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Dental caries in wild primates: Interproximal cavities on anterior teeth

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Abstract

Dental caries has been reported in a variety of primates, although it is still considered rare in wild populations. In this study, 11 catarrhine primate taxa (n = 339 individuals; 7946 teeth) were studied for the presence of caries. A differential diagnosis of lesions in interproximal regions of anterior teeth was undertaken, since they had been previously described as both carious and non-carious in origin. Each permanent tooth was examined macroscopically, with severity and position of lesions recorded. Two specimens were examined further, using micro-CT scans to assess demineralization. Differential diagnosis confirmed the cariogenic nature of interproximal cavities on anterior teeth (ICATs). Overall results show 3.3% of all teeth (i.e., anterior and posterior teeth combined) were carious (n = 262), with prevalence varying among species from 0% to >7% of teeth affected. Those with the highest prevalence of ICATs include *Pan troglodytes verus* (9.8% of anterior teeth), *Gorilla gorilla gorilla* (2.6%), *Cercopithecus denti* (22.4%), *Presbytis femoralis* (19.5%), and *Cercopithecus mitis* (18.3%). ICATs make up 87.9% of carious lesions on anterior teeth. These results likely reflect dietary and food processing differences among species, but also between the sexes (e.g., 9.3% of all female *P. troglodytes verus* teeth were carious vs. 1.8% in males). Processing cariogenic fruits and seeds with the anterior dentition (e.g., wadging) likely contributes to ICAT formation. Further research is needed in living primate populations to ascertain behavioral/dietary influences on caries occurrence. Given the presence of ICATs in frugivorous primates, their diagnosis in archaeological and paleontological specimens may shed light on diet and food processing behaviors in fossil primates.

KEYWORDS

dental caries, food processing, frugivory, tooth cavities

1 | INTRODUCTION

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

Caries research has historically focused on humans, with high prevalence of lesions often associated with an agriculturalist lifestyle or hunter-gatherer populations that consume specific cariogenic foods (Caglar et al., 2007; Esclassan et al., 2009; Humphrey et al., 2014; Lanfranco & Eggers, 2012; Nelson et al., 1999; Novak, 2015; Sealy et al., 1992; Šlaus et al., 2011; Srejić, 2001; Varrela, 1991; Walker & Hewlett, 1990; Watt et al., 1997). In non-agricultural hominins, typically less than 5% of teeth are carious (Kelley et al., 1991; Lacy, 2014; Larsen et al., 1991; Towle et al., 2021; Turner, 1979). Foods containing high levels of carbohydrates are implicated in caries formation, whereas tough and fibrous foods are often linked with low caries rates because of high wear rates and increased saliva production (Clarkson et al., 1987; Moynihan, 2000; Novak, 2015; Prowse et al., 2008; Rohnbogner & Lewis, 2016). Diets rich in fruits, seeds, and nuts are often associated with high caries rates, with varying susceptibility depending on the type of foods and how they are processed orally (Humphrey et al., 2014; Novak, 2015). A variety of other factors can affect the likelihood of caries, including the extent and type of crown wear and other pathologies/defects, such as enamel hypoplasia and periodontal disease (Calcagno & Gibson, 1991; Hillson, 2008; Towle & Irish, 2019, 2020). In humans, posterior teeth (molars and premolars) are most affected by caries.

Non-human primates also develop caries, particularly in captivity, and lesions have been described in extant and extinct wild populations (e.g., Cohen & Goldman, 1960; Colyer, 1936; Fuss et al., 2018; Lovell, 1990; Miles & Grigson, 2003; Schultz, 1935, 1956; Smith et al., 1977; Stoner, 1995). In captivity, non-human primates often have higher caries rates in posterior teeth, similar to humans (Anderson & Arnim, 1937; Bowen, 1968; Cohen & Bowen, 1966; Colyer, 1936). However, in wild primates, anterior teeth seem to be more affected (Colyer, 1931). Typically, lesions on anterior teeth form in interproximal regions of incisors (Lovell, 1990; Schultz, 1935; Smith et al., 1977; Stoner, 1995). The foods consumed and how they are orally processed have been implicated in the formation of these lesions, but an in-depth study on why these lesions form has not been conducted. These interproximal cavities on anterior teeth (ICATs) have not always been regarded as carious, or otherwise have been overlooked by researchers. For example, in Kilgore (1989) ICATs are described as being caused by attrition.

