Paranthropus robustus tooth chipping patterns do not support regular hard food mastication

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1. Introduction

When a tooth contacts a hard object with enough force, the enamel can fracture to create a chip (Chai and Lawn, 2007; Constantino et al., 2010). The fractured area can vary depending on mechanical and structural properties of the enamel and object (Thomas, 2000; Constantino et al., 2010; He and Swain, 2008; Lawn, Lee, Constantino, and Lucas, 2009; Scott and Winn, 2011). Chips are not generated through a gradual process, although cumulative effects related to enamel fatigue and demineralization may contribute to fracture likelihood and location (Gao et al., 2016; Sanchez-Gonzalez et al., 2020). Importantly, it can take many years of subsequent wear to erase evidence of a chip, making them a crucial marker of past behavior and diet (Belcastro et al., 2018; Towle et al., 2017; Constantino, Markham, and Lucas, 2012).

Enamel chips can be caused by a variety of factors, including food processing, environmental contaminants (e.g., sand or grit), dietary items and social behavior (Constantino et al., 2012; Sauther, Sussman, and Cuozzo, 2002; Scott and Winn, 2011; Stojanowski, Johnson, Paul, and Carver, 2015; Van Valkenburgh, 2009). These different influences can generate unique patterns across the dentition, and allow inferences of dietary and behavioral factors in archaeological and paleoanthropological samples (Belcastro et al., 2007; Constantino et al., 2010; Scott and Winn, 2011; Nystrom, Phillips-Conroy, and Jolly, 2004; Towle et al., 2017). A range of recent human populations, fossil hominins and extant primates have been studied for evidence of chipping (e.g., Belcastro et al., 2007; Bonfiglioli et al., 2004; Gould, 1968; Lous, 1970; Molnar et al., 1972; Silva, Gil, Soares, and da Silva, 2016; Turner and Cadien, 1969; Constantino et al., 2010; Grine et al., 2010; Robinson, 1954; Tobias, 1967; Johanson and Taieb, 1976; Ward et al., 2001; Fox and Frayer, 1997; Scott and Winn, 2011; Stojanowski et al., 2015; Larsen, 2015; Lous, 1970; Molnar et al., 1972; Fannin et al., 2020). However, until recently, differences in recording methods have made inter-study comparisons challenging.

Enamel chipping may provide critical insights into the feeding habits of enigmatic hominins, such as the ‘robust australopith’ clade, e.g., *Paranthropus boisei* and *P. robustus*. *Paranthropus* species have long been inferred to be hard object feeders (durophagous), with large bunodont posterior teeth and robust cranial features thought to reflect adaptations related to habitually masticating hard foods (Rak, 1983; Jolly, 1970; Teaford and Ungar, 2000;

Constantino et al., 2018). However, the diets of these species are still debated, with a variety of dietary scenarios described (e.g., Martínez et al., 2016; Williams, 2015; Strait et al., 2013; Smith et al., 2015; Cerling et al., 2011; Van der Merwe et al., 2008; Wood and Strait, 2004). Additionally, there is often an apparent disconnect between diet and craniodental morphology in *Paranthropus*.

Direct evidence from enamel microwear studies of *P. boisei* suggests little to no hard object feeding (Ungar et al., 2008). In *P. robustus,* higher enamel surface complexity may indicate hard foods were consumed more frequently (Ungar, 2019; Scott et al., 2005; Peterson et al., 2018), potentially in the context of 'fallback foods'. However, the role of hard plant tissues in generating microwear features is currently debated (van Casteren et al., 2020; Teaford et al., 2020). From stable carbon isotopes, the diets of *P. robustus* and *P. boisei* appear substantially different (Cerling et al., 2011; Ungar and Sponheimer, 2011). Isotopic results for *P. boisei* are in concordance with microwear and some biomechanical evidence, suggesting that hard foods such as seeds and nuts did not make up a significant part of their diet; rather, C4 graminoids (e.g., grasses and sedges) were likely common foods (Guatelli-Steinberg, 2016; Macho, 2014; Dominy et al., 2008; Yeakel et al., 2007; Cerling et al., 2011; Kaiser et al., 2019). A more recent study on comparative biomechanical and morphological data in primates also suggests a soft-food niche for *Paranthropus* (Marcé-Nogué et al., 2020). Based on this and other evidence, many researchers now regard *Paranthropus* as non-hard object eaters (Ungar and Hlusko, 2016; Grine and Daegling, 2017; Kaiser et al., 2019), while others consider them dietary generalists (e.g., eurytopy; Wood and Strait, 2004; Strait et al., 2013).

