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Towle, I, Irish, J and De Groote, I (2017) Behavioral inferences from the high levels of dental chipping in Homo naledi. American Journal of Physical Anthropology, 164 (1). pp. 184-192. ISSN 1096-8644

Behavioral inferences from the high levels of dental chipping in *Homo naledi*

Ian Towle[1], Joel D. Irish[1,2], Isabelle De Groote[1]

[1] Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, John Moores University, Liverpool, United Kingdom, L3 3AF

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

Number of text pages: 15

Number of reference pages: 5

Number of figures: 3

Number of Tables: 3

Abbreviated title: Dental chipping in *Homo naledi*

Key words: hominin diet, dental fractures, enamel, South Africa

Contact details:

Ian Towle

Room 352, James Parsons Building, Byrom Street, Liverpool, L3 3AF

07880330161

I.Towle@2014.ljmu.ac.uk

Abstract

Objectives: A variety of mechanical processes can result in ante-mortem dental chipping. In this study, chipping data in the teeth of *Homo naledi* are compared with those of other pertinent dental samples to give insight into their etiology.

Materials and Methods: Permanent teeth with complete crowns evidencing occlusal wear were examined macroscopically. The location, number, and severity of fractures were recorded and compared to those found in samples of two other South African fossil hominin species, as well as in samples of non-human primates (n= 3) and recent humans (n= 7).

Results: With 44% of teeth affected, *Homo naledi* exhibits far higher rates of chipping than the other fossil hominin samples***.*** Specifically, 50% of posterior teeth and 31% of anterior teeth display at least one chip. The maxillary teeth are more affected than the mandibular teeth (45% vs. 43%, respectively), 73% of molar chipping occurs on interproximal surfaces, and right teeth are more often affected than left teeth (50% vs. 38%).

Discussion: Results indicate that the teeth of *H. naledi* were exposed to acute trauma on a regular basis***.*** Because interproximal areas are more affected than buccal, and posterior teeth more than anterior, it is unlikely that non-masticatory cultural behavior was the cause. A diet containing hard and resistant food, or contaminants such as grit, is more likely. The small chip size, as well as steep occlusal wear and cupped dentine on some molars is supportive of the latter possibility. This pattern of chipping suggests *H. naledi* differed considerably – in terms of diet, environment, and/or specialized masticatory processing—relative to other African fossil hominins.

Ante-mortem dental chipping occurs when a tooth contacts a hard object with enough force to fracture the enamel (Chai & Lawn, 2007; Constantino et al., 2010), in a process akin to pressure flaking of stone tools. Fracture can occur with minimal plastic deformation because enamel is strong but brittle (Thomas, 2000). For example, in the human dentition enamel can withstand pressures >1000 N, equating to contact stress of up to 2.5 gigapascal; however, the fracture point varies depending on the properties of both the enamel and the object making contact with the enamel (Constantino et al., 2010; He & Swain, 2008; Lawn, Lee, Constantino, & Lucas, 2009; Scott & Winn, 2011). Chipping differs from other types of crown wear in that it is not a gradual process and does not leave a smooth occlusal surface. Irregular breaks are created on the occlusal edge of the enamel, though they may reach the dentine in severe cases. Such data therefore can offer some insight into the diet and behavior of past individuals and populations, especially because it often takes many years of subsequent attrition and abrasion to erase chips (Constantino, Markham, & Lucas, 2012). Chipping has been recorded in a range of different mammals, with considerable variation in the patterns and causes of fractures, which include food processing, accidents, diet, environmental contaminants, and social behavior (Constantino et al., 2012; Sauther, Sussman, & Cuozzo, 2002; Scott & Winn, 2011; Stojanowski, Johnson, Paul, & Carver, 2015; Van Valkenburgh, 2009). Different dietary items cause enamel fractures at different rates and sizes -- from soft fruits that rarely cause chipping to hard seeds and nuts that may lead to large chips. However, the propensity of some foods for dental chipping is more difficult to discern. Bark and low-quality terrestrial herbaceous vegetation tend to envelope the crown surface, thereby spreading out stresses to make chipping unlikely (Chai, Lee, Kwon, Lucas, & Lawn, 2009; Lucas, Constantino, Wood, & Lawn, 2008). Environmental contaminants may also be important, such as grit incorporated into the diet (Belcastro et al., 2007; Nystrom, Phillips-Conroy, & Jolly, 2004). The size and shape that an object must be to cause chipping are subjects of debate (e.g., Constantino et al., 2012; Daegling et al., 2013; Lucas et al., 2008); yet, the teeth affected, position on the tooth, and severity can all give insight into the etiology producing such chips (Belcastro et al., 2007; Constantino et al., 2010; Scott & Winn, 2011).

Comparatively low chipping rates are found in gorillas and chimpanzees relative to orangutans (Constantino et al., 2012). The rate in gorillas is a result of their infrequent ingestion of hard seeds and fruits, while feeding predominantly on foods like low quality herbaceous vegetation (Conklin-Brittain, Knott, & Wrangham, 2001; Doran et al., 2002). Similarly, chimpanzees commonly consume soft fruits (Conklin-Brittain et al., 2001). Orangutans, however, have far higher chipping rates than other great apes, with Constantino et al. (2012) reporting three to six times more chips on their posterior teeth. This high rate is attributed to the large hard foods that make up a significant part of their diet (Galdikas, 1982).

