

21

Abstract

22 Dental caries has been reported in a variety of primates, although is still considered rare in
23 wild populations. In this study, 11 catarrhine primates were studied for the presence of
24 caries. A differential diagnosis of lesions found in interproximal regions of anterior teeth was
25 undertaken, since they had been previously described as both carious and non-carious in
26 origin. Each permanent tooth was examined macroscopically, with severity and position of
27 lesions recorded. Two specimens were micro-CT scanned to assess demineralization. The
28 differential diagnosis confirmed the cariogenic nature of interproximal cavities on anterior
29 teeth (ICAT's). Overall results show 3.3% of teeth are carious, with prevalence varying
30 among species from 0% to over 7% of teeth affected. ICAT's occurred in *Pan troglodytes*
31 (9.8%), *Gorilla gorilla gorilla* (2.6%), *Cercopithecus denti* (22.4%), *Presbytis femoralis* (19.5%)
32 and *Cercopithecus mitis* (18.3%). They make up 87.9% of carious lesions on anterior teeth.
33 These results likely reflect dietary and food processing differences among species, but also
34 between the sexes (e.g., 9.3% of teeth of female chimpanzees were carious vs. 1.8% in
35 males). Processing cariogenic fruits and seeds with the anterior dentition (e.g., wadging)
36 likely contributes to ICAT formation. Further research is needed on living populations to
37 ascertain behavioral/dietary influences on caries occurrence in primates. Given the
38 constancy of ICAT's in frugivorous primates, their presence in archaeological and
39 paleontological specimens may shed light on diet and food processing behaviors in fossil
40 primates.

41 **Key words:** tooth cavities; food processing; dental caries; frugivory

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45 **Introduction**

46 Caries formation is influenced by dietary, behavioral, environmental, and genetic factors
47 (Kotecha et al., 2012; Slade et al., 2013). However, such lesions ultimately form from acids
48 produced by cariogenic bacteria metabolizing sugars and starches, leading to
49 demineralization of dental hard tissues (Byun et al., 2004; Larsen et al., 1991). Several
50 microorganisms have been implicated in this process, including *Streptococcus sobrinus* and
51 *S. mutans* (Nishikawara et al., 2007). The composition of the oral biofilm is a key component
52 in caries formation (Cornejo et al., 2013); however, the same bacteria are often a normal
53 part of the oral microbiome (Aas et al., 2008; Simón-Soro and Mira, 2015). Therefore, most
54 primates likely have the potential for caries formation if enough cariogenic foods are
55 consumed (Sheiham and James, 2015).

56 Caries research has historically focused on humans, with high prevalence of lesions
57 often associated with an agriculturalist lifestyle, or hunter-gatherer populations that
58 consume specific cariogenic foods (Caglar et al., 2007; Lanfranco & Eggers, 2012; Esclassan
59 et al., 2009; Novak, 2015; Slaus et al., 2011; Srejic, 2001; Varrel, 1991; Watt et al., 1997;
60 Walker and Hewlett, 1990; Sealy et al., 1992; Humphrey et al., 2014; Nelson et al., 1999). In
61 non-agricultural hominins, typically less than 5% of teeth are carious (Towle et al., 2021;
62 Turner, 1979; Lacy, 2014; Kelley et al., 1991; Larsen et al., 1991). In these groups, foods
63 containing high levels of carbohydrates are implicated in caries formation, whereas tough
64 and fibrous foods are often linked with low caries rates because of high wear rates and
65 increased saliva production (Clarkson et al., 1987; Moynihan, 2000; Novak, 2015; Prowse et
66 al., 2008; Rohnbogner & Lewis, 2016). Diets rich in fruits, seeds, and nuts are often

67 associated with high rates, with varying susceptibility depending on the type of foods and
68 how they are processed orally (Humphrey et al., 2014; Novak, 2015). A variety of other
69 factors can affect the likelihood of caries, including the extent and type of crown wear and
70 other pathologies/defects, such as enamel hypoplasia and periodontal disease (Hillson,
71 2008; Calcagno and Gibson, 1991; Towle and Irish, 2019; Towle and Irish, 2020).

72 Non-human primates also develop caries, particularly in captivity, and lesions have
73 been described in extant and extinct wild populations (e.g., Cohen and Goldman, 1960;
74 Colyer, 1936; Fuss et al., 2018; Lovell, 1990; Miles & Grigson, 2003; Schultz, 1935; 1956;
75 Smith et al., 1977; Stoner, 1995). In humans, posterior teeth are most commonly affected.
76 In non-human primates, anterior teeth evidence higher rates (Colyer, 1931), though in
77 captivity the pattern changes to posterior teeth (Anderson & Arnim, 1937; Bowen, 1968;
78 Cohen & Bowen, 1966; Colyer, 1936). Typically, lesions on anterior teeth form in
79 interproximal regions of incisors (Schultz, 1935; Smith et al., 1977; Stoner, 1995; Lovell,
80 1990). These Interproximal cavities on anterior teeth (ICAT) have not always been regarded
81 as carious, or otherwise have been overlooked (e.g., Kilgore, 1989).

82 Therefore, although ICAT's have been previously reported, a study on their
83 occurrence in a wide range of primate species is required. In this exploratory study, we use
84 micro-CT scans, and consider other potential forms of tissue removal that may lead to ICAT
85 formation. The influence of sex, age, and certain pathologies (e.g., abscesses and
86 periodontal disease) on the formation of carious lesions was also considered. A total of 11
87 catarrhine species were selected, with an emphasis on frugivores, given the cariogenic
88 potential of many fruits. We hypothesize that species known to regularly process sugary

89 fruits with their anterior dentition, including behaviors such as ‘wadging’, will display ICATs,
90 while those with a more varied diet will have a lower incidence.

91 **Methods**

92 All samples studied here are curated at the Primate Research Institute, Kyoto University,
93 Japan, and the Powell-Cotton Museum, UK. The 11 catarrhine species include: chimpanzee
94 (*Pan troglodytes*), Western lowland gorilla (*Gorilla gorilla gorilla*), Kloss's gibbon (*Hylobates*
95 *klossii*), hamadryas baboon (*Papio hamadryas*), pig-tailed langur (*Simias concolor*), Japanese
96 macaque (*Macaca fuscata*), Dent's mona monkey (*Cercopithecus denti*), blue monkey
97 (*Cercopithecus mitis*), mandrill (*Mandrillus* sp.), raffles' banded langur (*Presbytis femoralis*),
98 and Mentawai langur (*Presbytis potenziani*). All specimens were wild, and lived and died in
99 their natural habitat (Buck et al., 2018; Guatelli-Steinberg and Skinner, 2000; Kamaluddin et
100 al., 2019; Lukacs, 2001). The specimen numbers are presented in the supplementary
101 material.

