Tooth chipping patterns in *Paranthropus* do not support regular hard food mastication

Ian Towle[1], Joel D. Irish[2,3], Luke D. Fannin[4,5], Carolina Loch[1]

[1]Sir John Walsh Research Institute, Faculty of Dentistry, University of Otago, Dunedin 9054, New Zealand

[2] Research Centre in Evolutionary Anthropology and Palaeoecology, School of Biological and Environmental Sciences, Liverpool John Moores University, United Kingdom, L3 3AF

[3]Evolutionary Studies Institute and Centre for Excellence in PaleoSciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa

[4]Department of Anthropology, Dartmouth College, 3 Tuck Drive Hanover, NH 03755, USA

[5]Graduate Program in Ecology, Evolution, Environment, and Society, Dartmouth College, Hanover, NH 03755, USA

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Abstract

The paranthropines, including *Paranthropus boisei* and *Paranthropus robustus*, have often been considered hard-food specialists. The large post-canine teeth, thick enamel, and robust craniofacial features are often suggested to have evolved to cope with habitual mastication of hard foods. Yet, direct evidence for *Paranthropus* feeding behaviour often challenges these morphological interpretations. The main exception being antemortem tooth chipping which is still regularly used as evidence of habitual mastication of hard foods in this genus. In this study, data were compiled from the literature for six hominin species (including *P. boisei* and *P. robustus*) and 17 extant primate species, to analyse *Paranthropus* chipping patterns in a broad comparative framework. Severity of fractures, position on the dentition, and overall prevalence were compared among species. The results indicate that both *Paranthropus* species had a lower prevalence of tooth fractures compared to other fossil hominin species *(P. boisei*: 4%; *P. robustus*: 11%; *Homo naledi:* 37%; *Australopithecus africanus:* 17%; *Homo neanderthalensis:* 45%; Epipalaeolithic *Homo sapiens*: 29%); instead, their frequencies are similar to apes that masticate hard items in a non-regular frequency, including chimpanzees, gibbons, and gorillas (4%, 7% and 9% respectively). The prevalence is several times lower than in extant primates known to habitually consume hard items, such as sakis, mandrills, and sooty mangabeys (ranging from 28% to 48%). Comparative chipping analysis suggests that both *Paranthropus* species were unlikely habitual hard object eaters, at least compared to living durophage analogues.

Key words: Enamel fractures; *Paranthropus robustus*; *Paranthropus boisei*; tooth chipping

Introduction

When a tooth contacts a hard object with enough force, the enamel can break and fracture to create a chip (Chai & 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 & Swain, 2008; Lawn, Lee, Constantino, & Lucas, 2009; Scott & 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, & Lucas, 2012).

Enamel chips can be caused by a variety of factors, including food processing, environmental contaminants, specific dietary items and social behavior (Constantino et al., 2012; Sauther, Sussman, & Cuozzo, 2002; Scott & Winn, 2011; Stojanowski, Johnson, Paul, & Carver2015; Van Valkenburgh, 2009). These different influences can generate unique chipping 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 & Winn, 2011; Nystrom, Phillips-Conroy, & Jolly, 2004; Towle et al., 2017). A range of recent human populations, fossil hominins and extant primate samples 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, & da Silva, 2016; Turner & Cadien, 1969; Constantino et al., 2010; Grine et al., 2010; Robinson, 1954; Tobias, 1967; Johanson & Taieb, 1976; Ward et al., 2001; Fox & Frayer, 1997; Scott & Winn, 2011; Stojanowski et al., 2015; Larsen, 2015; Lous, 1970; Molnar et al., 1972; Fannin et al., 2020). While differences in recording methods make inter-study comparisons challenging, chipping may provide additional insight into patterns of primate diet alongside other analytical methods, such as microwear and stable isotopes (Strait et al., 2013).

In particular, enamel chipping may provide critical insights into the feeding habits of enigmatic hominins, such as the "robust australopith" clade, e.g., *Paranthropus boisei* and *Paranthropus 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 & Strait, 2004). Additionally, there is often an apparent disconnect between diet and cranio-dental 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 graminoid tissues (e.g., grasses and sedges) were likely a common food sources (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 dental anthropologists now regard *Paranthropus* as non-hard food eaters (Ungar and Hlusko, 2016; Grine and Daegling, 2017; Kaiser et al., 2019), while others consider them dietary generalists (e.g., eurytopy; Wood & Strait, 2004; Strait et al., 2013).