Nonetheless, some maintain that hard foods were commonly consumed by *Paranthropus,* and/or played a significant role in the craniodental evolution of the genus (e.g., Constantino et al., 2009; Constantino et al., 2018; Paine et al., 2019; Strait et al., 2013; Smith et al., 2015). Chipping is usually one of the main forms of evidence proposed to support these hypotheses, typically to show that hard object consumption was common (Constantino et al., 2010, Constantino et al., 2018; Ungar, 2019; Paine et al., 2019). Given the microwear and isotopic results discussed above, most of this recent research focuses on hard-food mastication in *P. robustus*. Earlier work suggested that ingestion of grit or bones may instead be responsible for the chipping of their teeth (Robinson, 1954; Tobias, 1967).

Therefore, despite being crucial in elucidating the diet of *P. robustus*, a broad comparison specifically focusing on chipping patterns relative to other hominins and extant primates is still lacking. In particular, although data in the current article comes from published sources, because *P. robustus* was not the focus of these studies, it has led to misunderstandings of interpretation. For example, Paine et al. (2019:104) stated that *P. robustus* had a "significant degree of hard object feeding," with Towle et al. (2017) cited to support this claim. In fact, Towle et al. (2017) reported that *P. robustus* has the lowest rate of chipping of any hominin studied, with a prevalence similar to gorillas. Additionally, in previous studies *Paranthropus* species are often only compared to one another, or to other fossil hominins. For example, the *P. robustus* diet is said to have contained a "significant amount of hard food content," based on higher chipping prevalence than in *P. boisei* (Constantino et al., 2018:76). Therefore, chipping is often considered evidence of regular hard food consumption in *P. robustus*, but extant comparisons are needed to determine if these conclusions are supported in primates that are known hard-object feeders.

In three recent studies that include comparisons of chipping in a total of 25 primate species (Towle and Loch, 2021; Fannin et al., 2020; Towle et al., 2017), all samples show at least some chips. Therefore, the presence of chipping in a sample on its own may tell us little about diet or behavior. Instead, the evaluation of the patterns in extant primates with associated ecological data allows an understanding of chipping relative to diet and behavior. In this study, we compared these patterns in a range of extant primates and fossil hominins, to test whether prevalence and patterns in *P. robustus* support habitual, or occasional, durophagy. The extant primates analyzed include several species considered hard-object feeding specialists (sooty mangabeys, mandrills and sakis). Other species either focus on particular non-hard food items or have been reported to rarely consume hard foods (including several ape and colobus species), and those with a more varied diet, including eurytopic and terrestrial species (e.g., Japanese macaques, mandrills and baboons). As well as prevalence, the size and distribution of chips across the dentition when compared to other species may help elucidate behavioral factors that led to their occurrence in *P. robustus*.

2. Materials and Methods

Data were compiled from the recent literature. Fossil hominin samples include specimens assigned to *Homo naledi*, *Australopithecus africanus*, *P. robustus*, and *H.*

neanderthalensis (following Towle et al., 2017; Belcastro et al., 2018). Extant primates studied include a range of Cercopithecidae species (n=11) and two species of Ceboidea (following Towle and Loch, 2021; Towle et al., 2017). Species classification and sample sizes (number of individuals and teeth) are presented in Table 1. An additional four species are added from Fannin et al. (2020), where only fourth premolars and first molars were studied. Therefore these data are only used in a separate comparison of these same teeth in each species (Figure 1). In all studies data collection methods were standardized, with only minor variations in technique. As well as overall prevalence of chipping, teeth were also divided into types to compare variation in chipping pattern across the dentition. Results refer to permanent teeth only.