102 All permanent teeth retained within the jaws of each specimen were examined
103 macroscopically. Those with substantial postmortem damage were excluded from analysis.
104 Two teeth were subsequently removed for micro-CT scanning to ascertain enamel/dentine
105 demineralization, and to visualize lesion progression (Boca et al., 2017; Rossi et al., 2004;
106 Swain & Xue, 2009). Scans were performed at the Primate Research Institute, Kyoto
107 University, using a SkyScan1275 Micro-CT scanner. The two teeth belonged to different
108 Dent's mona monkeys, one with a cavity on the mesial surface (upper right central incisor;
109 PRI 11580) and the other displaying only coloration changes in the same location (PRI
110 11578; lower left central incisor).

111 X-rays were generated at 100 kV, 100 μ A and 10W, with a 1mm copper filter placed
112 in the beam path. Resolution was set at 15 μ m pixel size, and rotation was set to 0.2-degree
113 for both teeth. Images were reconstructed using the Skyscan NRecon software (NRecon,
114 version 1.4.4, Skyscan) with standardized settings (smoothing: 3; ring artifact correction: 10;
115 beam hardening: 30%). Resin-hydroxyapatite phantoms were used to calibrate greyscales
116 and mineral densities in each specimen (Schwass et al. 2009). The calibration followed
117 Schwass et al. (2009) and Loch et al. (2013). Data collection from the scans was undertaken
118 using ImageJ. After calibration with phantoms, mineral concentration and total effective
119 density was calculated for four locations in each tooth (buccal, lingual, distal and mesial).
120 For the site with the potential carious lesion (mesial), three readings (oval ROI: 0.15mm
121 diameter) were taken in 10 slices (total 30 measurements), with the slice interval based on
122 the extent of the lesion. The individual ROI's were chosen at random within a distance of
123 0.5mm of the interproximal surface of the dentine (i.e., directly adjacent to the cavity in PRI
124 11580 and beneath the area of coloration change in PRI 11578). The same data were
125 collected for the other three locations (buccal, lingual and distal), on the same slices, with
126 random ROI's selected within 0.5mm of the dentine edge.

127 Caries prevalence by species was calculated as the percentage of carious teeth
128 among all permanent teeth analyzed, including antimeres. Color changes on the dental
129 tissues were not considered diagnostic, but were recorded when in association with
130 antemortem cavitation. Cavity severity and position on the crown were also recorded.
131 Severity was scored on a scale of 1 to 4 (Connell and Rauxloh, 2003): (1) enamel destruction;
132 (2) compromised dentine but pulp chamber not exposed; (3) destruction of dentine with
133 pulp exposure; (4) gross destruction with crown mostly destroyed. Location was recorded as
134 buccal, occlusal, distal, lingual and mesial. If it was not possible to determine location due to

135 severity, the lesion was recorded as 'gross'. Due to difficulty in ascertaining if certain lesions
136 would be best described as affecting the crown or root, teeth are not divided into these
137 categories; however, potential differences are discussed.

138 Caries can directly contribute to antemortem tooth loss, which has led to correction
139 methods (e.g., Duyar and Erdal, 2003; Kelley et al., 1991; Lukacs, 1995). The most likely
140 causes of antemortem tooth loss in extant primates are severe attrition, fractures, and
141 periodontal disease. Therefore, following other studies (e.g., Larsen et al., 1991; Meinl et al.,
142 2010), no correction methods were implemented. Data on abscesses and periodontal
143 disease were collected following Dias and Tayles (1997) and Ogden (2007), to assess if these
144 pathologies were associated with caries. Each individual was recorded as having caries,
145 periodontal disease, and abscesses (see Supplementary file). For abscesses and caries, the
146 individual needed to show at least one lesion in the dentition to be recorded as affected. For
147 periodontal disease, the individual needed to exhibit general resorption (rather than just
148 pockets) in the mandible and/or maxilla.

149 Species were also divided by sex to explore differences in caries occurrence. Wear
150 was scored following Scott (1979) for molars, and Smith (1984) for all other teeth. For sex
151 difference analyses, a Chi-square test with alpha level of 0.05 was used.

152 **Results**

153 Caries frequency was low (<1.5% of teeth) in over half the species. Posterior tooth
154 caries was particularly rare, though some species showed a moderate prevalence (Table 1).
155 Nearly 88% of all lesions on anterior teeth were interproximal, with mesial surfaces mostly
156 affected (Table 2). These ICATs were only present in chimpanzees, Western lowland gorillas,
157 Dent's mona monkeys, blue monkeys, and raffles' banded langurs. Most anterior lesions

158 were small (severity 1), although the chimpanzee and gorilla samples showed higher
159 frequencies of larger lesions (Table 3).

160 Micro-CT scans of two above mentioned teeth revealed that dentine was
161 substantially demineralized beneath both the cavitation and color change areas (Figure 1).
162 In both cases, a much lower mineral concentration and total effective density was evident
163 compared to other areas of the tooth (Table 4). The range and standard deviation of the
164 dentine mineral concentration within the carious locations was also much greater than in
165 sound dentine, adding further support for demineralization caused by caries. Below the
166 cavity in specimen PRI 11580, demineralization reached deep into the dentine, reaching
167 approximately 0.5mm before tissue returned to normal density (i.e., over 1.6g/cm³).

168

169 **[Table 1 here]**

170 **[Figure 1 here]**

171 **[Table 2 here]**

172 **[Table 3 here]**

173 **[Table 4 here]**

174 The five species displayed ICATs that were similar in shape and crown position, with
175 relatively circular lesions near the cementum-enamel junction (CEJ) on the interproximal
176 surfaces of anterior teeth (Figures 2a). In more severe cases, much of the crown was
177 destroyed (Figure 2b). In individuals with mild to moderate severity, lesions were limited to
178 the CEJ region, and often only affected the crown; however, in some cases, lesions initiated
179 on the root and followed the CEJ boundary, giving them a more oval appearance. In many

180 cases it was not possible to ascertain if the lesion initially involved the crown or root, as the
181 cavity covered both regions. Many individuals showed a dark coloration in these
182 interproximal regions, but no cavitation (Figure 3). Along with the micro-CT scan data, this
183 feature suggests these areas were early carious lesions.

184 **[Figure 2 here]**

185 Periodontal disease and extensive occlusal/interproximal wear were sometimes
186 associated with caries formation (Figs. 1 and 2). However, species with high caries levels do
187 not seem to have an overall increase in periodontal disease, with both carious and non-
188 carious individuals similarly affected. Small sample sizes for most species hampered
189 statistical comparisons (Supplementary file).

190 **[Figure 3 here]**

191 Only chimpanzees displayed a significant difference in prevalence of caries between
192 males and females (Supplementary Table 2). This analysis was hindered by small sample
193 sizes for Cercopithecidae. However, when pooled together, there was little difference in
194 caries frequency by sex (Cercopithecidae species combined; males: 25.49%; females:
195 17.57%; $X^2 = 1.1504$, 1 df, $p = 0.28$). While a slightly higher percent of male gorillas have
196 caries, this difference is not statistically significant (males: 11.43%; females: 6.52%; $X^2 =$
197 0.6062 , 1 df, $p = 0.44$). In contrast, female chimpanzees had significantly more caries than
198 males (males: 17.07%; females: 40%; $X^2 = 6.1639$, 1 df, $p = 0.01$).