Therefore, although ICATs have been previously reported, a study of their occurrence in a wide range of primate species is required. In this exploratory study, we use micro-CT scans to assess dental tissue demineralization, and consider other potential etiologies that may have led to ICAT formation, evaluating the likelihood of each. The influence of sex, age, and certain pathologies (e.g., abscesses and periodontal disease) on the formation of carious lesions was also considered. A total of 11 catarrhine species were selected for this survey, including species that vary in the degree to which they consume potentially cariogenic fruits. We hypothesize that species known to regularly process sugary fruits with the anterior dentition, including behaviors such as "wadging" (see below), will display ICATs, while those with a more varied diet will have a lower incidence of caries.

2 | METHODS

2.1 | Study sample

All samples studied here are curated at the Primate Research Institute, Kyoto University, Japan (PRI), and the Powell-Cotton Museum, UK (PCM). The 11 catarrhine species include: Western chimpanzee (*Pan troglodytes verus*), Western lowland gorilla (*Gorilla gorilla gorilla*), Kloss's gibbon (*Hylobates klossii*), hamadryas baboon (*Papio hamadryas*), pig-tailed langur (*Simias concolor*), Japanese macaque (*Macaca fuscata*), Dent's mona monkey (*Cercopithecus denti*), blue monkey (*Cercopithecus mitis*), mandrill (*Mandrillus* sp.), raffles' banded langur (*Presbytis femoralis*), and Mentawai langur (*Presbytis potenziani*). All were wild, and lived and died in their natural habitat (see Buck et al., 2018; Guatelli-Steinberg & Skinner, 2000; Kamaluddin et al., 2019; Lukacs, 2001). The specimen numbers are presented in the Supporting Information. This study only concerns osteological collections (i.e., not living individuals) and complied with protocols approved by both the PCM and PRI. The research also adheres to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates, and the legal requirements of both the UK and Japan. The authors have no conflict of interest to declare. The data that supports the findings of this study are available in the Supporting Information of this article. All permanent teeth retained within the jaws of each specimen were examined macroscopically. Those with substantial postmortem damage were excluded from analysis.

2.2 | Assessment of pathology and wear

Caries prevalence by species was calculated as the percentage of affected teeth among all permanent teeth analyzed, including antimeres. Comparisons were made for all teeth, as well as between the posterior (molars and premolars) and anterior dentition (canines and incisors). Color changes on dental tissues were not considered diagnostic, but were recorded when in association with antemortem cavitation. Cavity severity and position on the crown were also recorded. Severity was scored on a scale of 1–4 (Connell & Rauxloh, 2003): (1) enamel destruction; (2) compromised dentine but pulp chamber not exposed; (3) destruction of dentine with pulp exposure; (4) gross destruction with crown mostly destroyed. Location was recorded as buccal, occlusal, distal, lingual and mesial. If it was not possible to determine location due to severity, the lesion was recorded as 'gross'. Due to difficulty in ascertaining if certain lesions would be best described as affecting the crown or root, teeth were not divided into these categories; however, potential differences are discussed.

Caries can directly contribute to antemortem tooth loss, which has led to correction methods (e.g., Duyar & Erdal, 2003; Kelley et al., 1991; Lukacs, 1995). However, the most likely causes of antemortem tooth loss in extant primates are severe attrition, fractures, and periodontal disease. Therefore, following other studies (e.g., Larsen et al., 1991; Meinl et al., 2010), no correction methods were implemented here. Data on abscesses and periodontal disease were collected following Dias and Tayles (1997) and Ogden (2007), to assess if these pathologies were associated with caries. Each individual was recorded as having caries, periodontal disease, and abscesses (see Supporting Information). An individual was considered to be affected by abscesses and caries when they presented with at least one lesion in the dentition. For periodontal disease, the mandible and/or maxilla of the individual needed to exhibit general resorption (rather than just pockets).