Teeth with minimal wear were removed for prevalence in Towle et al. (2017), but are included here to allow direct comparisons with other samples, resulting in a slightly lower prevalence than previously reported. For example, an additional 35 *P. robustus* teeth are included here, giving a total of 270 permanent teeth. A further 132 *P. robustus* teeth are not included due to *postmortem* damage (as in Towle et al., 2017). However, a separate analysis is presented that does include both postmortem damaged and deciduous teeth in *P. robustus*, to assess if their inclusion may explain differences in chipping prevalence with other studies. The data on 57 deciduous *P. robustus* teeth come from previously unpublished data using the same methods as Towle et al. (2017).

Antemortem fractures were only recorded if subsequent attrition is evident on the chipped surface (i.e., the chip scar) to rule out postmortem damage (Scott and Winn, 2011; Belcastro et al., 2018). Smoothing and coloration were used for this purpose i.e., postmortem fractures displaying ‘fresh’ enamel brighter than the rest of the crown and with sharp edges (Towle and Loch, 2021). The number of chips on each tooth was also recorded, allowing inferences into the number of teeth with multiple chips (Belcastro et al., 2018; Towle et al., 2017; Towle and Loch, 2021).

Fractures were recorded on a three-point grading system following Bonfiglioli et al. (2004), except for the Towle and Loch (2021) extant primate species that were recorded on a comparable three-point system but with measurements removed to allow comparison with a larger range of primate tooth sizes. A summary of each grade is given below, with the descriptions in Towle and Loch (2021); followed by that of Bonfiglioli et al. (2004) for each grade:

1) Small enamel chip (crescent-shaped) on the outer edge of the enamel. Dentine is not exposed and the chip is restricted to the outer rim of the occlusal surface; slight crack or fracture (0.5 mm), or larger but superficial enamel flake loss
2) Larger chip that extends near to the enamel-dentine junction. A small area of dentine might be exposed; square irregular lesion (1 mm) with the enamel more deeply involved
3) Large irregular fracture in which a significant area of dentine is exposed. More dentine than enamel was removed by the fracture.; crack bigger than 1 mm involving enamel and dentine or a large, very irregular fracture that could destroy the tooth

3. Results

Prevalence and overall patterns of permanent tooth chipping for each species are summarized in Table 1. Hominins cover the range of prevalence in extant primates, with chipping common in *Homo* (37–45% of all permanent teeth) and relatively rare in *P. robustus* (11%). *Australopithecus africanus* falls between these two extremes, but closer to *P. robustus*, with 17% of teeth displaying at least one fracture. The prevalence of chipping in *P. robustus* is similar to the extant ape species studied, chimpanzees, gibbons and gorillas (Table 1). The rate in extant primates considered to be hard-food specialists (e.g., sakis and mandrills, 28% and 37% respectively) is several times greater than in *P. robustus* (Table 1). If all teeth are included from the Towle et al. (2017) dataset (i.e., including postmortem damaged teeth) there is a decrease of chipping prevalence in *P. robustus* to 7.46% (30/402). Additionally, if deciduous teeth are also included, this rate drops to 6.97% (32/459).

Further direct comparisons are made with additional species from Fannin et al. (2020) for first molars and fourth premolars in Figure 1, with *P. robustus* displaying the fourth lowest rate of fractures out of 20 species studied. Further, this equates to a chipping prevalence for these teeth approximately five times lower than both sooty mangabey and *H. naledi* (Figure 1). When divided into individual tooth types, all *P. robustus* teeth show consistently low chipping rates, except canines and third premolars with a moderate prevalence (21% and 23% respectively). Each *P. robustus* molar type (first, second and third) shows a low prevalence of chipping, with each displaying one of the lowest rates relative to the same tooth in other species (Table 2). Few *P. robustus* teeth exhibit multiple chips (6.7% of chipped teeth have more than one fracture). *Paranthropus robustus* also has a high ratio of larger chips relative to most other species (1.7 small chips for every large fracture); only chimpanzees, gibbons and Neanderthals have similar proportions of large chips (2.3, 1.9 and 0.9 small chips for every large fracture, respectively). When split into tooth categories, large chips were more frequent on anterior teeth and premolars in *P. robustus*, with molars showing a low rate of larger fractures similar to other species (Table 3).