199 When sex differences in caries occurrence were compared in terms of number of
200 teeth affected, female chimpanzees also had more caries ($X^2 = 20.890$, 1 df, $p = 0.00$), with
201 five times the number of teeth affected. This difference does not appear to relate to age,

202 based on crown wear (Table 5). Although most female chimpanzees exhibited more crown
203 wear, this difference in caries frequency remained stable once teeth were split into wear
204 categories. Females with low and medium levels of wear (combined wear score under 64 for
205 all four first molars; following Scott, 1979) displayed more carious teeth, with five times the
206 rate of males in the same wear category.

207 **[Table 5 here]**

208 **Discussion**

209 The results of this study suggest caries frequency was relatively low in the primates studied
210 (0-7.4% of teeth; Table 1). Anterior teeth had a higher frequency, and lesions were similar
211 among species in terms of position and physical characteristics. In particular, ICATs appear
212 to be relatively common in frugivorous and seed eating Cercopithecidae and Hominoidea,
213 likely related to the way dietary items are orally processed.

214 Although Kilgore (1989) suggested ICAT's may relate to severe enamel attrition from
215 stripping foods, demineralization visible deep into the dentine on the micro-CT scans is
216 strongly suggestive of caries. Attrition-related behavior could contribute to lesion formation,
217 by exposing the underlying dentine in interproximal areas. However, the present micro-CT
218 scan results, radiographs in Kilgore (1989), and thin sections in Miles and Grigson (2003),
219 seem to confirm that caries is the predominate factor for tissue loss in ICATs. Furthermore,
220 coloration changes in these regions are suggestive of early stage demineralization
221 associated with caries; thus, the true rate and effects of caries are likely much higher than
222 the present findings suggest. Other processes, such as attrition or non-bacterial erosion, are
223 unlikely to yield localized deep cavities and coloration change visible in ICATs.

224 Other researchers have reported ICATs as carious lesions (e.g., Colyer, 1936; Schultz,
225 1956). These studies also observed high caries rates in chimpanzees, with incisors commonly
226 affected. Colyer (1931) reported that in wild monkeys, anterior teeth were more commonly
227 affected than posterior teeth (66.2% vs. 33.80%), with interproximal surfaces presenting
228 most carious lesions (94.2%). When compared to previous photographs in the literature,
229 caries in anterior teeth appear similar to those described here (e.g., Figure 15 in Schultz,
230 1935; Figure 5 in Smith et al., 1977; Figure 4 in Stoner, 1995; Figure 5 in Lovell, 1990).
231 Therefore, in addition to the species studied here, other frugivorous primates (including
232 platyrrhine and catarrhine species) seem to display ICAT lesions (see Colyer, 1936; Lovell,
233 1990; Schultz, 1935; 1956; Smith et al., 1977; Stoner, 1995).

234 In contrast, ICATs seem rare in captive primates, with posterior teeth commonly
235 displaying carious lesions (Anderson & Arnim, 1937; Bowen, 1968; Cohen & Bowen, 1966;
236 Colyer, 1936). Such primates are often fed a cariogenic diet, but have higher caries rates in
237 the posterior teeth (Anderson and Arnim, 1937; Bowen, 1968; Cohen and Bowen, 1966). For
238 example, Colyer (1936) found that almost 90% of carious teeth in captive monkeys were
239 molars. These observations suggest the way in which foods are processed can contribute to
240 the generation of incisor lesions. In the present study, most ICATs were associated with
241 significant attrition/abrasion on the occlusal and interproximal surfaces. Tooth wear, along
242 with periodontal disease and continuous eruption of teeth, may create excessive space for
243 food and bacteria to accumulate below the crown between incisors. Additionally, heavy
244 wear can be associated with root surface exposure, through continuous tooth eruption or
245 periodontal disease, facilitating root caries formation (Hillson, 2008). Many sugary fruits are
246 also acidic, which might create a microenvironment that facilitates proliferation of
247 cariogenic bacteria.

248 Support for this multifactorial hypothesis in which multiple factors lead to ICAT
249 formation, is found in behavioral observations of wild chimpanzees. Chimpanzees tend to
250 use their lips in tandem with large broad spatulate incisors to process fruits and plants
251 (Hylander, 1975; Lambert, 1999; McGrew, 1999; Suzuki, 1969; Ungar, 1994; van Casteren et
252 al., 2018). Figs have a high concentration of sugars and other carbohydrates and require
253 substantial mechanical processing, which usually involves anterior teeth (Lambert, 1999;
254 Wrangham et al., 1993). Figs are consumed by most chimpanzees (e.g., Basabose, 2002;
255 Matthews et al., 2019; Nishida and Uehara, 1983; Potts et al., 2011; Tweheyo, and Lye,
256 2003; Watts et al., 2012), often involving holding the chewed fruits in the front part of the
257 mouth, in a behavior called 'wadging' (Lambert, 1999; Nishida et al., 1999). Chimpanzees
258 then suck the sugary liquids from the wedge, much of which will sieve through interproximal
259 surfaces of anterior teeth (Figure 4), likely creating a cariogenic microenvironment.
260 Chimpanzees often wedge figs with higher concentrations of sugars (i.e., *Ficus sur/capensis*,
261 *Ficus mucuso*) (Danish et al., 2006; Wrangham et al., 1993). Other cariogenic items are also
262 wadged, including honeycombs (Nishida et al., 1999).

263 **[Figure 4 here]**

264 Although gorillas had lower ICAT rates than chimpanzees, they still showed these
265 characteristic lesions. Gorillas also regularly eat fruits, many of which are high in soluble
266 sugars (Remis et al., 2001). The cercopithecidae species with ICATs (Dent's mona monkeys,
267 blue monkeys, and raffles' banded langurs) are all frugivores that process foods high in
268 fermentable carbohydrates with their anterior dentition. However, the specific types of
269 foods that contribute to lesions formation likely vary. Carious lesions in raffles' banded
270 langurs may relate to a diet of seeds high in carbohydrates (i.e., starch), processed using

271 incisors (Davies and Bennett, 1988). This process could have led to not only high caries rates
272 in the anterior dentition, but also to high rates of tooth chipping (Towle and Loch, 2021).
273 Dent's mona and blue monkeys also eat substantial quantities of different fruits (Olaeru,
274 2017; Takahashi et al., 2019). Further research is needed to ascertain which foods may
275 contribute to ICATs in these species. For example, blue monkeys show substantial variation
276 in feeding ecology across their range (Tesfaye et al., 2013), meaning that a study of caries in
277 populations with detailed dietary and behavioral record is important to elucidate the
278 processes leading to ICAT formation.