Wear was scored following Scott (1979) for molars, and Smith (1984) for all other teeth, to assess the impact of age (using tooth wear as a proxy) on caries prevalence. Species were also divided by sex to explore differences in caries occurrence. For sex difference analyses, a Chi-square test with an alpha level of 0.05 was used.

2.3 | Demineralization analysis

Two teeth were subsequently removed for Micro-CT scanning to ascertain enamel/dentine demineralization, and to visualize lesion progression (Boca et al., 2017; Rossi et al., 2004; Swain & Xue, 2009). Scans were performed at the Primate Research Institute, Kyoto University, using a SkyScan1275 Micro-CT scanner. The two teeth belonged to different *C. denti* individuals, one with a cavity on the mesial surface (upper right central incisor; PRI 11580) and the other displaying only coloration changes in the same location (PRI 11578; lower left central incisor).

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

3 | RESULTS

Caries frequency varied across species and was low (<1.5% of teeth) in over half the species (*G. gorilla gorilla*, *M. fuscata*, *P. hamadryas*, *S. concolor*, *H. klossii*, and *P. potenziani*). Posterior tooth caries were particularly rare (0%–3.4%, Table 1), while caries prevalence in anterior dentition was more variable (0%–22.4%, Table 1). Nearly 88% of all lesions on anterior teeth were interproximal, with mesial surfaces mostly affected (Table 2). These ICATs were only present in *P. troglodytes verus*, *G. gorilla gorilla*, *C. denti*, *C. mitis*, and *P. femoralis*. Most anterior lesions were small (severity 1), although *P. troglodytes verus* and *G. gorilla gorilla* samples showed higher frequencies of larger lesions (Table 3).

Micro-CT scans of the two teeth that exhibited ICATs revealed that dentine was substantially demineralized beneath both the cavitation and color change areas (Figure 1). In both cases, a much lower mineral concentration and total effective density were evident compared to other areas of the tooth (Table 4). The range and standard deviation of the dentine mineral concentration within the carious locations were also much greater than in sound dentine, adding further support for demineralization caused by caries. Below the cavity in specimen PRI 11580, demineralization reached a maximum of approximately 0.5 mm into the dentine before tissue returned to normal density (i.e., over 1.6 g/cm^3).

ICATs in the five species that displayed them were similar in shape and crown position, with relatively circular lesions near the cementum-enamel junction (CEJ) on the interproximal surfaces of anterior teeth (Figure 2a). In more severe cases, much of the crown was destroyed (Figure 2b). In individuals with mild to moderate severity, lesions were limited to the CEJ region, and often only affected the crown; however, in some cases, lesions had initiated on the root and followed the CEJ boundary, giving them a more oval appearance. In many cases, it was not possible to ascertain if the lesion initially involved the crown or root, as the cavity covered both regions. Many individuals showed a dark coloration in these interproximal regions, but no cavitation (Figure 3). Along with the Micro-CT scan data, this feature suggests these areas were early carious lesions.

Periodontal disease and extensive occlusal/interproximal wear were sometimes associated with caries formation (Figures 1 and 2). However, species with high caries levels do not seem to have an overall increase in periodontal disease, with both carious and non-carious individuals' similarly affected (Supporting Information).

Only *P. troglodytes verus* displayed a significant difference in caries prevalence between males and females (Table S2). This analysis was hindered by small sample sizes for Cercopithecidae. However, when pooled together, there was little difference in caries frequency by sex (Cercopithecidae species combined; males: 25.49%; females: 17.57%; $\chi^2 = 1.150$, 1 df, $p = 0.28$). While a slightly higher percentage of male *G. gorilla gorilla* had caries, this difference was not statistically significant (males: 11.43%; females: 6.52%; $\chi^2 = 0.606$, 1 df, $p = 0.44$). In contrast, female *P. troglodytes verus* had significantly more caries than males (males: 17.07%; females: 40%; $\chi^2 = 6.164$, 1 df, $p = 0.01$). Female *P. troglodytes verus* also had five times the number of teeth

TABLE 1 Caries prevalence for permanent teeth for each species studied, split by anterior and posterior teeth