4. Discussion and conclusions

Chipping prevalence in extant primates links well with dietary and behavioral observations. Hard object-feeding primates have a high prevalence (Towle and Loch, 2021; Fannin et al., 2020). Species considered hard-object feeding specialists are >25%, with the diets of sooty mangabeys, mandrills and sakis containing significant amounts of hard foods (e.g., durophagy; Kinzey and Norconk, 1993; Fleagle and McGraw, 1999; McGraw et al., 2011; Pampush et al., 2013; Fannin et al., 2020; vanCasteren et al., 2020). The overall prevalence in *P. robustus* is far below this threshold (11%). Furthermore, the prevalence in first molars and fourth premolars (for which most data are currently available) shows *P. robustus* with one of the lowest rates.

Based on these results, *P. robustus* experienced significantly fewer crown chips than other hominin species, and several times less than extant primates consuming hard objects (e.g., food items and/or grit). The prevalence in *P. robustus* is similar to species not known to regularly masticate hard items, including several apes, colobines, and guenons. The findings do not corroborate *P. robustus* as a habitual hard-object feeder, at least to the extent of modern durophagous primates such as sakis, mandrills, and sooty mangabeys. Daegling et al. (2013) suggested that the large posterior teeth of Paranthropus may show a greater occurrence of chips due to greater surface area. Crown fractures are also more likely to form on teeth with enamel defects or unusual wear (Soukup, 2019). The pitting enamel hypoplasia present on a large proportion of *P. robustus* molars (Towle and Irish, 2019) suggests they may have been more fracture prone. Thus, durophagy may have been even less frequent than the low chipping rate suggests. The low rate of multiple chips on a single tooth supports this conclusion.

Other factors influence chipping prevalence as well. In humans, chips are generally more common on anterior teeth due to food processing, trauma, or non-masticatory cultural behavior, though frequencies vary substantially among groups (Scott and Winn, 2011; Stojanowski et al., 2015; Bonfiglioli et al., 2004; Gould, 1968; Larsen, 2015; Lous, 1970; Molnar et al., 1972). Grit is also masticated by many primates, and likely influences chipping rates in certain species (e.g., Van Casteren et al., 2019; Fannin et al., 2020; Towle et al., 2017). Both factors are associated with an increase in frequency. Therefore, a low rate of chipping in *P. robustus* likely suggests that trauma related to food consumption and other factors such as grit mastication were rare. This rate is perhaps unexpected since *P. robustus* was likely more terrestrial and inhabited open environments, unlike most of other primates in the sample.

A possible exception is the moderate rate of large fractures on canines and third premolars, which may suggest a modest level of trauma in these regions. A low rate on *P. robustus* incisors suggests a non-masticatory explanation, since large fractures on these teeth would also be expected (Belcastro et al., 2018). Similarly, the size of fractures and the fact that molar and incisors seem relatively unaffected may suggest grit was not the cause of chipping, although further research is needed to test this hypothesis. One possible explanation could be specific masticatory behaviors, such as placing hard foods in these positions for the initial phase of mastication (e.g., breaking seeds or nuts). That said, the small sample size for individual tooth types makes inferences difficult, and the chipping rate is still only moderate relative to other species. Therefore, although it is possible that *P. robustus* did occasionally masticate hard foods, there is little evidence to suggest it was a common practice, and does not seem to have involved their large molars.