279 Sex differences in caries prevalence are also important, since differences have been
280 observed in humans and other great apes (Lanfranco and Eggers, 2012; Lukacs and
281 Largaespada, 2006; Lukacs, 2011; Stoner, 1995). Dietary and behavioral differences are
282 known between male and female chimpanzees (Gilby et al., 2017; Nakamura et al., 2015;
283 Wrangham and Smuts, 1980). Pregnancy and differences in oral pH, saliva, physiology, life
284 history, and microbiome between the sexes may also be predisposing factors (e.g., Fuss et
285 al., 2018; Lukacs and Largaespada, 2006; Stoner, 1995). The results of the present study
286 support other research suggesting sex differences in caries rates among the great apes,
287 although the present sample of gorillas did not show significant differences.

288 Recent literature has shown caries is not as rare as previously thought in fossil
289 hominin and extant great apes (e.g., Arnaud et al., 2016; Lacy, 2014; Lacy et al., 2012;
290 Lanfranco & Eggers, 2012; Liu et al., 2015; Margvelashvili et al., 2016; Miles & Grigson, 2003;
291 Stoner, 1995; Towle et al., 2019; Trinkaus et al., 2000). There is also growing evidence that
292 caries was common in other extinct primates (e.g., Fuss et al., 2018; Han and Zhao, 2002;
293 Selig and Silcox, 2020). This study adds further evidence that caries has likely been relatively

294 common in many primate lineages. Additionally, lesion position in the dentition may offer
295 insights into diet and behavior of extinct species, based on comparisons with extant
296 primates. In particular, because of ICATs' uniform appearance in multiple frugivore species,
297 these may be useful for behavioral interpretations. Given the difference in female and male
298 chimpanzees, caries prevalence may also shed light on sexually dimorphic feeding behaviors
299 and physiology in past primate populations.

300

301 **Acknowledgments**

302 We thank I. Livne from the Powell-Cotton Museum and the Study Material Committee from
303 the Primate Research Institute (PRI), Kyoto University, for access to their collections, and T.
304 Ito for assistance during data collection. Research was supported by a Sir Thomas Kay Sidey
305 Postdoctoral fellowship from the University of Otago to Ian Towle and a studentship from
306 Liverpool John Moores University, and was partly performed under the Cooperative
307 Research Program of the PRI (2019-C-20).

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309 **References**

- 310 Aas, J. A., Griffen, A. L., Dardis, S. R., Lee, A. M., Olsen, I., Dewhirst, F. E., ... & Paster, B. J. (2008).
311 Bacteria of dental caries in primary and permanent teeth in children and young adults. *Journal of*
312 *Clinical Microbiology*, 46(4), 1407-1417.
- 313 Anderson, B. G., & Arnim, S. S. (1937). The incidence of dental caries in seventy-six monkeys. *The*
314 *Yale Journal of Biology and Medicine*, 9(5), 443.

- 315 Arnaud, J., Benazzi, S., Romandini, M., Livraghi, A., Panetta, D., Salvadori, P. A., Volpe, L., & Peresani,
316 M., 2016. A Neanderthal deciduous human molar with incipient carious infection from the Middle
317 Palaeolithic De Nadale cave, Italy. *American Journal of Physical Anthropology*, 162(2), 370–376.
- 318 Basabose, A. K. 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi,
319 Democratic Republic of Congo. *American Journal of Primatology*, 58(1), 1-21.
- 320 Boca, C., Truyen, B., Henin, L., Schulte, A. G., Stachniss, V., De Clerck, N., ... & Bottenberg, P. (2017).
321 Comparison of micro-CT imaging and histology for approximal caries detection. *Scientific Reports*,
322 7(1), 1-9.
- 323 Bowen, W. H. (1968). Dental caries in monkeys. *Advances in Oral Biology*, 3, 185-216.
- 324 Buck, L. T., De Groote, I., Hamada, Y., & Stock, J. T. (2018). Humans preserve non-human primate
325 pattern of climatic adaptation. *Quaternary Science Reviews*, 192, 149-166.
- 326 Byun, R., Nadkarni, M. A., Chhour, K. L., Martin, F. E., Jacques, N. A., & Hunter, N., 2004.
- 327 Caglar, E., Kuscu, O. O., Sandalli, N., & Ari, I. (2007). Prevalence of dental caries and tooth wear in a
328 Byzantine population (13th cad) from northwest Turkey. *Archives of Oral biology*, 52(12), 1136-1145.
- 329 Calcagno, J. M., & Gibson, K. R., 1991. Selective compromise: evolutionary trends and mechanisms in
330 hominid tooth size. In: Kelley, M. A., & Larsen, C. S., (Eds), *Advances in Dental Anthropology*, 59-76.
331 New York: Wiley-Liss.
- 332 Clarkson, B. H., Krell, D., Wefel, J. S., Crall, J., & Feagin, F. F., 1987. In vitro caries-like lesion
333 production by *Streptococcus mutans* and *Actinomyces viscosus* using sucrose and starch. *Journal of*
334 *Dental Research*, 66(3), 795-798.
- 335 Cohen, B., & Bowen, W. H. (1966). Dental caries in experimental monkeys. A pilot study. *British*
336 *Dental Journal*, 121, 269-276.

- 337 Cohen, D. W., & Goldman, H. M. (1960). Oral disease in primates. *Annals of the New York Academy*
338 *of Sciences*, 85, 889-909.
- 339 Colyer, F. (1931). *Abnormal Conditions of the Teeth of Animals in their Relationship to Similar*
340 *Conditions in Man*. London: The Dental Board of the United Kingdom.
- 341 Colyer, F. (1936). *Variations and Diseases of the Teeth of Animals*. Variations and Diseases of the
342 *Teeth of Animals*. London: Bale & Danielsson.
- 343 Connell, B., & Rauxloh, P., 2003. A rapid method for recording human skeletal data. MoL unpub rep.
344 <http://www.museumoflondon.org.uk/English/Collections/OnlineResources/CHB/About>
345 [Us/WORDdtb.htm](http://www.museumoflondon.org.uk/English/Collections/OnlineResources/CHB/About).
- 346 Cornejo, O. E., Lefébure, T., Pavinski Bitar, P. D., Lang, P., Richards, V. P., Eilertson, K., ... & Burne, R.
347 A. (2013). Evolutionary and population genomics of the cavity causing bacteria *Streptococcus*
348 *mutans*. *Molecular Biology and Evolution*, 30(4), 881-893.
- 349 Danish, L., Chapman, C. A., Hall, M. B., Rode, K. D., & Worman, C. O. D. (2006). The role of sugar in
350 diet selection in redtail and red colobus monkeys. *Feeding ecology in apes and other primates*, 48,
351 473.
- 352 Davies, A. G., Bennett, E. L., & Waterman, P. G. (1988). Food selection by two South-east Asian
353 colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry.
354 *Biological Journal of the Linnean Society*, 34(1), 33-56.
- 355 Dias, G., & Tayles, N. (1997). 'Abscess cavity'—a misnomer. *International Journal of*
356 *Osteoarchaeology*, 7(5), 548-554.
- 357 Duyar, I., & Erdal, Y. S., 2003. A new approach for calibrating dental caries frequency of skeletal
358 remains. *Journal of Comparative Human Biology*, 54(1), 57-70.