			All teeth			Anterior teeth			Posterior teeth		
Species	Common name	Individuals (m, f, unk)	# Teeth	Carious teeth	%	# Teeth	Carious teeth	%	# Teeth	Carious teeth	%
Pan troglodytes verus	Chimpanzee	109 (41, 65, 3)	2498	165	6.6	914	112	12.3 (9.8)	1584	53	3.4
Gorilla gorilla gorilla	Western lowland gorilla	83 (35, 46, 2)	2090	20	1	779	20	2.6 (2.6)	1311	0	0
Macaca fuscata	Japanese macaque	48 (18, 22, 8)	1011	12	1.2	298	0	0	713	12	1.7
Papio hamadryas	Hamadryas baboon	20 (2, 7, 11)	518	6	1.2	182	0	0	336	6	1.8
Simias concolor	Pig-tailed langur	20 (9, 11)	409	0	0	132	0	0	277	0	0
Hylobates klossii	Kloss's gibbon	15 (0, 0, 15)	316	4	1.3	84	0	0	232	4	1.7
Cercopithecus denti	Dent's mona monkey	10 (5, 5)	265	19	7.2	85	19	22.4 (22.4)	180	0	0
Mandrillus sp.	Mandrill	10 (6, 2, 2)	128	2	1.6	20	0	0	108	2	1.9
Cercopithecus mitis	Blue monkey	8 (3, 5)	242	16	6.6	82	15	18.3 (18.3)	160	1	0.6
Presbytis femoralis	Raffles' banded langur	8 (5, 5)	242	18	7.4	82	16	19.5 (19.5)	160	2	1.3
Presbytis potenziani	Mentawai langur	8 (5, 3)	227	0	0	69	0	0	158	0	0
All species combined		339	7946	262	3.3	2727	182	6.7	5219	80	1.5

Note: Figure in parenthesis is the percentage of ICAT teeth (i.e., anterior teeth with mesial and/or distal carious lesions).

TABLE 2 Percentage of carious lesions recorded for each surface on anterior teeth for the five species with anterior tooth lesions

Species	Buccal	Mesial	Lingual	Distal	Gross	Occlusal
Pan troglodytes verus	8.1	68.5	2.7	11.7	9	0
Gorilla gorilla gorilla	0	70	0	30	0	0
Cercopithecus denti	0	69.2	0	30.8	0	0
Cercopithecus mitis	0	81.3	0	18.8	0	0
Presbytis femoralis	0	63.2	5.3	31.6	0	0

Note: greatest prevalence occurs in mesial region of teeth for all taxa.

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

Species	Severity 1	Severity 2	Severity 3	Severity 4
Pan troglodytes verus	55.4	33.9	4.5	6.3
Gorilla gorilla gorilla	65	35	0	0
Cercopithecus denti	79.2	16.7	4.2	0
Cercopithecus mitis	76.5	23.5	0	0
Presbytis femoralis	100	0	0	0

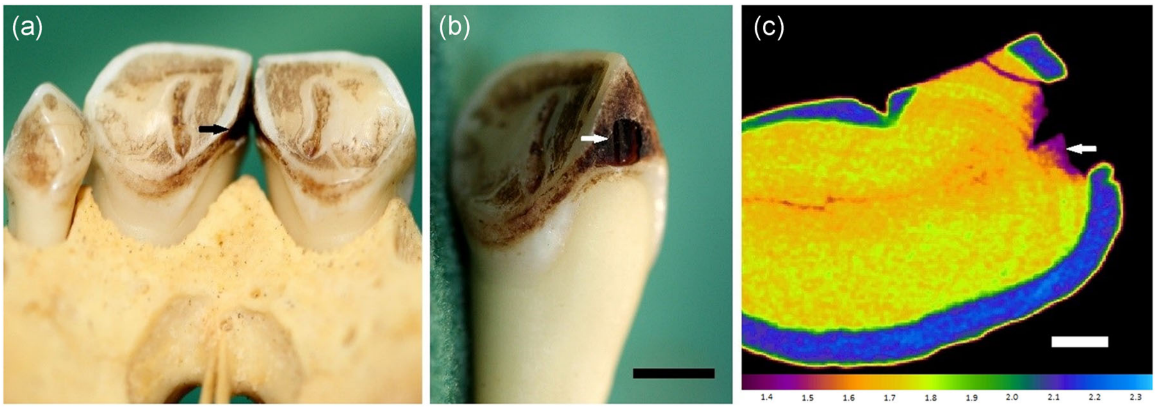

FIGURE 1 Carious lesions on the mesial surface of an upper right central incisor in a Dent's mona monkey (*Cercopithecus denti*; PRI 11580) individual. (a) carious lesion (black arrow) showing the relationship to the adjacent left central incisor; (b) close up of the lesion (white arrow), scale bar 5 mm; (c) Micro-CT slice of the same lesion, showing demineralization deep into the dentine (white arrow). Color ramp: total effective density (g/cm^3); scale bar: 1 mm

