of dietary partitioning. An immense number of Plio-Pleistocene hominin bearing sites can
534 be found in South Africa, some yielding hominin specimens of a single species (e.g. Malapa, *A. sediba*;
535 Gondolin, *P. robustus*), and some yielding several hominin species (e.g. Kromdraai, *P. robustus* and early
536 *Homo*; Swartkrans, *P. robustus* and early *Homo*; Sterkfontein, *P. robustus*, *A. africanus*, and early *Homo*),
537 making it likely and probable that early *Homo* was sympatric with *P. robustus* and *A. africanus*,
538 respectively (e.g. (Brain, 1981; Braga and Thackeray, 2003; Moggi-Cecchi et al., 2006)). Although *A.*
539 *sediba* and early *Homo* have not yet been found in the same member at the same site, it is possible that
540 the two were living sympatrically due to their overlapping temporal and close geographic ranges (Berger
541 et al., 2010; Pickering et al., 2011).

542 With diet, there is strong evidence that *A. africanus* and *P. robustus* had overlapping diets, likely
543 in preferred foods, with some dietary partitioning in fallback foods (see Grine et al., 2012 and sources
544 there within). Similar dietary overlap likely existed between these species and the early *Homo* living in
545 South Africa. Competition over resources between early *Homo* and *A. africanus*, *P. robustus*, and early
546 *Homo* could have provided a selective force that led to the niche specialization observed in the diets of
547 *A. sediba* (high C₃ consumption) (Cerling et al., 2011; Henry et al., 2012), *P. robustus* (derived
548 masticatory apparatus, consumption of hard, brittle food items) (Scott et al., 2005), and South African
549 Early *Homo* (derived masticatory apparatus, consumption of compliant foods) (Ungar et al., 2006a,
550 2006b).

551 Although time-averaging can affect how we interpret occupation of a site, character
552 displacement analysis using dental topographic variables may provide a framework for assessing the
553 likelihood of overlap among fossil hominins based on the patterns observed in living apes. That is to say,
554 the results of our study indicate that character displacement may be useful for quantifying the potential
555 of ecological overlap in fossil taxa. In our study, DNE scores outperformed relative molar size in
556 detecting divergence between living populations and more closely reflected the observed overlap
557 among populations of great apes. This suggests that, when available, DNE may be a useful metric for
558 quantifying character displacement in fossil hominins and determining their likelihood of overlap,
559 although we caution the use of this method when comparing allopatric populations that may have
560 different regional ecologies (i.e. comparing southern African to East African hominins). Character
561 displacement may also be generalizable to other skeletal proxies of diet (e.g. mandibular cross-sectional
562 geometry, skull shape), although this has not been rigorously tested in extant apes or fossil hominins.

563 **Conclusion**

564 Contrary to findings among other primate groups, dental topography does not reliably
565 predict broad dietary categories within apes. However, differences in dental topography can separate
566 higher and lower fiber diets within sympatric groups of apes. This divergence was significant in a
567 character displacement analysis, suggesting that some degree of ecological competition may influence
568 dental topography in extant apes. A combined character displacement and dental topographic analysis
569 may be informative for reconstructing the dietary niches of fossil apes, including fossil hominins.
570 Although this conclusion presupposes that fossil taxa are subject to similar selection pressures as
571 modern taxa, including the presence of ecological overlap, it may open new avenues for understanding
572 the community compositions of early hominins and the formation of specific ecological niches among
573 hominin taxa.

574 If natural selection via character displacement operated to produce contrasting tooth shapes in
575 multiple groups of extant apes, as is suggested by our analyses, these results are likely applicable to
576 extinct apes and the fossil hominins. If this proves to be true, it is possible that competition between
577 early Australopithecine lineages resulted in character displacement and divergent evolution leading to
578 the evolution of both robust Australopithecines and early *Homo*.

579

580

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997 *Figure 1: Distribution of extant great apes in Africa. Note there are no overlapping ranges between species and subspecies of*
998 *Gorilla, or species and subspecies of Pan. However, there are some overlapping ranges between Gorilla and Pan.*

999 *Figure 2: Diversity in ape mandibular M2's. Each tooth has a DNE value close to the mean of the taxon, indicating it is the most*
1000 *"average" shaped tooth. From top to bottom left for both views, moving clockwise: G. g. gorilla (CMNH B1845), G. b. graueri*
1001 *(MRAC RG881), G. b. beringei (NMNH 396935), P. p. pygmaeus (SAPM 1981-30), P. paniscus (MRAC RG29057), P. t.*
1002 *schweinfurthii (MRAC RG6043), and P. t. troglodytes (CMNH B1720). Figures were created using CloudCompare v2.6.1*
1003 *(<http://www.danielgm.net/cc/>).*

1004 *Figure 3: Effects of reducing the number of triangles that represent the surface of a G. b. graueri tooth (MRAC RG881).*