- 359 Esclassan, R., Grimoud, A. M., Ruas, M. P., Donat, R., Sevin, A., Astie, F., ... & Crubezy, E. (2009).
360 Dental caries, tooth wear and diet in an adult medieval (12th–14th century) population from
361 Mediterranean France. *Archives of Oral Biology*, 54(3), 287-297.
- 362 Fuss, J., Uhlig, G., & Böhme, M., 2018. Earliest evidence of caries lesion in hominids reveal sugar-rich
363 diet for a Middle Miocene dryopithecine from Europe. *PLoS One*, 13(8), e0203307.
- 364 Gilby, I. C., Machanda, Z. P., O'Malley, R. C., Murray, C. M., Lonsdorf, E. V., Walker, K., ... & Pusey, A.
365 E. (2017). Predation by female chimpanzees: toward an understanding of sex differences in meat
366 acquisition in the last common ancestor of Pan and Homo. *Journal of Human Evolution*, 110, 82-94.
- 367 Guatelli-Steinberg, D., & Skinner, M. (2000). Prevalence and etiology of linear enamel hypoplasia in
368 monkeys and apes from Asia and Africa. *Folia Primatologica*, 71(3), 115-132.
- 369 Han, K., & Zhao, L. 2002. Dental caries of *Gigantopithecus blacki* from Hubei Province of China. *Acta*
370 *Anthropologica Sinica*, 21(3), 191-196.
- 371 Hillson S., 2008. The current state of dental decay In: Irish JD, Nelson GC, editors. Technique and
372 application in dental anthropology. Cambridge, UK: Cambridge University Press, 111–135.
- 373 Humphrey, L. T., De Groote, I., Morales, J., Barton, N., Collcutt, S., Ramsey, C. B., & Bouzouggar, A.
374 (2014). Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-
375 gatherers from Morocco. *Proceedings of the National Academy of Sciences*, 111(3), 954-959.
- 376 Hylander, W. L. 1975. Incisor size and diet in anthropoids with special reference to Cercopithecidae.
377 *Science*, 189(4208), 1095-1098.
- 378 Johnsen, D. C., Gerstenmaier, J. H., DiSantis, T. A., & Berkowitz, R. J. (1986). Susceptibility of nursing-
379 caries children to future approximal molar decay. *Pediatric Dentistry*, 8(3), 168-70.

- 380 Kamaluddin, S. N., Tanaka, M., Wakamori, H., Nishimura, T., & Ito, T. (2019). Phenotypic plasticity in
381 the mandibular morphology of Japanese macaques: captive–wild comparison. *Royal Society Open*
382 *Science*, 6(7), 181382.
- 383 Kelley, M. A., Levesque, D. R., & Weidl, E., 1991. Contrasting patterns of dental disease in five early
384 northern Chilean groups. In: Kelley, M. A., & Larsen, C. S. (Eds.), *Advances in dental anthropology*,
385 203-213. New York: Wiley-Liss.
- 386 Kilgore, L. 1989. Dental pathologies in ten free-ranging chimpanzees from Gombe National Park,
387 Tanzania. *American Journal of Physical Anthropology*, 80(2), 219-227.
- 388 Kotecha, P. V., Patel, S. V., Bhalani, K. D., Shah, D., Shah, V. S., & Mehta, K. G., 2012. Prevalence of
389 dental fluorosis & dental caries in association with high levels of drinking water fluoride content in a
390 district of Gujarat, India. *Indian Journal of Medical Research*, 135(6), 873-877.
- 391 Lacy, S. A., 2014. Oral health and its implications in late Pleistocene Western Eurasian humans. St.
392 Louis: Washington University.
- 393 Lacy, S. A., Wu, X. J., Jin, C. Z., Qin, D. G., Cai, Y. J., & Trinkaus, E., 2012. Dentoalveolar
394 paleopathology of the early modern humans from Zhirendong, south China. *International Journal of*
395 *Paleopathology*, 2(1), 10-18.
- 396 Lambert, J. E. (1999). Seed handling in chimpanzees (*Pan troglodytes*) and redbtail monkeys
397 (*Cercopithecus ascanius*): Implications for understanding hominoid and cercopithecine
398 fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology*, 109(3),
399 365-386.
- 400 Lanfranco, L.P., Eggers, S., 2012. Caries through time: an anthropological overview. In: Li, M. (Ed.),
401 *Contemporary Approach to Dental Caries*. INTECH Open Access Publisher.

- 402 Larsen, C. S. (1991). Dental caries evidence for dietary change: an archaeological context. *Advances*
403 *in Dental Anthropology*, 179-202.
- 404 Larsen, C. S., Shavit, R., & Griffin, M. C., 1991. Dental caries evidence for dietary change: an
405 archaeological context. In: Kelley, M. A., & Larsen, C. S. (Eds.), *Advances in dental anthropology*, 179-
406 202. New York: Wiley-Liss.
- 407 Liu, W., Martínón-Torres, M., Cai, Y. J., Xing, S., Tong, H. W., Pei, S. W., ... & Li, Y. Y., 2015. The
408 earliest unequivocally modern humans in southern China. *Nature*, 526(7575), 696.
- 409 Loch, C., Schwass, D.R., Kieser, J.A., Fordyce, R.E., 2013. Use of Microcomputed tomography for
410 dental studies in modern and fossil odontocetes: potential applications and limitations. NAMMCO
411 Scientific Publications, 10, doi: <http://dx.doi.org/10.7557/3.2616>.
- 412 Lovell, N. C., 1990. Skeletal and dental pathology of free-ranging mountain gorillas. *American Journal*
413 *of Physical Anthropology*, 81(3), 399-412.
- 414 Lukacs, J. R. (2001). Enamel hypoplasia in the deciduous teeth of early Miocene catarrhines:
415 evidence of perinatal physiological stress. *Journal of Human Evolution*, 40(4), 319-329.
- 416 Lukacs, J. R. (2011). Sex differences in dental caries experience: clinical evidence, complex etiology.
417 *Clinical Oral Investigations*, 15(5), 649-656.
- 418 Lukacs, J. R., & Largaespada, L. L. (2006). Explaining sex differences in dental caries prevalence:
419 Saliva, hormones, and “life-history” etiologies. *American Journal of Human Biology*, 18(4), 540-555.
- 420 Lukacs, J. R., 1995. The ‘caries correction factor’: a new method of calibrating dental caries rates to
421 compensate for antemortem loss of teeth. *International Journal of Osteoarchaeology*, 5(2), 151-156.