Nonetheless, some researchers maintain that hard foods were commonly consumed in *Paranthropus,* or particular species (usually *P. robustus*), and/or played a significant role in cranio-dental 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). Earlier work suggested that ingestion of grit or bones may instead be responsible for the chipping in this genus (Robinson, 1954; Tobias, 1967).

Despite being crucial in elucidating the evolution and diet of *Paranthropus*, a broad comparison of chipping patterns in both *Paranthropus* species relative to other hominins and extant primates is still lacking. For example, Paine et al. (2019, Page 104) stated that *P. robustus* had a "significant degree of hard object feeding," with Towle et al. (2017) cited to support this claim. In reality, 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). Therefore, chipping is often considered evidence of regular hard food consumption, but without comparisons with extant primates these conclusions cannot be justified. All primate species studied show chipping (Towle and Loch, 2021; Fannin et al., 2020), from dietary items as well as accidents and unintentional ingestion of hard objects. The evaluation of chipping patterns in extant primates with associated ecological data allows an understanding of chipping relative to diet and behavior. In this study, we compared chipping patterns in a range of extant primates and fossil hominins, to test whether the prevalence and patterning in *Paranthropus* support habitual, or occasional, durophagy.

Materials and Methods

Data were compiled from the recent literature. Hominin samples include specimens assigned to *H. naledi*, *A. africanus*, *P. robustus*, *P. boisei*, *H., neanderthalensis* and *H. sapiens* (following Towle et al., 2017; Constantino et al., 2018; Constantino and Lawn, 2019; Bonfiglioli et al., 2004; Belcastro et al., 2018). Extant primates include chimpanzees (*Pan troglodytes troglodytes*), Western lowland gorillas (*Gorilla gorilla gorilla*), Kloss's gibbons (*Hylobates klossii*), hamadryas baboons (*Papio hamadryas*), pig-tailed langurs (*Simias concolor*), Japanese macaques (*Macaca fuscata*), Dent's mona monkey (*Cercopithecus denti*), blue monkeys (*Cercopithecus mitis*), mandrills (*Mandrillus leucophaeus* and *Mandrillus sphinx*), Raffles' banded langurs (*Presbytis femoralis*), Mentawai langurs (*Presbytis potenziani*), brown woolly monkeys (*Lagothrix lagothricha*), Sakis (*Pithecia* sp.), sooty mangabeys (*Cercocebus atys*), olive colobus monkeys (*Procolobus verus*), Western red colobus (*Piliocolobus badius*) and king colobus (*Colobus polykomos*) (following Towle and

Loch, 2021; Towle et al., 2017; Fannin et al., 2020). In these studies, data collection methods were standardized, with only minor variations in techniques observed. A summary of methods is given below. Some hominin species, particularly *P. robustus and A. africanus*, have been studied on several occasions with regard to chipping prevalence (e.g., Grine et al., 2010; Robinson, 1956; Wallace, 1973; Tobias, 1967). Here, data from Towle et al. (2017) are used for these species, but with different criteria for tooth inclusion to match other studies. Specifically, teeth with minimal wear were removed for chipping prevalence in Towle et al., (2017) but are included in the present study, resulting in slightly different frequencies.

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 total number of chips on each tooth was also recorded for some samples (Belcastro et al., 2018; Towle et al., 2017; Towle and Loch, 2021). Results refer to all permanent teeth, unless stated otherwise.

Fractures were recorded on a three-point grading system following either Bonfiglioli et al. (2004) or Towle and Loch (2021), the latter with slight modifications that remove direct measurements to allow a broader range of comparisons among primates:

(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.
(2) Larger chip that extends near to the enamel-dentine junction. A small area of dentine might be exposed.
(3) Large irregular fracture in which a significant area of dentine is exposed. More dentine than enamel was removed by the fracture.