1005 *Figure 4: Four possible ape phylogenies encompassing the extremes in subspecies divergence. Tree1 and Tree4 assume G. b.*
1006 *beringei and G. b. graueri diverged 10,000 years after the split with G. g. gorilla, while Tree2 and Tree3 assume the split*
1007 *occurred 10,000 years ago. A similar pattern is seen in the Pan troglodytes clade.*

1008 *Figure 5: Schematic of character displacement. A behavioral or morphological character is measured in two sympatric (i.e.*
1009 *overlapping) taxa, and the difference between character expression in the two taxa is summarized as " D_S ." When the same*
1010 *character is measured in allopatric (i.e. isolated) populations of the same two taxa, the divergence is summarized as " D_A ." When*
1011 *D_S is greater than D_A , character displacement is indicated. A greater D_S than D_A is represented in this schematic by the thickness*
1012 *of the lines, rather than their length. Solid circles represent one taxon and patterned circles represent another taxon. Although*
1013 *described here for one character, character displacement analyses may include multiple characters.*

1014 *Figure 6: DNE results. Sympatric species are framed in dotted boxes, while allopatric species are framed in a solid box. Our*
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1014

Table 1: Dental topographic studies on extinct primate taxa

Genus	Taxon	Dental Topographic Measures	Source
<i>Archaeoindris</i>	<i>fontoyntii</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Paleopropithecus</i>	<i>Ingens</i> ,	DNE, OPCR	(Godfrey et al., 2012)
<i>Paleopropithecus</i>	<i>maximus</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Paleopropithecus</i>	<i>kelyus</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Babokita</i>	<i>radofilai</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Mesopropithecus</i>	<i>globiceps</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Mesopropithecus</i>	<i>pithecoides</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Mesopropithecus</i>	<i>dolichobrachion</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Archaeolemur</i>	<i>majori</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Archaeolemur</i>	<i>sp. cf. edwardsi</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Hadropithecus</i>	<i>stenognathus</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Pachylemur</i>	<i>insignis</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Pachylemur</i>	<i>jullyi</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Megaladapis</i>	<i>edwardsi</i>	DNE, OPCR	(Godfrey et al., 2012)
<i>Platychoerops</i>	<i>antiquus</i>	OPC, RFI	(Boyer et al., 2012)
<i>Platychoerops</i>	<i>daubrei</i>	OPC, RFI	(Boyer et al., 2010, 2012)
<i>Plesiadapis</i>	<i>tricuspidens</i>	OPC, RFI	(Boyer et al., 2010, 2012)
<i>Plesiadapis</i>	<i>cookei</i>	DNE, OPCR, OPC, RFI	(Boyer et al., 2010; Prufrock et al., 2016a; b)
<i>Chiromyoides</i>	<i>spp.</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Nannodectes</i>	<i>intermedius</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Nannodectes</i>	<i>gazini</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Nannodectes</i>	<i>simpsoni</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Plesiadapis</i>	<i>praecursor</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Plesiadapis</i>	<i>anceps</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Plesiadapis</i>	<i>rex</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Plesiadapis</i>	<i>churchilli</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Plesiadapis</i>	<i>fodinatus</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Plesiadapis</i>	<i>dubius</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Pronothodectes</i>	<i>matthewi</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Pronothodectes</i>	<i>jepi</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Pronothodectes</i>	<i>gaoi</i>	DNE, OPCR, RFI	(Prufrock et al., 2016a; b)
<i>Acidomomys</i>	<i>hebeticus</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Arcius</i>	<i>fuscus</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Arcius</i>	<i>lapparenti</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Arcius</i>	<i>rougieri</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Edworthia</i>	<i>lerbekmoi</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Elwynella</i>	<i>oreas</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Ignacius</i>	<i>clarkforkensis</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Ignacius</i>	<i>fremontensis</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Ignacius</i>	<i>frugivorus</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)

<i>Ignacius</i>	<i>graybullianus</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Paromomys</i>	<i>farrandi</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Paromomys</i>	<i>maturus</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>archus</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>citatus</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>fortior</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>jepseni</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>pagei</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>praecox</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>praecox-fortior</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>simonsi</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Phenacolemur</i>	<i>willwoodensis</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Premnoides</i>	<i>douglasi</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Purgatorius</i>	<i>coracis</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Purgatorius</i>	<i>janisae</i>	DNE, OPCR, RFI	(López-Torres et al., 2017)
<i>Homo</i>	<i>rudolfensis</i>	RFI*, slope	Ungar, 2004
<i>Homo</i>	<i>erectus</i>	RFI*, slope	Ungar, 2004
<i>Homo</i>	<i>habilis</i>	RFI*, slope	Ungar, 2004
<i>Australopithecus</i>	<i>afarensis</i>	RFI*, slope	Ungar, 2004
<i>Australopithecus</i>	<i>africanus</i>	Slope	Ungar, 2007
<i>Paranthopus</i>	<i>robustus</i>	Slope	Ungar, 2007

Table 1: Sample for this study. Museum abbreviations are as follows: CMNH=Cleveland Museum of Natural History, AMNH=American Museum of Natural History, MRAC= Musée royal de l'Afrique centrale (Royal Museum for Central Africa) in Tervuren, SAPM= Staatssammlung für Anthropologie und Paläoanatomie München (State Museum of Anthropology and Paleoanatomy in Munich), NMNH = National Museum of Natural History.