- 422 Margvelashvili, A., Zollikofer, C. P., Lordkipanidze, D., Tafforeau, P., & Ponce de León, M. S., 2016.
423 Comparative analysis of dentognathic pathologies in the Dmanisi mandibles. *American Journal of*
424 *Physical Anthropology*, 160(2), 229-253.
- 425 Matthews, J. K., Ridley, A., Niyigaba, P., Kaplin, B. A., & Grueter, C. C. (2019). Chimpanzee feeding
426 ecology and fallback food use in the montane forest of Nyungwe National Park, Rwanda. *American*
427 *Journal of Primatology*, 81(4), e22971.
- 428 Meinl, A., Rottensteiner, G. M., Huber, C. D., Tangl, S., Watzak, G., & Watzek, G., 2010. Caries
429 frequency and distribution in an early medieval Avar population from Austria. *Oral Diseases*, 16(1),
430 108-116.
- 431 Miles, A. E. W., & Grigson, C., 2003. Colyer's Variations and Diseases of the Teeth of Animals.
432 Cambridge: Cambridge University Press.
- 433 Moynihan, P., 2000. Foods and factors that protect against dental caries. *Nutrition Bulletin*, 25(4),
434 281-286.
- 435 Nakamura, M., Hosaka, K., Itoh, N., & Zamma, K. (Eds.). (2015). Mahale chimpanzees: 50 years of
436 research. Cambridge University Press.
- 437 Nelson, G. C., Lukacs, J. R., & Yule, P. 1999. Dates, caries, and early tooth loss during the Iron Age of
438 Oman. *American Journal of Physical Anthropology*, 108(3), 333-343.
- 439 Nishida, T., & Uehara, S. 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-
440 term record from the Mahale Mountains, Tanzania. *African Study Monographs*, 3:109-130.
- 441 Nishida, T., Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. 1999. Ethogram and ethnography
442 of Mahale chimpanzees. *Anthropological Science*, 107(2), 141-188.

- 443 Nishikawara, F., Nomura, Y., Imai, S., Senda, A., & Hanada, N., 2007. Evaluation of cariogenic
444 bacteria. *European Journal of Dentistry*, 1(1), 31-39.
- 445 Novak, M., 2015. Dental health and diet in early medieval Ireland. *Archives of Oral Biology*, 60(9),
446 1299-1309.
- 447 Ockerse, T., & De Jager, C. L. (1957). Dental caries produced in the vervet monkey (a preliminary
448 report). *Brit. dent. J.*, 102, 93-96.
- 449 Ogden, A. (2007). Advances in the palaeopathology of teeth and jaws. *Advances in human*
450 *palaeopathology*, 283-307.
- 451 Olaleru, F. (2017). Seasonality and nutrient composition of the plant diets of mona monkeys
452 (*Cercopithecus mona*) in University of Lagos, Nigeria. *The Zoologist*, 15(1), 13-21.
- 453 Potts, K. B., Watts, D. P., & Wrangham, R. W. 2011. Comparative feeding ecology of two
454 communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. *International Journal*
455 *of Primatology*, 32(3), 669-690.
- 456 Prowse, T. L., Saunders, S. R., Schwarcz, H. P., Garnsey, P., Macchiarelli, R., & Bondioli, L., 2008.
457 Isotopic and dental evidence for infant and young child feeding practices in an imperial Roman
458 skeletal sample. *American Journal of Physical Anthropology*, 137(3), 294-308.
- 459 Remis, M. J., Dierenfeld, E. S., Mowry, C. B., & Carroll, R. W. (2001). Nutritional aspects of western
460 lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at Bai Hokou, Central
461 African Republic. *International Journal of Primatology*, 22(5), 807-836.
- 462 Rohnbogner, A., & Lewis, M., 2016. Dental caries as a measure of diet, health, and difference in non-
463 adults from urban and rural Roman Britain. *Dental Anthropology*, 29(1), 16-31.

- 464 Rossi, M., Casali, F., Romani, D., Bondioli, L., Macchiarelli, R., & Rook, L., 2004. MicroCT Scan in
465 paleobiology: application to the study of dental tissues. *Nuclear Instruments and Methods in Physics*
466 *Research Section B: Beam Interactions with Materials and Atoms*, 213, 747-750.
- 467 Schultz, A. H. (1935). Eruption and decay of the permanent teeth in primates. *American Journal of*
468 *Physical Anthropology*, 19(4), 489-581.
- 469 Schultz, A. H. (1956). The occurrence and frequency of pathological and teratological conditions and
470 of twinning among non-human primates. *Primatologia*, 1, 965-1014.
- 471 Scott, E. C. 1979. Dental wear scoring technique. *American Journal of Physical Anthropology*, 51(2),
472 213-217.
- 473 Sealy, J. C., Patrick, M. K., Morris, A. G., & Alder, D. 1992. Diet and dental caries among later stone
474 age inhabitants of the Cape Province, South Africa. *American Journal of Physical Anthropology*,
475 88(2), 123-134.
- 476 Selig, K. R., & Silcox, M. T. 2020, March. Identification and Implications of Carious Lesions in a Large
477 Sample of Early Eocene Stem Primates from the Bighorn Basin of Wyoming. *American Journal of*
478 *Physical Anthropology*, Vol. 171, pp. 257-258.
- 479 Sheiham, A., & James, W. P. T. (2015). Diet and dental caries: the pivotal role of free sugars
480 reemphasized. *Journal of Dental Research*, 94(10), 1341-1347.
- 481 Simón-Soro, A., & Mira, A. (2015). Solving the etiology of dental caries. *Trends in Microbiology*, 23(2),
482 76-82.
- 483 Slade, G. D., Sanders, A. E., Do, L., Roberts-Thomson, K., & Spencer, A. J., 2013. Effects of fluoridated
484 drinking water on dental caries in Australian adults. *Journal of Dental Research*, 92(4), 376-382.

- 485 Šlaus, M., Bedic, Z., Rajic, P., Vodanovic, M. & Kunic, A., (2011). Dental Health at the transition from
486 the Late Antique to the Early Medieval Period on Croatia's Eastern Adriatic Coast. *International*
487 *Journal of Osteoarchaeology*, 21: 577–590.
- 488 Smith, B. H. 1984. Patterns of molar wear in hunter–gatherers and agriculturalists. *American Journal*
489 *of Physical Anthropology*, 63(1), 39-56.
- 490 Smith, J. D., Genoways, H. H., & Jones jr, K. (1977). Cranial and dental anomalies in three species of
491 platyrrhine monkeys from Nicaragua. *Folia Primatologica*, 28(1), 1-42.
- 492 Srejić, M. D. (2001). Dental paleopathology in a Serbian medieval population. *Anthropologischer*
493 *Anzeiger*, 113-122.
- 494 Stoner, K. E., 1995. Dental pathology in *Pongo satyrus borneensis*. *American Journal of Physical*
495 *Anthropology*, 98(3), 307-321.
- 496 Suzuki, A. 1969. An ecological study of chimpanzees in a savanna woodland. *Primates*, 10(2), 103-
497 148.
- 498 Swain, M. V., & Xue, J. (2009). State of the art of micro-CT applications in dental research.
499 *International Journal of Oral Science*, 1(4), 177-188.
- 500 Takahashi, M. Q., Rothman, J. M., Raubenheimer, D., & Cords, M. (2019). Dietary generalists and
501 nutritional specialists: Feeding strategies of adult female blue monkeys (*Cercopithecus mitis*) in the
502 Kakamega Forest, Kenya. *American Journal of Primatology*, 81(7), e23016.
- 503 Tethyragus (Artiodactyla, Mammalia) del Mioceno Medio de Somosaguas (Pozuelo de Alarcón,
504 Madrid). *Colóquios de Paleontología* 57: 7-14.
- 505 Tesfaye, D., Fashing, P. J., Bekele, A., Mekonnen, A., & Atickem, A. (2013). Ecological flexibility in
506 Boutourlini's blue monkeys (*Cercopithecus mitis boutourlinii*) in Jibat Forest, Ethiopia: a comparison