Results

Prevalence and overall patterns for each species are summarized in Table 1. Hominins cover the range of prevalence observed in extant primates, with chipping common in *Homo* (37-45% of teeth) and rare in *Paranthropus* (4-11% of teeth). *Australopithecus africanus* falls between these two extremes with 17% of teeth displaying at least one fracture. The chipping prevalence in *Paranthropus* is similar to such extant species as chimpanzees,

gibbons, gorillas, olive colobus, Western red colobus, and king colobus (4-10% of teeth; Table 1). The rate in extant primates considered hard-food specialists (e.g., sakis, mandrills and sooty mangabeys - 28-48% of teeth) is several times greater than in both *Paranthropus* species (*P. boisei*, 4.4%; *P. robustus*, 11.1%; Figure 1). Additionally, species that occasionally masticate hard foods, either seasonally or as fallback foods, show intermediate rates, though still higher than either *Paranthropus* species (e.g., brown woolly monkeys: 19%; Dent's mona monkey: 20%).

The chipping pattern varied among species, with either posterior or anterior teeth affected to a higher degree in certain groups, likely reflecting food processing differences. Smaller chips are common on interproximal surfaces of *H. naledi*, and to a lesser extent in other hominin species. In *H. naledi* the posterior teeth are mainly affected, whereas in Neanderthals anterior teeth exhibit more chips. In *Australopithecus*, the posterior teeth are most affected, with premolars particularly prone to fracture (25%). All *P. robustus* tooth types show consistently low chipping rates, except for canines with a moderate prevalence (21%) compared to premolars (12%), molars (10%), and incisors (9%). Few *P. robustus* teeth exhibit multiple chips (6.7% of chipped teeth have more than one fracture). *Paranthropus robustus* also shows a high ratio of larger chips relative to most other species (1.7 small chip for every large fracture), with only chimpanzees, gibbons and Neanderthals having similar proportions of large chips (2.3, 1.9 and 0.9 small for every large fracture, respectively).

Table 1. Prevalence of chipping in different primate species, by tooth type, jaw, and size of chips. Data refers to permanent teeth unless stated.

Species	Common name	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)
Paranthropus boisei[1]				4.4*	-		Constantino & Lawn (2019)
Homo neanderthalensis	Neanderthals	31.53 (35/111)	64.86 (48/74)	44.86 (83/185)	9.00	0.90	Belcastro et al. (2018)
Homo sapiens	Humans	32.8*	21.1*	29.25 (167/571)	-		Bonfiglioli et al. (2004)
Gorilla gorilla gorilla	Western lowland gorilla	11.70 (137/1171)	5.25 (32/610)	9.49 (169/1781)	4.14	10.27	Towle et al. (2017)
Pan troglodytes	Chimpanzee	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	16.11 (29/180)	27.06 (23/85)	19.62 (52/265)	1.92	5.50	Towle and Loch (2021)
Cercopithecus mitis	Blue monkey	18.13 (29/160)	9.76 (8/82)	15.29 (37/242)	13.51	6.40	Towle and Loch (2021)
Mandrillus spp.	Mandrill	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	31.88 (51/160)	40.24 (33/82)	34.71 (84/242)	11.90	4.60	Towle and Loch (2021)
Presbytis potenziani	Mentawai langur	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	5.60 (13/232)	11.90 (10/84)	7.28 (23/316)	0.00	1.88	Towle and Loch (2021)
Macaca fuscata	Japanese macaque	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	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	21.79 (34/156)	11.27 (8/71)	18.50 (42/227)	0.00	7.40	Towle and Loch (2021)
Pithecia spp.	Saki	35.09 (60/171)	11.59 (8/69)	28.33 (68/240)	23.53	5.80	Towle and Loch (2021)
Papio hamadryas	Hamadryas baboon	26.49 (89/336)	9.89 (18/182)	20.66 (107/518)	8.41	7.23	Towle and Loch (2021)
Cercocebus atys[2]	Sooty mangabey	48.40 (59/122)					Fannin et al. (2020)
Procolobus verus[2]	Olive colobus monkey	10.34 (3/29)					Fannin et al. (2020)
Piliocolobus badius[2]	Western red colobus	6.22 (25/402)					Fannin et al. (2020)
Colobus polykomos[2]	King colobus	5.15 (6/116)					Fannin et al. (2020)

[1]Includes deciduous teeth; [2]Only includes P4's and M1's; *sample size not provided