Taxon	Sample size	Museums
Frugivores		
<i>Pan troglodytes troglodytes</i>	9	CMNH
<i>Pan troglodytes schweinfurthii</i>	8	AMNH, MRAC
<i>Gorilla gorilla gorilla</i>	8	AMNH, CMNH
<i>Pongo pygmaeus pygmaeus</i>	10	SAPM
<i>Pan paniscus</i>	9	MRAC
Folivores		
<i>Gorilla beringei beringei</i>	9	NHNH
<i>Gorilla beringei graueri</i>	8	MRAC

Table 1: Mann-Whitney U-test comparing DNE values between species (not phylogenetically corrected). Test statistics are presented followed by the P-value in brackets. Student t-tests had the same pattern of results.

Mann-Whitney U-test (W [P-value])	<i>G. b. beringi</i>	<i>P. paniscus</i>	<i>G. b. graueri</i>	<i>P. t. schweinfurthii</i>	<i>G. g. gorilla</i>	<i>P. t. troglodytes</i>
<i>P. p. pygmaeus</i>	54 [0.4967]	70 [0.0435]	26 [0.237]	57 [0.1457]	56 [0.1728]	88 [<0.0001]*
<i>G. b. beringi</i>		63 [0.0503]	9 [0.0079]*	50 [0.1996]	44 [0.4807]	81 [<0.0001]*
<i>P. paniscus</i>			3 [0.0006]*	30 [0.6058]	28 [0.4807]	78 [0.0003]*
<i>G. b. graueri</i>				59 [0.003]*	57 [0.007]*	72 [<0.0001]*
<i>P. t. schweinfurthii</i>					22 [0.3282]	66 [0.0025]*
<i>G. g. gorilla</i>						70 [0.0003]*

*significant using a Bonferroni adjusted P-value of 0.0083

Table 4: Results of character displacement analysis. Two pairs of sympatric Gorilla and Pan populations were compared to one pair of allopatric Gorilla and Pan (i.e. *G. b. beringei* and *P. paniscus*) in three different versions of the analysis: macromorphological variables alone, DNE scores alone, and a combination of both.

A. Macromorphological variables

Comparison	D _S	D _A	D _S -D _A	P
<i>G. g. gorilla</i> and <i>P. t. troglodytes</i>	0.031	0.015	0.016	0.229
<i>G. b. graueri</i> and <i>P. t. schweinfurthii</i>	0.042	0.011	0.031	0.046
All sympatric <i>Gorilla</i> and sympatric <i>Pan</i>	0.017	0.024	-0.007	0.672

B. DNE scores

Comparison	D _S	D _A	D _S -D _A	P
<i>G. g. gorilla</i> and <i>P. t. troglodytes</i>	115.959	59.788	56.171	0.051
<i>G. b. graueri</i> and <i>P. t. schweinfurthii</i>	142.993	21.822	121.170	0.006
All sympatric <i>Gorilla</i> and sympatric <i>Pan</i>	115.791	35.053	80.739	0.033

C. Combined analysis (macromorphological variables & DNE scores)

Comparison	D _S	D _A	D _S -D _A	P
<i>G. g. gorilla</i> and <i>P. t. troglodytes</i>	109.425	18.331	91.093	0.014
<i>G. b. graueri</i> and <i>P. t. schweinfurthii</i>	141.299	39.216	102.083	0.015
All sympatric <i>Gorilla</i> and sympatric <i>Pan</i>	131.190	21.679	109.511	0.026

Table5

Table 5: Pairwise comparison of hominin taxa, depicting which were likely sympatric (Sym, likely), probably sympatric (Sym, prob), geographically separated (Geog sep), temporally separated (Temp sep), or geographically and temporally separated (none-of-the-above).