TABLE 4 Average mineral concentration and total effective density (g/cm^3) for each dentine position studied, along with standard deviation (±) 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 ± 0.12 (0.43–0.85)	1.43 ± 0.05 (1.36–1.52)
Buccal	1.29 ± 0.06 (1.17–1.43)	1.70 ± 0.02 (1.65–1.75)
Distal	1.18 ± 0.03 (1.10–1.23)	1.65 ± 0.01 (1.62–1.67)
Lingual	1.17 ± 0.04 (1.10–1.24)	1.65 ± 0.02 (1.62–1.68)
PRI 11578		
Mesial (lesion)	0.84 ± 0.08 (0.73–1.02)	1.52 ± 0.03 (1.48–1.59)
Buccal	1.20 ± 0.03 (1.13–1.26)	1.66 ± 0.01 (1.63–1.69)
Distal	1.20 ± 0.01 (1.17–1.23)	1.66 ± 0.01 (1.65–1.68)
Lingual	1.24 ± 0.03 (1.17–1.30)	1.68 ± 0.01 (1.65–1.70)

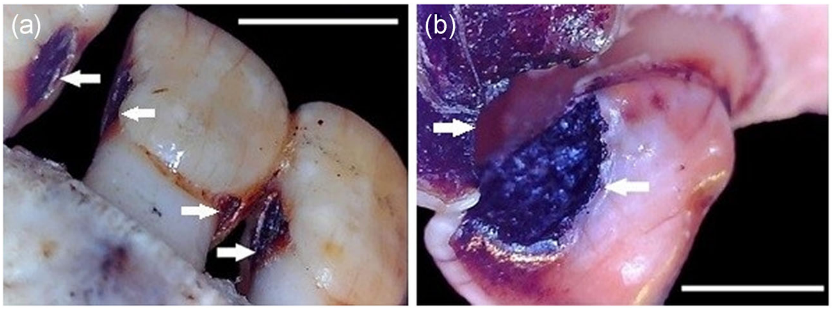

FIGURE 2 Interproximal caries in chimpanzee (*Pan troglodytes verus*): (a) M60: carious lesions on mandibular left lateral incisor and both central incisors (indicated by white arrows); (b) M155: carious lesions in maxillary right central and lateral incisors (indicated by white arrows). Both specimens were curated at PCM. Scale bars = 5 mm

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: 5 mm

TABLE 5 Caries prevalence for male and female *Pan troglodytes verus*

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[a]	3.9	2.6
Mean molar wear[a]	16.4	10.8
Wear score 1 taken out		
Total teeth	1192	255
Carious teeth	121	6
Mean I, C, and PM wear[a]	4.31	3.5
Mean molar wear[a]	16.76	11.6
% caries teeth	10.2	2.4
Medium to low wear[b]		
Total teeth	511	227
Carious teeth	50	5
Mean I, C, and PM wear[a]	3.5	3.6
Mean molar wear[a]	13.2	11.2
% carious teeth	9.8	2.2

Note: Displayed for all teeth, unworn/little-worn teeth removed, and with heavily worn teeth excluded. I: incisors; C: canines; PM: premolars.

[a]Molar wear is calculated using Scott (1979) and all other teeth following Smith (1984).

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

affected compared to males ($\chi^2 = 20.890$, 1 df, $p = 0.00$). This difference does not appear to relate to age, based on crown wear (Table 5).