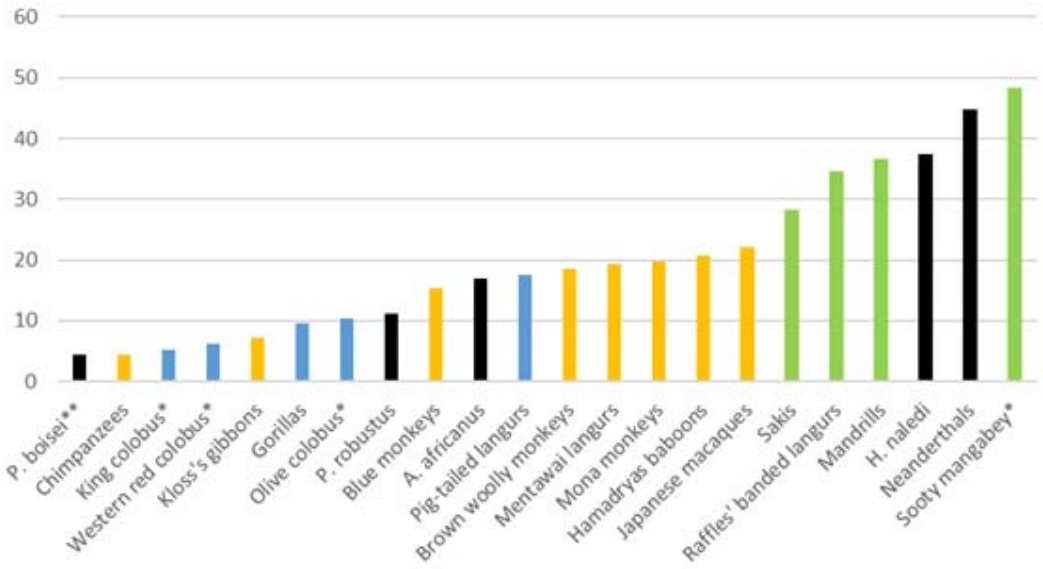

Figure 1. Chipping prevalence (%) for all permanent teeth split by broad diet category. Blue = folivores; Yellow = frugivores; Green = hard object specialists (diet categories from DeCasien et al., 2017; Scott et al., 2018; Davies and Bennett, 1988). Black = hominins.

*Only includes P4s and M1s.

**Includes deciduous teeth.

Discussion

Chipping prevalence in extant primates links well with dietary and behavior observations. Hard object-feeding primates have a high chipping prevalence (Towle and Loch, 2021). Extant apes, gorillas, gibbons and chimpanzees have relatively low frequencies of chipping, especially compared to orangutans (Constantino et al., 2012; Towle et al. 2021), likely due to orangutans' proclivity for large seeds and nuts (Galdikas, 1982; Vogel et al., 2008; Lucas et al., 2012). Species considered to be hard object feeding specialists have a chipping prevalence >25%, with diets of sooty mangabeys, mandrills, sakis and Raffles' banded langur containing significant amounts of hard foods (e.g., durophagy; Kinzey & Norconk, 1993; Fleagle & McGraw, 1999; McGraw et al., 2011; Pampush et al., 2013; Fannin et al., 2020; vanCasteren et al., 2020; Davies and Bennett, 1988).

There are other factors that influence chipping prevalence in certain species. In humans, fractures are generally more common on anterior teeth due to food processing, trauma, or non-masticatory cultural behavior (Scott & Winn, 2011; Stojanowski et al., 2015; Bonfiglioli et al., 2004; Gould, 1968; Larsen, 2015; Lous, 1970; Molnar et al., 1972). In *H. neanderthalensis*, the high rate of fractures is thought to be caused by non-masticatory activities, but in *H. naledi* it likely relates to ingesting environmental contaminants, such as grit (Fiorenza & Kullmer, 2013; Fox & Frayer, 1997; Towle et al., 2017). Grit is also masticated by many extant primates, and likely influences chipping rates in certain species (e.g., Van Casteren et al., 2019; Fannin et al., 2020).

Based on these results, the current study indicates that both *Paranthropus* species experienced significantly fewer crown chipping than other hominin species, and several times less than extant primates known to regularly masticate hard objects (food items and/or grit). The chipping prevalence of *Paranthropus* was similar to species that rarely masticate hard items, including several groups of apes, colobines, and guenons. The findings do not corroborate that either *Paranthropus* species were habitual hard-object feeders, 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* showed a greater prevalence 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 *Paranthropus* 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 in both *Paranthropus* species suggests.