	A. afarensis	A. africanus	A. anamensis	A. bahrelghazali	A. deyiremeda	A. garhi	A. sediba	Homo sp. early	K. platyops	P. aethiopicus	P. boisei	P. robustus
<i>Australopithecus afarensis</i>	-----	Geog sep (prob)	Temp sep	Geog sep	Sym, likely	Temp sep	none- of-the- above	Temp sep	Sym, likely	Temp sep	Temp sep	none-of- the- above
<i>Australopithecus africanus</i>	Geog sep (prob)	-----	Geog sep (prob)	Geog sep (prob)	Geog sep (prob)	Geog sep	Sym, prob	Sym, prob	Geog sep (prob)	Geog sep	Geog sep	Sym, prob
<i>Australopithecus anamensis</i>	Temp sep	Geog sep (prob)	-----	Geog sep (prob)	Temp sep	none- of- the- above	none- of-the- above	Temp sep	Temp sep (prob)	Temp sep (prob)	Temp sep	none-of- the- above
<i>Australopithecus bahrelghazali</i>	Geog sep	Geog sep (prob)	Geog sep (prob)	-----	Geog sep (prob)	none- of- the- above	none- of-the- above	none- of-the- above	Geog sep (prob)	none-of- the-above	none- of- the- above	none-of- the- above
<i>Australopithecus deyiremeda</i>	Sym, likely	Geog sep (prob)	Temp sep	Geog sep (prob)	-----	Temp sep	none- of-the- above	Temp sep	Sym, prob	Temp sep (prob)	Temp sep (prob)	none-of- the- above
<i>Australopithecus garhi</i>	Temp sep	Geog sep	none-of- the-above	none-of-the- above	Temp sep	-----	none- of-the- above	Sym, likely	Temp sep (prob)	Sym, prob	Sym, prob	none-of- the- above
<i>Australopithecus sediba</i>	none-of- the- above	Sym, prob	none-of- the-above	none-of-the- above	none-of- the-above	none- of- the- above	-----	Sym, likely	none-of- the- above	none-of- the-above	Geog sep	Sym, likely
<i>Homo sp. early</i>	Temp sep	Sym, prob	Temp sep	none-of-the- above	Temp sep	Sym, likely	Sym, likely	-----	Temp sep	Sym, likely	Sym, likely	Sym, likely
<i>Kenyanthropus platyops</i>	Sym, likely	Geog sep (prob)	Temp sep (prob)	Geog sep (prob)	Sym, prob	Temp sep (prob)	none- of-the- above	Temp sep	-----	Temp sep	Temp sep	none-of- the- above
<i>Paranthropus</i>	Temp	Geog sep	Temp sep	none-of-the-	Temp sep	Sym,	none-	Sym,	Temp	-----	Sym,	Geog

<i>aethiopicus</i>	sep		(prob)	above	(prob)	prob	of-the- above	likely	sep		likely	sep (prob)
<i>Paranthropus boisei</i>	Temp sep	Geog sep	Temp sep	none-of-the- above	Temp sep (prob)	Sym, prob	Geog sep	Sym, likely	Temp sep	Sym, likely	-----	Geog sep
<i>Paranthropus robustus</i>	none-of- the- above	Sym, prob	none-of- the-above	none-of-the- above	none-of- the-above	none- of- the- above	Sym, likely	Sym, likely	none-of- the- above	Geog sep (prob)	Geog sep	-----