- 507 of habitat use, ranging behavior, and diet in intact and fragmented forest. *International Journal of*
508 *Primatology*, 34(3), 615-640.
- 509 Towle, I., Riga, A., Irish, J. D., Dori, I., Menter, C., & Moggi-Cecchi, J., 2019. Root caries on a
510 *Paranthropus robustus* third molar from Drimolen. *American Journal of Physical Anthropology*,
511 170(2).
- 512 Towle, I., & Irish, J. D. (2020). Recording and interpreting enamel hypoplasia in samples from
513 archaeological and palaeoanthropological contexts. *Journal of Archaeological Science*, 114, 105077.
- 514 Towle, I., & Irish, J. D. (2019). A probable genetic origin for pitting enamel hypoplasia on the molars
515 of *Paranthropus robustus*. *Journal of human evolution*, 129, 54-61.
- 516 Towle, I., Irish, J. D., Groote, I. D., Fernée, C., & Loch, C. (2021). Dental caries in South African fossil
517 hominins. *South African Journal of Science*, 117(3-4), 1-8. <http://dx.doi.org/10.17159/sajs.2021/8705>
- 518 Trinkaus, E., Smith, R. J., & Lebel, S., 2000. Dental caries in the Aubesier 5 Neandertal primary molar.
519 *Journal of Archaeological Science*, 27(11), 1017-1021.
- 520 Turner, C. G. (1979). Dental anthropological indications of agriculture among the Jomon people of
521 central Japan. X. Peopling of the Pacific. *American Journal of Physical Anthropology*, 51(4), 619-635.
- 522 Tweheyo, M., & Lye, K. A. 2003. Phenology of figs in Budongo Forest Uganda and its importance for
523 the chimpanzee diet. *African Journal of Ecology*, 41(4), 306-316.
- 524 Ubelaker, D. H., Phenice, T. W., & Bass, W. M. (1969). Artificial interproximal grooving of the teeth in
525 American Indians. *American Journal of Physical Anthropology*, 30(1), 145-149.
- 526 Ungar, P. S. 1994. Patterns of ingestive behavior and anterior tooth use differences in sympatric
527 anthropoid primates. *American Journal of Physical Anthropology*, 95(2), 197-219.

- 528 van Casteren, A., Oelze, V. M., Angedakin, S., Kalan, A. K., Kambi, M., Boesch, C., Hjalmar S. Kühl,
529 Langergraber, K. E., Piel, A. K., Stewart, F. A., & Kupczik, K. 2018. Food mechanical properties and
530 isotopic signatures in forest versus savannah dwelling eastern chimpanzees. *Communications*
531 *Biology*, 1(1), 109.
- 532 Varrela, T. M., 1991. Prevalence and distribution of dental caries in a late medieval population in
533 Finland. *Archives of Oral Biology*, 36(8), 553-559.
- 534 Walker, P. L., & Hewlett, B. S. 1990. Dental health diet and social status among Central African
535 foragers and farmers. *American Anthropologist*, 92(2), 383-398.
- 536 Watt, M. E., Lunt, D. A., & Gilmour, W. H., 1997. Caries prevalence in the permanent dentition of a
537 mediaeval population from the south-west of Scotland. *Archives of Oral Biology*, 42(9), 601-620.
- 538 Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012). Diet of chimpanzees (*Pan troglodytes*
539 *schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. *American*
540 *Journal of Primatology*, 74(2), 114-129.
- 541 Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees
542 in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*. Supplement, 13-31.
- 543 Wrangham, R. W., Conklin, N. L., Etot, G., Obua, J., Hunt, K. D., Hauser, M. D., & Clark, A. P. (1993).
544 The value of figs to chimpanzees. *International Journal of Primatology*, 14(2), 243-256.

Figure legends

Figure 1. Carious lesions on the mesial surface of an upper right central incisor in a Dent's mona monkey (*Cercopithecus denti*; PRI 11580) individual. A) carious lesion (black arrow) showing the relationship to the adjacent left central incisor; B) close up of the lesion (white arrow), scale bar 5mm; C) Micro-CT slice of the same lesion, showing demineralization deep into the dentine (white arrow).

Figure 2. Interproximal caries in chimpanzees (*Pan troglodytes*): A) M60: carious lesions on mandibular left lateral incisor and both central incisors (indicated by white arrows); B) M155: carious lesions in maxillary right central and lateral incisors (indicated by white arrows). Both scale bars are 5mm.

Figure 3. Raffles' banded langur (*Presbytis femoralis*; PRI 4565) lower incisors displaying potential periodontal disease and early stages of caries in the interproximal areas, but no clear evidence of cavitation. Scale bar 5mm.

Figure 4. An adult female chimpanzee in Kibale National Park, Uganda, eating figs (*Ficus sur/capensis*) by creating a wedge in the anterior dentition.

Table 1. Caries prevalence for permanent teeth for each species studied, split by anterior and posterior teeth. Figure in parenthesis is the percentage of ICAT teeth (i.e., anterior teeth with mesial and/or distal carious lesions).

Species	Common name	Anterior teeth			Posterior teeth			All teeth		
		# Teeth	carious teeth	%	# Teeth	carious teeth	%	# Teeth	carious teeth	%
<i>Pan troglodytes</i>	Chimpanzee	914	112	12.3 (9.8)	1584	53	3.4	2498	165	6.6
<i>Gorilla gorilla gorilla</i>	Western lowland gorilla	779	20	2.6 (2.6)	1311	0	0	2090	20	1
<i>Cercopithecus denti</i>	Dent's mona monkey	85	19	22.4 (22.4)	180	0	0	265	19	7.2
<i>Cercopithecus mitis</i>	Blue monkey	82	15	18.3 (18.3)	160	1	0.6	242	16	6.6
<i>Mandrillus sp.</i>	Mandrill	20	0	0	108	2	1.9	128	2	1.6
<i>Presbytis femoralis</i>	Raffles' banded langur	82	16	19.5 (19.5)	160	2	1.3	242	18	7.4
<i>Presbytis potenziani</i>	Mentawai langur	69	0	0	158	0	0	227	0	0
<i>Hylobates klossii</i>	Kloss's gibbon	84	0	0	232	4	1.7	316	4	1.3
<i>Macaca fuscata</i>	Japanese macaque	298	0	0	713	12	1.7	1011	12	1.2
<i>Simias concolor</i>	Pig-tailed langur	132	0	0	277	0	0	409	0	0
<i>Papio hamadryas</i>	Hamadryas baboon	182	0	0	336	6	1.8	518	6	1.2
All species combined		2727	182	6.7	5219	80	1.5	7946	262	3.3

Table 2. Percentage of carious lesions recorded for each surface on anterior teeth for the five species with anterior tooth lesions. Bold figures indicate position with highest caries prevalence.