Constantino et al. (2018) reported a chipping rate of 5% for *P. robustus*, which is similar to a more recent finding by some of the same authors of 4.4% of teeth in *P. boisei* (Constantino & Lawn, 2019). The difference in prevalence for *P. robustus* in Towle et al. (2017) compared to Constantino et al. (2018) likely relates to stricter criteria for inclusion in the former study (i.e., deciduous and postmortem damaged teeth were removed from analysis), with both studies recording approximately 30 chipped teeth. Unfortunately, it is not stated which specimens were studied in Constantino et al. (2018), making direct comparisons difficult. Therefore, the actual prevalence between the *Paranthropus* species is likely similar.

It has been suggested that *Paranthropus* preferred soft or tough foods, but relied on certain harder variants as 'fallback foods' (Constantino and Wright, 2009; Ungar et al., 2008). This hypothesis suggests *Paranthropus* evolved large teeth and robust cranial structures to cope with dietary items that were rarely consumed, but required requisite adaptations. This hypothesis has been challenged, with other scenarios favored (Daegling et al., 2013; Scott et al., 2014). 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, an occasional hard object-feeding primate (seasonal or as fallback foods) can show elevated chipping frequencies. For example, while the diet of brown woolly monkeys is primarily soft fruits, at certain times of the year they consume seeds and hard fruits (Peres, 1994; Defler and Defler, 1996), which could explain their relatively high chipping prevalence.

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 & Lawn, 2007). As such, species-specific enamel attributes (e.g., thickness and mechanical properties) likely evolved for functional reasons (Cuy et al., 2002); species that regularly eat hard foods likely evolved dental characteristics in response (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). Thick enamel likely does add protection, but the low fracture prevalence in both *Paranthropus* species may suggest fractures were not the evolutionary force behind this change. Instead, it may be that the genus evolved large thickly enameled posterior teeth as a response to dental wear.

Other enamel characteristics also need to be considered with microstructure (e.g., Hunter-Schreger band thickness and prism density) and overall tooth morphology potentially contributing to reduce fracture or limit 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 *Paranthropus* was rare relative to other hominins and extant durophagous primates. The ability of such enamel chips to deduce the selective pressures influencing the paranthropines' unique craniofacial hypodigm remains opaque, since the identify of any one

chip as a response to hard foods remains difficult to disentangle from variation in habitat use patterns. Additionally, differences in tooth properties among species, and how these differences influence fracture likelihood, need to be more adequately explored. Future work is needed to determine the causal factors for the few chips that exist in the paranthropine dentition. However, based on extant primate comparisons, at present, these chips should not be used as evidence to suggest *Paranthropus* species regularly masticated hard foods.

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References

Belcastro, M. G., Mariotti, V., Riga, A., Bonfiglioli, B., & Frayer, D. W. (2018). Tooth fractures in the Krapina Neandertals. *Journal of Human Evolution*, *123*, 96-108.

Beynon, A. D., & Wood, B. A. (1986). Variations in enamel thickness and structure in East African hominids. *American Journal of Physical Anthropology*, *70*(2), 177-193.

Cerling, T. E., Mbua, E., Kirera, F. M., Manthi, F. K., Grine, F. E., Leakey, M. G., ... & Uno, K. T. (2011). Diet of Paranthropus boisei in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences*, *108*(23), 9337-9341.

Cofran, Z. (2014). Mandibular development in *Australopithecus robustus*. *American Journal of Physical Anthropology*, 154(3), 436-446.

Constantino, P. J., & Lawn, B. R. (2019, March). Dental Fracture Mechanics: What broken teeth can reveal about diet and feeding behavior. In *American Journal of Physical Anthropology* (Vol. 168, pp. 47-48). Hoboken, Wiley.

Constantino, P. J., & Wright, B. W. (2009). The importance of fallback foods in primate ecology and evolution. *American Journal of Physical Anthropology*, 140(4), 599-602.

Constantino, P. J., Borrero-Lopez, O., & Lawn, B. R. (2018). Mechanisms of tooth damage and Paranthropus dietary reconstruction. *Biosurface and Biotribology*, *4*(3), 73-78.