Figure
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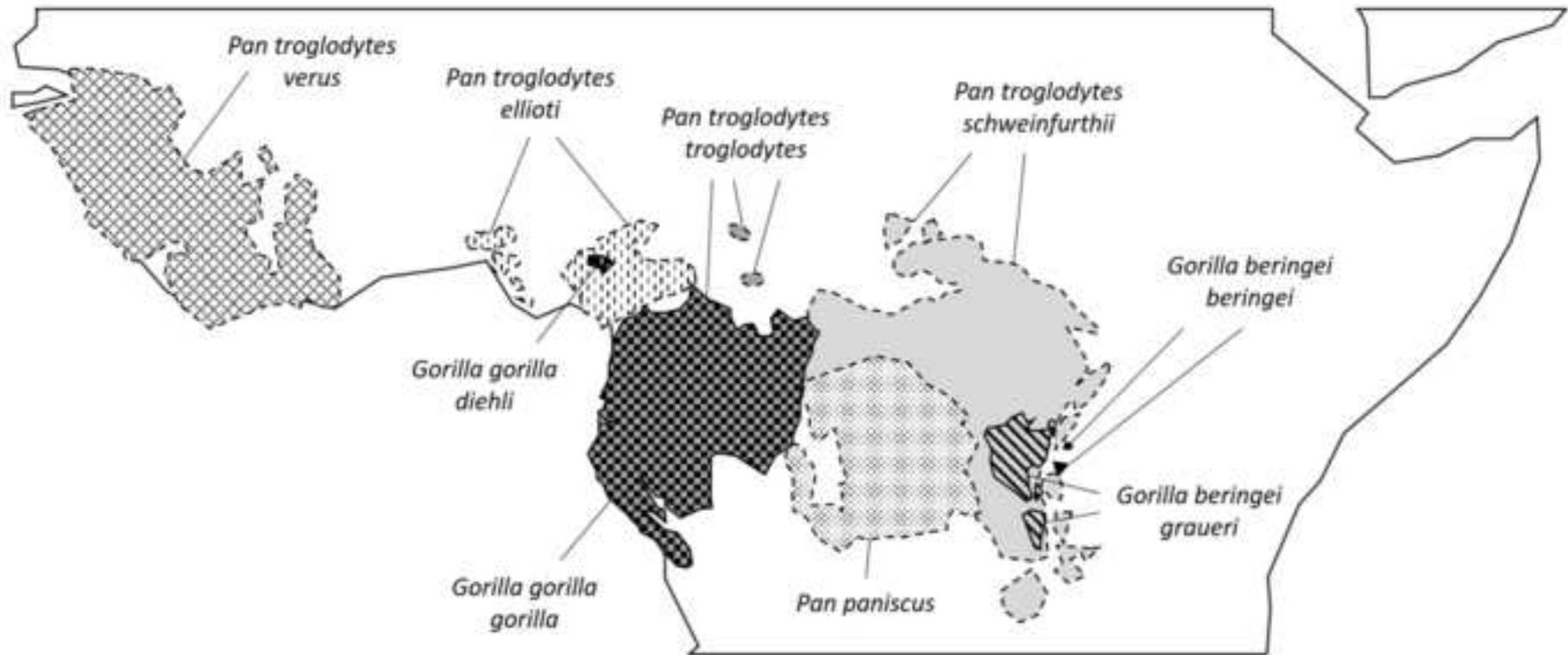
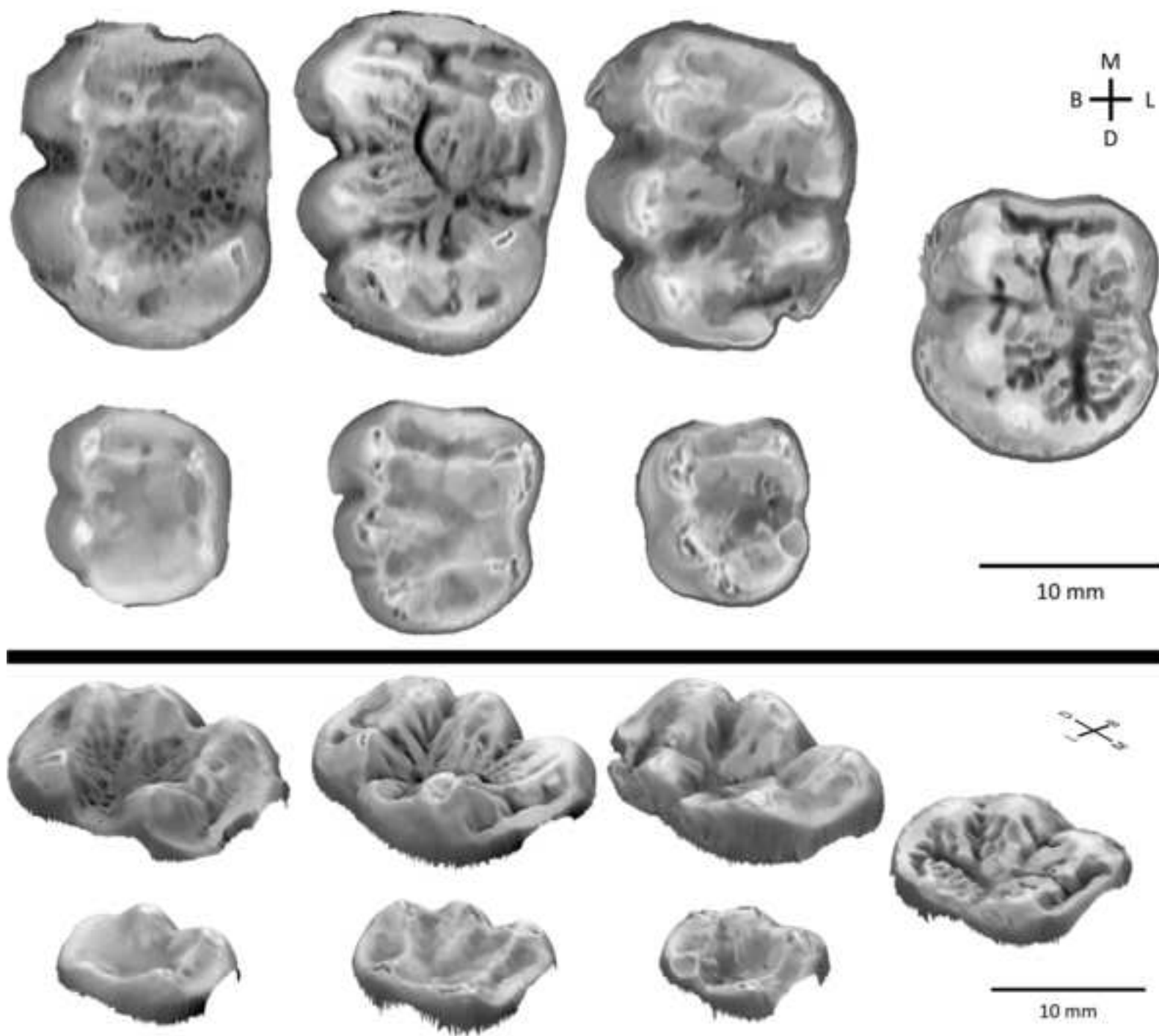
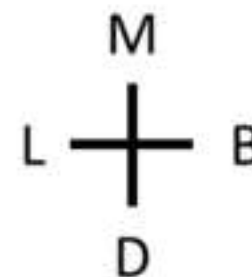
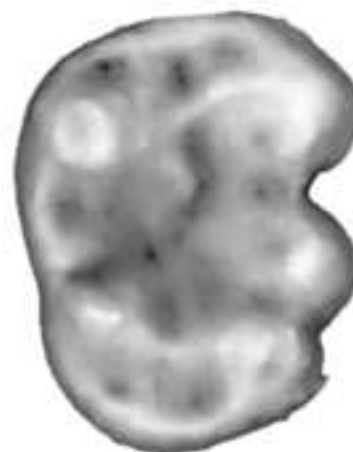