Species	Common name	Buccal	Mesial	Lingual	Distal	Gross	Occlusal
<i>Pan troglodytes</i>	Chimpanzee	8.1	68.5	2.7	11.7	9	0
<i>Gorilla gorilla gorilla</i>	Western lowland gorilla	0	70	0	30	0	0
<i>Cercopithecus denti</i>	Dent's mona monkey	0	69.2	0	30.8	0	0
<i>Cercopithecus mitis</i>	Blue monkey	0	81.3	0	18.8	0	0
<i>Presbytis femoralis</i>	Raffles' banded langur	0	63.2	5.3	31.6	0	0

Table 3. Percentage of carious lesions recorded for each severity grade on anterior teeth of species with interproximal lesions.

Species	Common name	Severity 1	Severity 2	Severity 3	Severity 4
<i>Pan troglodytes</i>	Chimpanzee	55.4	33.9	4.5	6.3
<i>Gorilla gorilla gorilla</i>	Western lowland gorilla	65	35	0	0
<i>Cercopithecus denti</i>	Dent's mona monkey	79.2	16.7	4.2	0
<i>Cercopithecus mitis</i>	Blue monkey	76.5	23.5	0	0
<i>Presbytis femoralis</i>	Raffles' banded langur	100	0	0	0

Table 4. Average mineral concentration and total effective density (g/cm^3) for each dentine position studied, along with standard deviation (\pm) and minimum and maximum values (in parenthesis), for a tooth with a large cavity (PRI 11580) and a tooth showing coloration changes but no cavitation (PRI 11578).

	Average Mineral Concentration	Average Total Effective Density
PRI 11580		
Mesial (lesion)	0.60 \pm 0.12 (0.43-0.85)	1.43 \pm 0.05 (1.36-1.52)
Buccal	1.29 \pm 0.06 (1.17-1.43)	1.70 \pm 0.02 (1.65-1.75)
Distal	1.18 \pm 0.03 (1.10-1.23)	1.65 \pm 0.01 (1.62-1.67)
Lingual	1.17 \pm 0.04 (1.10-1.24)	1.65 \pm 0.02 (1.62-1.68)
PRI 11578		
Mesial (lesion)	0.84 \pm 0.08 (0.73-1.02)	1.52 \pm 0.03 (1.48-1.59)
Buccal	1.20 \pm 0.03 (1.13-1.26)	1.66 \pm 0.01 (1.63-1.69)
Distal	1.20 \pm 0.01 (1.17-1.23)	1.66 \pm 0.01 (1.65-1.68)
Lingual	1.24 \pm 0.03 (1.17-1.30)	1.68 \pm 0.01 (1.65-1.70)

Table 5. Caries prevalence for male and female chimpanzees. Displayed for all teeth, unworn/little-worn teeth removed, and with heavily worn teeth excluded. I: incisors; C: canines; PM: premolars.

Sample	Females	Males
Totals (%)		
Total teeth	1301	334
Carious teeth	121	6
Carious teeth %	9.3	1.8
% of individuals with caries	44.9	8.3
Mean I, C and PM wear**	3.9	2.6
Mean molar wear**	4.1	2.7
Wear score 1 taken out		
Total teeth	1192	255
Carious teeth	121	6
Mean I, C and PM wear**	4.31	3.5
Mean molar wear**	4.19	2.9
% caries teeth	10.2	2.4
Medium to low wear*		
Total teeth	511	227
Carious teeth	50	5
Mean I, C and PM wear**	3.5	3.6
Mean molar wear**	3.3	2.8
% carious teeth	9.8	2.2

*Individuals with a combined wear score of under 64 for all four first molars. Teeth with a wear score of 1 are excluded

**Molar wear is calculated using Scott (1979) and all other teeth following Smith (1984)

Supplementary Table 1. Geographic origin of the samples studied, along with information on the number of individuals split by sex.

Species	Common name	Location	Total individuals	Males	Females	Unspecified
<i>Pan troglodytes</i>	Chimpanzee	Cameroon (between 3.75-4.25 degrees North; 13.75-14.25 degrees East)	109	41	65	3
<i>Gorilla gorilla gorilla</i>	Western lowland gorilla	Cameroon (between 3.75-4.25 degrees North; 13.75-14.25 degrees East)	83	35	46	2
<i>Hylobates klossii</i>	Kloss's gibbon	Siberut Island, Sumatra, Indonesia	15	0	0	15
<i>Simias concolor</i>	Pig-tailed langur	Mentawai islands (Malibakbak; Silabu; Samekmek; Pasakiat), West Sumatra, Indonesia	20	9	11	0
<i>Papio hamadryas</i>	Hamadryas baboon	Mojo, Ethiopia	20	2	7	11
<i>Macaca fuscata</i>	Japanese macaque	Japan (Chiba; Koshima Island; Yakushima Island)	48	18	22	8
<i>Cercopithecus denti</i>	Dent's mona monkey	Democratic Republic of the Congo (Kalehe; Waikale; Kimbala; Kakolokelwa)	10	5	5	0
<i>Cercopithecus mitis</i>	Blue monkey	Walikale, North Kivu Province, Democratic Republic of the Congo	8	3	5	0
<i>Mandrillus spp.</i>	Mandrill	Cameroon	10	6	2	2
<i>Presbytis femoralis</i>	Raffles' banded langur	Lubuk Jantan (near Koto Alam), West Sumatra, Indonesia	8	3	5	0
<i>Presbytis potenziani</i>	Mentawai langur	Simaileppet Island, West Sumatra, Indonesia	8	5	3	0

Supplementary Table 2. Number of individuals with and without caries, split by sex.

Species	Female				Male			
	Caries	No caries	Total individuals	% with caries	Caries	No caries	Total individuals	% with caries
Blue monkey	3	2	5	60.00	3	0	3	100.00
Dent's mona monkey	3	2	5	60.00	4	1	5	80.00
Mandrill	0	5	5	0.00	1	5	6	16.67
Raffles' banded langur	3	2	5	60.00	1	2	3	33.33
Mentawai langur	0	3	3	0.00	0	5	5	0.00
Japanese macaque	1	21	22	4.55	4	14	18	22.22
Pig-tailed langur	0	11	11	0.00	0	9	9	0.00
Hamadryas baboon	3	15	18	16.67	0	2	2	0.00
Chimpanzee	26	39	65	40.00	7	34	41	17.07
Western lowland gorilla	3	43	46	6.52	4	31	35	11.43

A



B



C