4 | DISCUSSION

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

Although Kilgore (1989) suggested ICATs may relate to severe enamel attrition from stripping foods, demineralization visible deep into the dentine on the Micro-CT scans was strongly suggestive of caries. Attrition-related behavior could contribute to lesion formation, by exposing the underlying dentine in interproximal areas. However, the present Micro-CT scan results, radiographs in Kilgore (1989), and thin sections in Miles and Grigson (2003), seem to confirm that caries is the predominant factor for hard tissue loss in ICATs. Furthermore, coloration changes in these regions are suggestive of early-stage demineralization associated with caries; thus, the true rate and effects of caries are likely much higher than the present findings suggest, due to the conservative approach adopted here when recording lesions. A study of a large number of lesions showing only discoloration is required before these can be confidently included in caries frequencies, and such a study requires care since taphonomic processes can lead to similar coloration changes. Additional processes, such as attrition or non-bacterial erosion, are unlikely to yield localized deep cavities and coloration change visible in ICATs.

Other researchers have reported ICATs as carious lesions (e.g., Colyer, 1936; Schultz, 1956), reporting high caries rates in primates, with incisors commonly affected. Colyer (1931) reported that anterior teeth were more commonly affected than posterior teeth (66.2% vs. 33.8%) in wild monkeys, with interproximal surfaces presenting most lesions (94.2%). When compared to previous photographs in the literature, caries in anterior teeth appear similar to those described here (e.g., Figure 15 in Schultz, 1935; Figure 5 in Smith et al., 1977; Figure 4 in Stoner, 1995; Figure 5 in Lovell, 1990). Therefore, in addition to the present species studied, other frugivorous primates (including platyrrhines and catarrhines) seem to display ICATs (see Coyler, 1936; Lovell, 1990; Schultz, 1935, 1956; Smith et al., 1977; Stoner, 1995).

In contrast, ICATs seem rare in captive primates, with posterior teeth commonly displaying carious lesions (Anderson & Arnim, 1937; Bowen, 1968; Cohen & Bowen, 1966; Colyer, 1936). Such primates are often fed a cariogenic diet but have higher caries rates in the posterior teeth (Anderson & Arnim, 1937; Bowen, 1968; Cohen & Bowen, 1966). For example, Colyer (1936) found that almost 90% of carious teeth in captive monkeys were molars. These observations suggest the way in which foods are processed can contribute to the generation of incisor lesions. In the present study, most ICATs were associated with significant attrition/abrasion on the occlusal and interproximal surfaces. Tooth wear, along with periodontal disease and continuous eruption of teeth, may create excessive space for food and bacteria to accumulate below the crown between incisors. Additionally, heavy wear can be associated with root surface exposure, through continuous tooth eruption or periodontal disease, facilitating root caries formation (Hillson, 2008). Many sugary fruits are also highly acidic, which might create a microenvironment that facilitates the proliferation of cariogenic bacteria. Although salivary pH will counteract this acidity, certain dental locations in the mouth may be more prone to acid effects (Cuozzo et al., 2008; Pollard, 1995; Poole et al., 1981; Ungar, 1995).

Support for this multifactorial hypothesis is found in behavioral observations of wild chimpanzees, as they tend to use their lips in tandem with large broad spatulate incisors to process fruits and plants (Hylander, 1975; Lambert, 1999; McGrew, 1999; Suzuki, 1969; Ungar, 1994; van Casteren et al., 2018). Figs are commonly consumed by many primates, including most chimpanzees (e.g., Basabose, 2002; Matthews et al., 2019; Nishida & Uehara, 1983; Potts et al., 2011; Tweheyo & Lye, 2003; Watts et al., 2012). However, chimpanzees often process figs differently than other primates using a behavior called “wadging,” which involves holding a large mass of chewed fruits in the anterior part of the mouth (Lambert, 1999; Nishida et al., 1999). Chimpanzees then suck the sugary liquids from the wadge, much of which will sieve through interproximal surfaces of anterior teeth (Figure 4). Importantly, wadging is more common with figs that have higher concentrations of sugars (i.e. *Ficus sur/capensis*, *Ficus mucuso*; Danish et al., 2006; Wrangham et al., 1993). Other sugary foods are also wadged, including honeycomb (Nishida et al., 1999), which likely creates a cariogenic environment in the interproximal surfaces of anterior teeth, which likely explains the high prevalence of lesions there.