Constantino, P. J., Lucas, P. W., Lee, J. J. W., & Lawn, B. R. (2009). The influence of fallback foods on great ape tooth enamel. *American Journal of Physical Anthropology*, 140(4), 653-660.

Daegling, D. J., Judex, S., Ozcivici, E., Ravosa, M. J., Taylor, A. B., Grine, F. E., ... & Ungar, P. S. (2013). Viewpoints: feeding mechanics, diet, and dietary adaptations in early hominins. *American Journal of Physical Anthropology*, 151(3), 356-371.

Defler, T. R., & Defler, S. B. (1996). Diet of a group of *Lagothrix Lagothricha Lagothricha* in southeastern Colombia. *International Journal of Primatology*, 17(2), 161-190.

Dominy, N. J., Vogel, E. R., Yeakel, J. D., Constantino, P., & Lucas, P. W. (2008). Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evolutionary Biology*, 35(3), 159-175.

Dominy, N. J. (2012). Hominins living on the sedge. *Proceedings of the National Academy of Sciences*, 109.50 (2012): 20171-20172.

Fannin, L. D., Guatelli-Steinberg, D., Geissler, E., Morse, P. E., Constantino, P. J., & McGraw, W. S. (2020). Enamel chipping in Taï Forest cercopithecids: Implications for diet reconstruction in paleoanthropological contexts. *Journal of Human Evolution*, *141*, 102742.

Fleagle, J. G., & McGraw, W. S. (1999). Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. *Proceedings of the National Academy of Sciences*, *96*(3), 1157-1161.

Gao, S. S., An, B. B., Yahyazadehfar, M., Zhang, D., & Arola, D. D. (2016). Contact fatigue of human enamel: Experiments, mechanisms and modeling. *Journal of The Mechanical Behavior of Biomedical Materials*, 60, 438-450.

Grine, F. E., & Daegling, D. J. (2017). Functional morphology, biomechanics and the retrodiction of early hominin diets. *Comptes Rendus Palevol*, 16(5-6), 613-631.

Grine, F. E., Ungar, P. S., Teaford, M. F., & El-Zaatari, S. (2006). Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *Journal of Human Evolution*, 51(3), 297-319.

Grine, F. E., Judex, S., Daegling, D. J., Ozcivici, E., Ungar, P. S., Teaford, M. F., ... & Walker, A. (2010). Craniofacial biomechanics and functional and dietary inferences in hominin paleontology. *Journal of Human Evolution*, 58(4), 293-308.

Guatelli-Steinberg, D. (2016). What teeth reveal about human evolution. Cambridge, Cambridge University Press.

Jolly, C. J. (1970). The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man*, 5(1), 5-26

Kaiser, T. M., Marce-Nogue, J., Puschel, T. A., & Daasch, A. (2019, March). Morpho-functional traits of the mandible suggest no hard food adaptation in the hominin lineage. In *American Journal of Physical Anthropology*, 168, 118-118.

Kinzey, W. G., & Norconk, M. A. (1993). Physical and chemical properties of fruit and seeds eaten byPithecia andChiropotes in Surinam and Venezuela. *International Journal of Primatology*, *14*(2), 207-227.

Laden, G., & Wrangham, R. (2005). The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. *Journal of Human Evolution*, 49(4), 482-498.

Lucas, P. W., Gaskins, J. T., Lowrey, T. K., Harrison, M. E., Morrogh-Bernard, H. C., Cheyne, S. M., & Begley, M. R. (2012). Evolutionary optimization of material properties of a tropical seed. *Journal of the Royal Society Interface*, 9(66), 34-42.

Macho, G. A., & Shimizu, D. (2009). Dietary adaptations of South African australopiths: inference from enamel prism attitude. *Journal of Human Evolution*, 57(3), 241-247.

Macho, G. A. (2014). Baboon feeding ecology informs the dietary niche of Paranthropus boisei. PLoS One, 9(1), e84942.

Marcé-Nogué, J., Püschel, T.A., Daasch, A., Kaiser, T.M. (2020). Broad-scale morpho-functional traits of the mandible suggest no hard food adaptation in the hominin lineage. *Sci Rep*, 10, 6793. https://doi.org/10.1038/s41598-020-63739-5

Martínez, L. M., Estebaranz-Sánchez, F., Galbany, J., & Pérez-Pérez, A. (2016). Testing dietary hypotheses of East African hominines using buccal dental microwear data. *PloS one*, 11(11), e0165447.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (2011). Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, *144*(1), 140-153.