Figure2
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181,661
faces

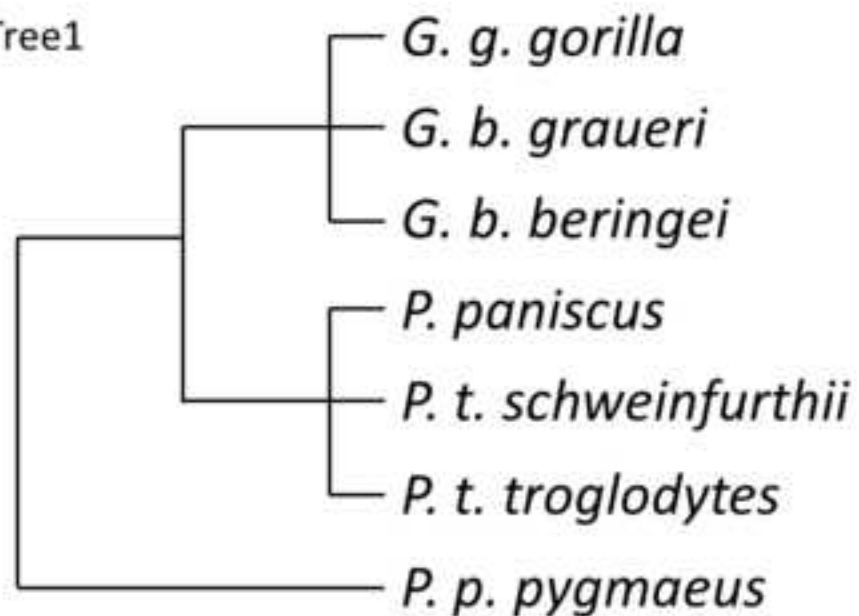
20,000
faces

9,997
faces

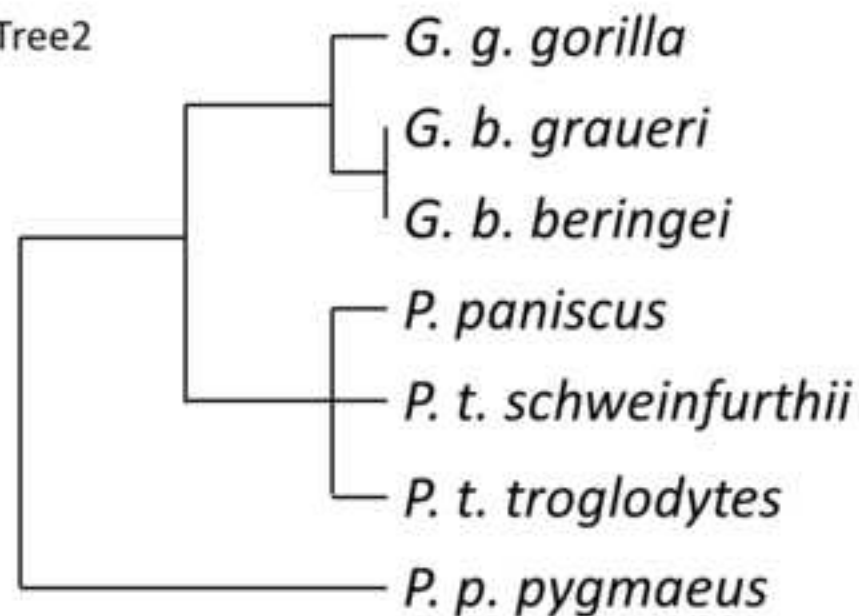
Figure4

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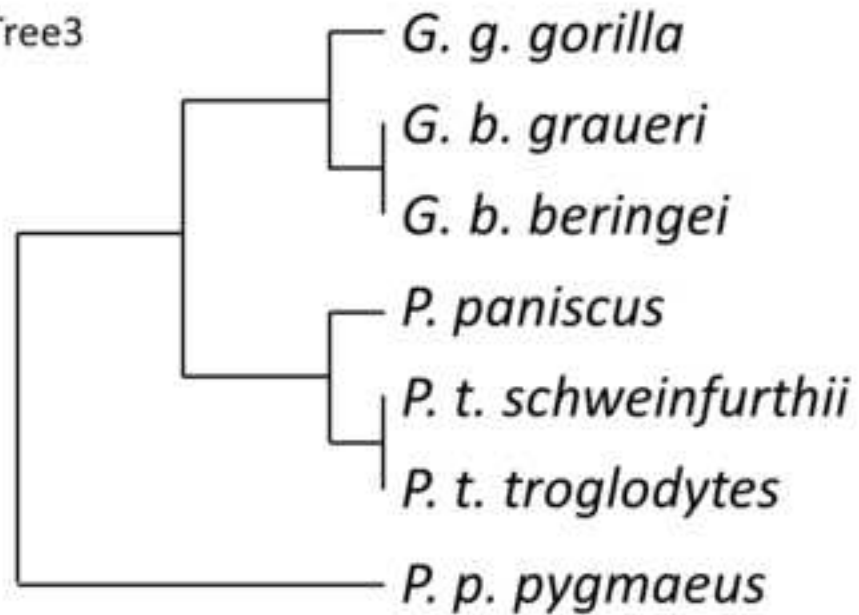
Tree1