Some hominin species, particularly *P. robustus and A. africanus*, were studied previously for chipping prevalence (e.g., Grine et al., 2010; Robinson, 1956; Wallace, 1973; Tobias, 1967; Constantino et al., 2018). Comparisons with these studies are difficult due to methodological differences and the teeth included (e.g., tooth sub-samples studied; inclusion of postmortem damaged teeth) and sample size (e.g., more samples have become available since the earlier studies). Constantino et al. (2018) reported a prevalence of 5% chipping for 557 *P. robustus* teeth. The difference for *P. robustus* in Towle et al. (2017) and Constantino et al. (2018) therefore likely relates to stricter criteria for inclusion in the former study (see above), with both studies recording approximately 30 chipped teeth. If all teeth are included from Towle et al (2017), i.e., including deciduous and postmortem damaged teeth, the prevalence is reduced to 6.97%. Therefore, chipping in *P. robustus* seems consistently low across studies when attempts are made to unify methods. Although a study using the methods described here has not yet been published on a large sample of *P. boisei* teeth, recent results on chipping in this group suggests lower rates than *P. robustus* (Constantino et al., 2018; Constantino and Lawn, 2019). Thus, *Paranthropus* as a whole may be characterized by infrequent chipping.

It has been suggested that *Paranthropus* preferred soft or tough foods, but relied on harder 'fallback foods' (Constantino and Wright, 2009; Ungar et al., 2008). This hypothesis suggests they evolved large teeth and robust cranial structures to cope with dietary items that were rarely consumed. Extant primate chipping patterns may offer some insight. Species that evolved specialized dental characteristics for softer foods can still occasionally eat hard foods (e.g., van Casteren et al., 2019). Additionally, a primate that feeds occasionally on hard objects (e.g., seasonal or fallback foods) can evidence elevated chipping frequencies. To illustrate, while the diet of brown woolly monkeys is primarily based on soft fruits, at certain times of the year they consume seeds and hard fruits (Peres, 1994; Defler and Defler, 1996); this shift could explain their relatively high chipping prevalence, although further research is needed into the mechanical properties of these foods.

The orientation of the hard object and underlying enamel microstructure is crucial in chip formation, as are the size and shape of the tooth, the object, and resultant biomechanical forces (Xu et al., 1998; Lucas et al., 2008; Chai and Lawn, 2007). As such, species-specific enamel attributes (e.g., thickness and mechanical properties) likely evolved for functional reasons (Cuy et al., 2002; but see Constantino et al., 2012 who found relatively uniform mechanical properties among extant primates); species that regularly eat hard foods likely evolved dental characteristics in response to high biomechanical demands (Ungar and Lucas, 2010). It has been suggested that thick enamel may have evolved in some hominins, including *Paranthropus*, to delay fracture-related tooth loss (Kay, 1981; Lucas et al., 2008). Although chipping cannot conclusively be used to infer whether thick enamel evolved to counter attrition or fracture, it seems chipping should not be used to support the hypothesis that thick enamel evolved to protect against fracture in *Paranthropus*. This is especially the case since molars are often the focus of such research, and in *P. robustus* a low chipping prevalence is evident in these teeth.

Other enamel characteristics also need to be considered with microstructure (e.g., Hunter-Schreger band thickness and enamel prism density) and overall tooth morphology as potential contributors to reducing fracture or limiting chip size (Constantino et al., 2009). Further comparative studies can elucidate the functional and evolutionary implications of enamel structure in *Paranthropus*. The present study suggests that dental chipping in hominins most commonly regarded as hard-food eaters, *P. robustus*, was rare relative to other hominins and extant durophagous primates. The ability of such enamel chips to deduce selective pressures influencing the unique craniofacial morphology of *Paranthropus* remains opaque. Additionally, differences in tooth properties among species, and how they influence fracture likelihood, need to be more adequately explored (Constantino et al., 2012, Cuy et al., 2002, and Darnell et al., 2010). Future work is needed to determine the causal factors for the low chipping frequency in *Paranthropus*. However, based on extant primate comparisons, chipping should not be used as evidence that *P. robustus* regularly masticated hard foods.