Nystrom, P., Phillips-Conroy, J. E., & Jolly, C. J. (2004). Dental microwear in anubis and hybrid baboons (*Papio hamadryas*, sensu lato) living in Awash National Park, Ethiopia. *American Journal of Physical Anthropology*, 125(3), 279-291.

Paine, O. C., Koppa, A., Henry, A. G., Leichliter, J. N., Codron, D., Codron, J., ... & Sponheimer, M. (2019). Seasonal and habitat effects on the nutritional properties of savanna vegetation: Potential implications for early hominin dietary ecology. *Journal of Human Evolution*, *133*, 99-107.

Peres, C. A. (1994). Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagotricha cana*) in central Amazonia: comparisons with other atelines. *International Journal of Primatology*, 15(3), 333-372.

Peterson, A., Abella, E. F., Grine, F. E., Teaford, M. F., & Ungar, P. S. (2018). Microwear textures of *Australopithecus africanus* and *Paranthropus robustus* molars in relation to paleoenvironment and diet. *Journal of Human Evolution*, 119, 42-63.

Rabenold, D., & Pearson, O. M. (2011). Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. *PLoS One*, 6(12), e28379.

Rak Y. 1983. The australopithecine face. New York, Academic Press.

Richmond, B. G., Green, D. J., Lague, M. R., Chirchir, H., Behrensmeyer, A. K., Bobe, R., ... & Merritt, S. R. (2020). The upper limb of Paranthropus boisei from Ileret, Kenya. *Journal of Human Evolution*, 141, 102727.

Robinson, J.T., (1956). The Dentition of the Australopithecinae. Transvaal MuseumMemoir, 9. Transvaal Museum, Pretoria

Rosenberger, A. L., & Strier, K. B. (1989). Adaptive radiation of the ateline primates. *Journal of Human Evolution*, 18(7), 717-750.

Sanchez-Gonzalez, E., Pinilla-Cienfuegos, E., Borrero-Lopez, O., Rodríguez-Rojas, F., & Guiberteau, F. (2020). Contact damage of human dental enamel under cyclic axial loading with abrasive particles. *Journal of the Mechanical Behavior of Biomedical Materials*, *102*, 103512.

Scott, J. E., Campbell, R. M., Baj, L. M., Burns, M. C., Price, M. S., Sykes, J. D., & Vinyard, C. J. (2018). Dietary signals in the premolar dentition of primates. *Journal of Human Evolution*, *121*, 221-234.

Scott, J. E., McAbee, K. R., Eastman, M. M., & Ravosa, M. J. (2014). Experimental perspective on fallback foods and dietary adaptations in early hominins. *Biology Letters*, 10(1), 20130789.

Scott, R. S., Ungar, P. S., Bergstrom, T. S., Brown, C. A., Grine, F. E., Teaford, M. F., & Walker, A. (2005). Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature*, 436(7051), 693.

Sender, R. S., Hilko, A. S., Schwartz, G. T., & Strait, D. S. (2020, March). Biomechanical implications of variation in Hunter-Schreger Bands in early hominins. In American Journal of Physical Anthropology (vol. 171, pp. 258-258). 111 river st, hoboken 07030-5774, NJ USA: Wiley.

Smith, A. L., Benazzi, S., Ledogar, J. A., Tamvada, K., Pryor Smith, L. C., Weber, G. W., ... & Al-Fadhalah, K. (2015). The Feeding Biomechanics and Dietary Ecology of *Paranthropus boisei*. *The Anatomical Record*, *298*(1), 145-167.

Soukup, J. (2019). Traumatic Dentoalveolar Injuries. Wiggs's Veterinary Dentistry: Principles and Practice, 109-130.

Sponheimer, M., Passey, B. H., De Ruiter, D. J., Guatelli-Steinberg, D., Cerling, T. E., & Lee-Thorp, J. A. (2006). Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science*, 314(5801), 980-982.

Strait, D. S., Constantino, P., Lucas, P. W., Richmond, B. G., Spencer, M. A., Dechow, P. C., ... & Weber, G. W. (2013). Viewpoints: diet and dietary adaptations in early hominins: the hard food perspective. *American Journal of Physical Anthropology*, 151(3), 339-355.