Tree2



Tree3



Tree4

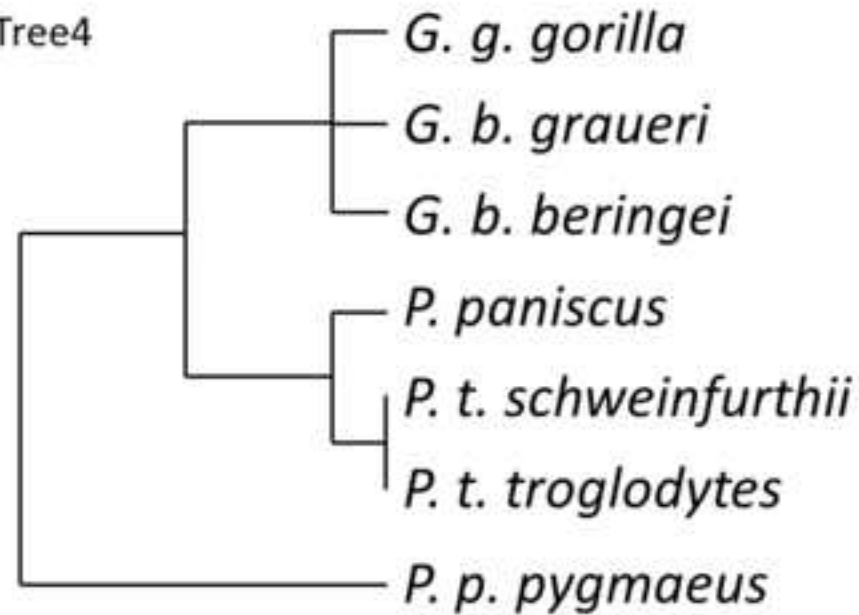


Figure5
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