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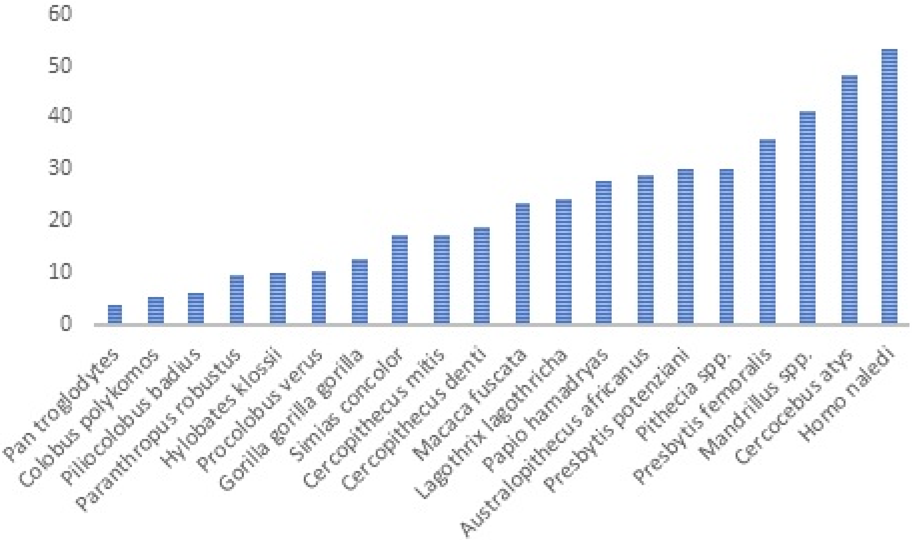
Figure legend

Figure 1. Chipping prevalence for first molars and fourth premolars for different extant primate and fossil hominin species. Species are organized by increasing chipping prevalence.


60
50
40
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Pan troglodytes
Colobus polykomos
Piliocolobus badius
Paranthropus robustus
Hylobates klossi
Procolobus verus
Gorilla gorilla gorilla
Simias concolor
Cercopithecus mitis
Cercopithecus denti
Macaca fuscata
Lagothrix lagothricha
Papio hamadryas
Australopithecus africanus
Presbytis potenziani
Pithecia spp.
Presbytis femoralis
Mandrillus spp.
Cercocebus atys
Homo naledi

Table 1

Prevalence of chipping in different primate species, by tooth type, jaw, and size of chips. Data refers to all permanent teeth unless stated.