Teaford MF, Ungar PS. (2000). Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Sciences*, 97, 13 506–13 511.

Teaford, M. F., Ungar, P. S., Taylor, A. B., Ross, C. F., & Vinyard, C. J. (2020). The dental microwear of hard-object feeding in laboratory Sapajus apella and its implications for dental microwear formation. *American Journal of Physical Anthropology*, 171(3), 439-455.

Thiery, G., Lazzari, V., Ramdarshan, A., & Guy, F. (2017). Beyond the map: enamel distribution characterized from 3D dental topography. *Frontiers in Physiology*, 8, 524.

Tobias, P.V., (1967). The Cranium of Australopithecus (Zinjanthropus) boisei. OlduvaiGorge, vol. 2. Cambridge University Press, Cambridge.

Towle, I., & Irish, J. D. (2019). A probable genetic origin for pitting enamel hypoplasia on the molars of *Paranthropus robustus*. *Journal of Human Evolution*, 129, 54-61.

Towle, I., Irish, J. D., & De Groote, I. (2017). Behavioral inferences from the high levels of dental chipping in *Homo naledi*. *American Journal of Physical Anthropology*, 164(1), 184-192.

Towle, I., Loch, C., Irish, J. D., Veneziano, A., & Ito, T. (2021). Chipping and wear patterns in extant primate and fossil hominin molars: 'Functional' cusps are associated with extensive wear but low levels of fracture. *Journal of Human Evolution*, 151, 102923. DOI: 10.1016/j.jhevol.2020.102923

Towle, I., Loch, C., Tooth chipping prevalence and patterns in extant primates. (2021). *American Journal of Physical Anthropology*, 1– 8. DOI: https://doi.org/10.1002/ajpa.24232

Ungar PS, Grine FE, Teaford MF. (2008). Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE*, 3:e2044.

Ungar PS, Scott RS, Grine FE, Teaford MF. (2010). Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. *Philosophical Transactions of the Royal Society B*, 365, 3345–3354.

Ungar, P. S. (2019). Inference of diets of early hominins from primate molar form and microwear. *Journal of Dental Research*, 98(4), 398-405.

Ungar, P. S., & Hlusko, L. J. (2016). The evolutionary path of least resistance. *Science*, 353(6294), 29-30.

Ungar, P. S., Lucas, P. W. (2010). Tooth form and function in biological anthropology. In: Larsen CS, editor. A companion to biological anthropology. Malden, MA: Wiley-Blackwell. p516–529.

van Casteren, A., Strait, D. S., Swain, M. V., Michael, S., Thai, L. A., Philip, S. M., ... & McGraw, W. S. (2020). Hard plant tissues do not contribute meaningfully to dental microwear: evolutionary implications. *Scientific Reports*, 10(1), 1-9.

van Casteren, A., Wright, E., Kupczik, K., & Robbins, M. M. (2019). Unexpected hard-object feeding in Western lowland gorillas. *American Journal of Physical Anthropology*, 170(3), 433-438.

Van der Merwe, N. J., Masao, F. T., & Bamford, M. K. (2008). Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *South African Journal of Science*, *104*(3-4), 153-155.

Vogel, E. R., van Woerden, J. T., Lucas, P. W., Atmoko, S. S. U., van Schaik, C. P., & Dominy, N. J. (2008). Functional ecology and evolution of hominoid molar enamel thickness: Pan troglodytes schweinfurthii and Pongo pygmaeus wurmbii. *Journal of Human Evolution*, 55(1), 60-74.

Wallace, J.A., 1973. Tooth chipping in the australopithecines. *Nature* 244, 117–118.

Williams, F. L. E. 2015. Dietary proclivities of *Paranthropus robustus* from Swartkrans, South Africa. *Anthropological Review*, 78(1), 1-19.

Wood, B., & Strait, D. 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution*, 46(2), 119-162.

Yeakel, J. D., Bennett, N. C., Koch, P. L., & Dominy, N. J. 2007. The isotopic ecology of African mole rats informs hypotheses on the evolution of human diet. *Proceedings of the Royal Society B: Biological Sciences*, 274(1619), 1723-1730.