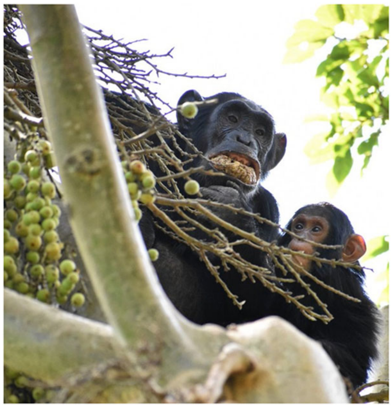

FIGURE 4 An adult female chimpanzee in Kibale National Park, Uganda, eating figs (*Ficus sur/capensis*) by creating a wadge against the anterior dentition

In this study, although *G. gorilla gorilla* has lower ICAT rates than *P. troglodytes verus*, they still showed these characteristic lesions. Gorillas also regularly eat fruits, many of which are high in soluble sugars (Remis et al., 2001). The cercopithecid species with ICATs (*C. denti*, *C. mitis*, and *P. femoralis*) are all frugivores that process foods high in fermentable carbohydrates using their anterior dentition. However, the specific food types that contribute to caries formation likely vary. Caries in *P. femoralis* may relate to a diet of seeds high in carbohydrates (i.e., starch), processed using incisors (Davies et al., 1988). This process could have led to not only high caries rates in the anterior dentition, but to high rates of tooth chipping (Towle & Loch, 2021). *Cercopithecus denti* and *C. mitis* also eat substantial quantities of different fruits (Olaleru, 2017; Takahashi et al., 2019). Further research is needed to ascertain which foods may contribute to ICATs in these species. For example, *C. mitis* show substantial variation in feeding ecology across their range (Tesfaye et al., 2013), meaning that a study of caries in populations with detailed dietary and behavioral record is important to elucidate the processes leading to ICAT formation.

Sex differences in caries prevalence are also important, since differences have been observed in humans and other great apes and are linked to a variety of social, behavioral, and physiological differences (Lanfranco & Eggers, 2012; Lukacs & Largaespada, 2006; Lukacs, 2011; Stoner, 1995). Although most female *P. troglodytes verus* exhibited more crown wear, this difference in caries frequency remained stable once teeth were split into wear categories. Females with low and medium levels of wear (combined wear score under 64 for all four first molars; following Scott, 1979) displayed more carious teeth, with five times the rate of males in the same wear category. Therefore, in this sample, female *P. troglodytes verus* were more likely to exhibit caries compared to males, and also exhibited caries in five times more teeth. Dietary and behavioral differences are known between male and female chimpanzees (Gilby et al., 2017; Nakamura et al., 2015; Wrangham & Smuts, 1980). Pregnancy and differences in oral pH, saliva, physiology, life history, and microbiome between the sexes may also be predisposing factors for caries formation (e.g., Fuss et al., 2018; Lukacs & Largaespada, 2006; Stoner, 1995). The results of the present study support other reports of sex differences in caries rates among great apes, although the present sample did not show differences between male and female *G. gorilla gorilla*.

Recent literature has shown that caries in fossil hominin and extant great apes is not as rare as previously thought (e.g., Arnaud et al., 2016; Lacy et al., 2012; Lacy, 2014; Lanfranco & Eggers, 2012; Liu et al., 2015; Margvelashvili et al., 2016; Miles & Grigson, 2003; Stoner, 1995; Towle & Irish, De Groote, et al., 2021; Towle et al., 2019; Trinkaus et al., 2000). There is also growing evidence that caries was common in other extinct primates (e.g., Fuss et al., 2018; Han & Zhao, 2002; Selig & Silcox, 2021). This study adds further evidence that caries was likely relatively common in some primate lineages. ICATs are the result of bacterial/chemical demineralization of the dental tissues, and this study shows they are linked to feeding behaviors, with such lesions being rare in captive primates. Therefore, their position in the dentition may offer insights into diet and behavior of extinct species, based on comparisons with extant primates. In particular, because of ICATs' uniform appearance in multiple frugivore species, these lesions may be useful for behavioral interpretations. Given the difference in prevalence in female and male *P. troglodytes verus*, caries prevalence may also shed light on sexually dimorphic feeding behaviors and physiology in past primate populations.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supporting Information of this article.

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