Species	Common name	Number of individuals	Posterior teeth	Anterior teeth	All teeth %	Multiple chipped teeth %	Small:large chip ratio	Reference
Homo naledi			46.39 (45/97)	20.75 (11/53)	37.33 (56/150)	50.00	8.33	Towle et al. (2017)
Australopithecus africanus			20.16 (50/248)	7.32 (6/82)	16.97 (56/330)	16.07	10.20	Towle et al. (2017)
Paranthropus robustus			10.90 (23/211)	11.86 (7/59)	11.11 (30/270)	6.67	1.73	Towle et al. (2017)
Homo neanderthalensis	Neanderthals		31.53 (35/111)	64.86 (48/74)	44.86 (83/185)	9.00	0.90	Belcastro et al. (2018)
Gorilla gorilla gorilla	Western lowland gorilla	83	11.70 (137/1171)	5.25 (32/610)	9.49 (169/1781)	4.14	10.27	Towle et al. (2017)
Pan troglodytes	Chimpanzee	109	4.52 (65/1439)	4.13 (33/800)	4.38(98/2239)	2.04	2.27	Towle et al. (2017)
Cercopithecus denti	Dent's mona monkey	10	16.11 (29/180)	27.06 (23/85)	19.62 (52/265)	1.92	5.50	Towle and Loch (2021)
Cercopithecus mitis	Blue monkey	8	18.13 (29/160)	9.76 (8/82)	15.29 (37/242)	13.51	6.40	Towle and Loch (2021)
Mandrillus spp.	Mandrill	10	36.11 (39/108)	40.00 (8/20)	36.72 (47/128)	23.40	6.83	Towle and Loch (2021)
Presbytis femoralis	Raffles' banded langur	8	31.88 (51/160)	40.24 (33/82)	34.71 (84/242)	11.90	4.60	Towle and Loch (2021)
Presbytis potenziani	Mentawai langur	8	20.25 (32/158)	17.39 (12/69)	19.38 (44/227)	11.36	43.00	Towle and Loch (2021)
Hylobates klossii	Kloss's gibbon	15	5.60 (13/232)	11.90 (10/84)	7.28 (23/316)	0.00	1.88	Towle and Loch (2021)
Macaca fuscata	Japanese macaque	48	24.68 (171/693)	15.33 (44/287)	21.94 (215/980)	12.56	5.76	Towle and Loch (2021)
Simias concolor	Pig-tailed langur	20	16.61 (46/277)	19.70 (26/132)	17.60 (72/409)	12.50	7.00	Towle and Loch (2021)
Lagothrix lagothricha	Brown woolly monkey	7	21.79 (34/156)	11.27 (8/71)	18.50 (42/227)	0.00	7.40	Towle and Loch (2021)
Pithecia spp.	Saki	8	35.09 (60/171)	11.59 (8/69)	28.33 (68/240)	23.53	5.80	Towle and Loch (2021)
Papio hamadryas	Hamadryas baboon	20	26.49 (89/336)	9.89 (18/182)	20.66 (107/518)	8.41	7.23	Towle and Loch (2021)

Table 2

Prevalence of chipping (%) in different primate species, split by individual permanent tooth types. I: incisor; C: canine; PM: premolar; M: molar.

Species	Common name	I1	I2	C	PM3	PM4	M1	M2	M3
Homo naledi		40 (6/15)	12.5 (2/16)	13.64 (3/22)	42.11 (8/19)	42.11 (8/19)	60.71 (17/28)	36.84 (7/19)	41.67 (5/12)
Australopithecus africanus		17.39 (4/23)	4.35 (1/23)	2.78 (1/36)	18.60 (8/43)	32.43 (12/37)	29.53 (13/49)	17.91 (12/67)	9.62 (5/52)
Paranthropus robustus		9.38 (3/32)	7.69 (1/13)	21.43 (3/14)	23.33 (7/30)	4.65 (2/43)	13.46 (7/52)	4.65 (2/43)	11.63 (5/43)
Gorilla gorilla gorilla	Western lowland gorilla	4.05 (9/222)	5.12 (11/215)	6.94 (12/173)	3.76 (8/213)	9.26 (20/216)	15.22 (44/289)	10.89 (28/257)	18.88 (37/196)
Pan troglodytes	Chimpanzee	2.79 (8/287)	4.06 (11/271)	5.79 (14/242)	2.22 (6/270)	1.87 (5/268)	5.18 (20/386)	3.46 (10/289)	10.62 (24/226)
Cercopithecus denti	Dent's mona monkey	38.71 (12/31)	34.62 (9/26)	7.14 (2/28)	8.57 (3/35)	10.81 (4/37)	26.32 (10/38)	15.79 (6/38)	18.75 (6/32)
Cercopithecus mitis	Blue monkey	17.86 (5/28)	4 (1/25)	6.90 (2/29)	3.13 (1/32)	15.63 (5/32)	18.75 (6/32)	25 (8/32)	28.13 (9/32)
Mandrillus spp.	Mandrill	55.56 (5/9)	50 (3/6)	0 (0/5)	13.64 (3/22)	33.33 (7/21)	50 (10/20)	50 (11/22)	34.78 (8/23)
Presbytis femoralis	Raffles' banded langur	52.17 (12/23)	46.15 (12/26)	34.48 (10/29)	18.75 (6/32)	31.25 (10/32)	40.63 (13/32)	31.25 (10/32)	37.5 (12/32)
Presbytis potenziani	Mentawai langur	18.18 (4/22)	22.22 (6/27)	10 (2/20)	6.45 (2/31)	31.25 (10/32)	29.03 (9/31)	31.25 (10/32)	3.13 (1/32)
Hylobates klossii	Kloss's gibbon	2.78 (1/36)	12.5 (4/32)	31.25 (5/16)	4.26 (2/47)	6.52 (3/46)	13.33 (6/45)	3.85 (2/52)	0 (0/42)
Macaca fuscata	Japanese macaque	22.62 (19/84)	16.28 (14/86)	9.40 (11/117)	17.91 (24/134)	18.66 (25/134)	27.92 (43/154)	25.17 (36/143)	33.59 (43/128)
Simias concolor	Pig-tailed langur	29.79 (14/47)	13.33 (6/45)	15 (6/40)	8.62 (5/58)	10.53 (6/57)	24.07 (13/54)	28.07 (16/57)	11.76 (6/51)
Lagothrix lagothricha	Brown woolly monkey	10.53 (2/19)	11.11 (3/27)	15.79 (3/19)	15.38 (4/26)	25.93 (7/27)	22.22 (4/18)	22.22 (6/27)	33.33 (6/18)
Pithecia spp.	Saki	13.33 (2/15)	16.67 (4/24)	8.70 (2/23)	26.67 (8/30)	24.14 (7/29)	37.5 (9/24)	44.44 (12/27)	50 (13/26)
Papio hamadryas	Hamadryas baboon	8.47 (5/59)	9.68 (6/62)	11.48 (7/61)	15.87 (10/63)	17.65 (12/68)	37.5 (27/72)	37.68 (26/69)	21.88 (14/64)