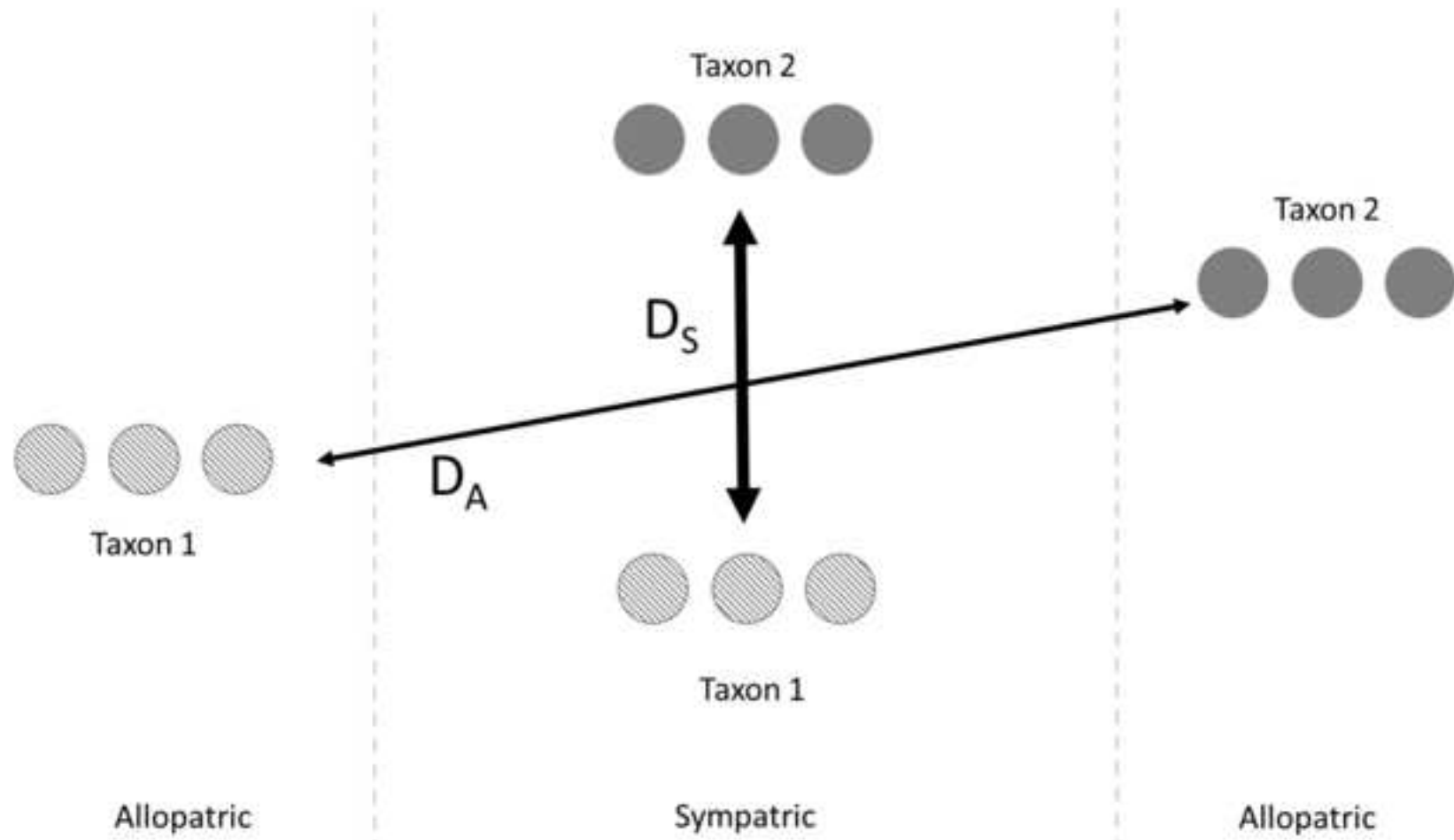
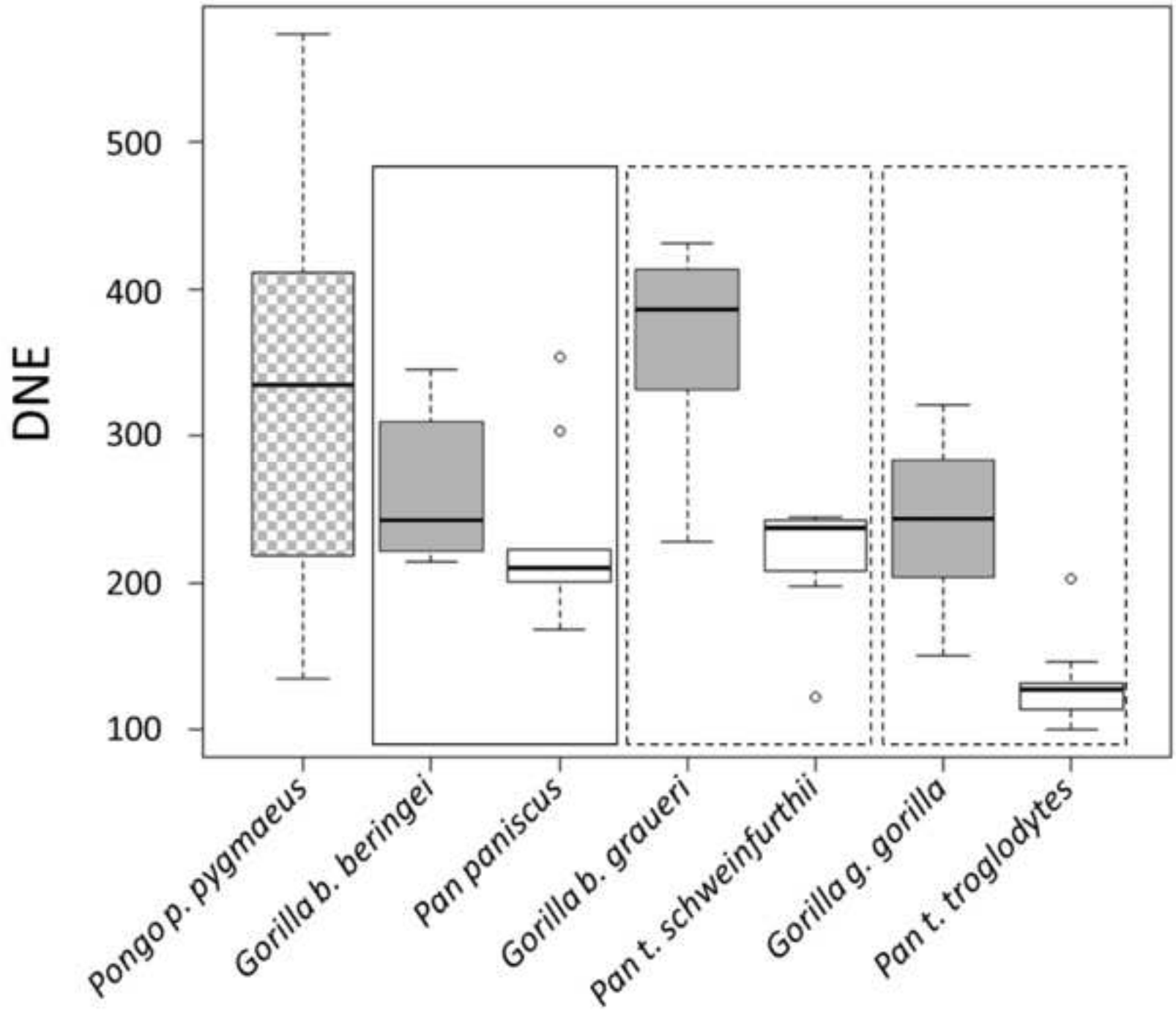


Figure6
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