Table 3

Prevalence of large chips, split by tooth type. Number of large chips (severity 2 and 3) as a percentage of total chips.

Species	Common name	Molars	Premolars	Canines	Incisors
Paranthropus robustus		14.29 (2/14)	44.44 (4/9)	100 (3/3)	50 (2/4)
Homo naledi		17.24 (5/29)	6.25 (1/16)	0 (0/3)	0 (0/8)
Australopithecus africanus		6.67 (2/30)	10 (2/20)	100 (1/1)	0 (0/5)
Gorilla gorilla gorilla	Western lowland gorilla	7.34 (8/109)	10.71 (3/28)	0 (0/12)	20 (4/20)
Chimpanzees	Chimpanzee	35.19 (19/54)	27.27 (3/11)	42.86 (6/14)	10.53 (2/19)
Cercopithecus denti	Dent's mona monkey	22.73 (5/22)	0 (0/7)	0 (0/2)	14.29 (3/21)
Cercopithecus mitis	Blue monkey	8.70 (2/23)	33.33 (2/6)	0 (0/2)	16.67 (1/6)
Mandrillus spp.	Mandrill	17.24 (5/29)	10 (1/10)	n/a (0/0)	0 (0/8)
Presbytis femoralis	Raffles' banded langur	8.57 (3/35)	37.5 (6/16)	30 (3/10)	12.5 (3/24)
Presbytis potenziani	Mentawai langur	5 (1/20)	0 (0/12)	0 (0/2)	0 (0/10)
Hylobates klossii	Kloss's gibbon	50 (4/8)	20 (1/5)	40 (2/5)	20 (1/5)
Macaca fuscata	Japanese macaque	22.13 (27/122)	2.04 (1/49)	18.18 (2/11)	3.03 (1/33)
Simias concolor	Pig-tailed langur	11.43 (4/35)	9.09 (1/11)	0 (0/6)	20 (4/20)
Lagothrix lagothricha	Brown woolly monkey	18.75 (3/16)	0 (0/11)	33.33 (1/3)	0 (0/5)
Pithecia spp.	Saki	8.82 (3/34)	26.67 (4/15)	0 (0/2)	0 (0/6)
Papio hamadryas	Hamadryas baboon	11.94 (8/67)	9.09 (2/22)	14.29 (1/7)	18.18 (2/11)