A variety of recent human populations have also been studied (e.g., Belcastro et al., 2007; Bonfiglioli, Mariotti, Facchini, Belcastro, & Condemi, 2004; Gould, 1968; Lous, 1970; Molnar et al., 1972; Scott & Winn, 2011; Silva, Gil, Soares, & da Silva, 2016; Turner & Cadien, 1969), and the findings are useful for inferring chipping etiologies in fossil hominins. In general, hunter-gatherers tend to have higher rates in their posterior teeth, whereas agriculturalists have more chipping of the anterior teeth. In addition, the former groups are most affected by diet or environmental contaminants, while the latter are more often affected by diet and tool use (Scott & Winn, 2011; Stojanowski et al., 2015). Non-masticatory behavior is usually the focus of chipping studies in *Homo sapiens*, with different activities leading to a variety of patterns (e.g., Bonfiglioli et al., 2004; Gould, 1968; Larsen, 2015; Lous, 1970; Molnar at al., 1972).

Chipping frequencies have also been recorded in hominin fossils, with South African specimens particularly well studied (Constantino et al., 2010; Grine et al., 2010; Robinson, 1954; Tobias, 1967). For example, there has been much debate in the literature concerning what the frequencies of dental chipping in *Paranthropus robustus* and *Australopithicus africanus* indicate in terms of diet. Alternate explanations include: grit introduced into the masticatory process from eating roots (Robinson, 1954), crunching of bones (Tobias, 1967), and consumption of seeds and nuts (Constantino et al., 2010). Chipping has also been noted in the teeth of *A. afarensis* (Johanson & Taieb, 1976), *A. anamensis* (Ward, Leakey, & Walker, 2001), *P. boisei* (Tobias, 1967), and *H. neanderthalensis* (Fox & Frayer, 1997). Neanderthal teeth exhibit high rates that are likely caused, at least in part, by non-masticatory processes (Fiorenza & Kullmer, 2013; Fox & Frayer, 1997).

Although dental chipping can be useful in reconstructing hominin diets, a few issues have not yet been thoroughly addressed in the literature, including the effects that enamel microstructure, thickness, and morphology have on susceptibility to fracture, and the time spent in occlusion and wear of the tooth. It has been suggested that fractures may follow lines of weakness such as lamellae and tufts, which means cracks can form differentially or more easily at certain locations (Lucas et al., 2008). Similarly, orientation of enamel microstructure, as well as the dietary object is important (Xu et al., 1998). Most research on fractures assumes that enamel has similar properties across the occlusal surface, as well as between tooth types and populations. However, more recent work suggests that enamel mechanical properties differ across the surface of a single tooth, as well as between teeth (Cuy, Mann, Livi, Teaford, & Weihs, 2002; Macho & Shimizu, 2009; Ziscovici, Lucas, Constantino, Bromage, & Van Casteren, 2014). Enamel property differences among species could also mean that two closely related species with nearly identical diets have markedly different patterns of chipping. In this regard, it was proposed that thick enamel may have evolved in certain lineages to resist tooth loss through fracture (Kay, 1981; Lucas et al., 2008). This possibility could lead to bias in the data if these same species evolved other adaptations to cope with consuming large amounts of hard foods. Efforts to quantify bite forces in extinct species may be especially influenced by such factors (Chai & Lawn, 2007; Chai, Lee, & Lawn, 2011; Constantino et al., 2010; Constantino et al., 2012). However, species differences are just beginning to be researched (e.g., Ziscovici et al., 2014). There are also issues concerning how samples are chosen, such as the inclusion of incomplete crowns and differences in the presentation of results that may yield substantial differences among studies of the same species (Daegling et al., 2013).

That said, if care is taken in choosing the methods and enamel property differences are considered, dental chipping should be able to provide some insight into the diet and behavior of extinct species. By recording position, severity, and frequency, a unique sample-specific pattern may be obtained for comparison with other samples. In this study, chipping data were recorded in the permanent teeth of *H. naledi* for comparison with other samples of South African fossil hominins, as well as extant primates and recent humans. The results help to characterize further the newly-defined species from South Africa's Rising Star cave system, along with other publications (e.g., Feuerriegel et al., 2016; Harcourt-Smith et al., 2015; Kivell et al, 2015; Williams, Garcia-Martinez, Bastir, & Berger, 2017) – several of which also concern the teeth (Berger et al., 2015; Cofran, Skinner, & Walker, 2016; Skinner, Lockey, Gunz, Hawks, & Delezene, 2016).

1. Materials and Methods

At the time of data collection, over 1,500 *H. naledi* specimens were available for study, from which ≥15 individuals are represented (Berger et. al., 2015; Dirks et. al., 2015). The dental sample itself consists of 156 permanent teeth, all of which were observed directly by the first author. Following Daegling et al. (2013), six damaged teeth and 24 others not subject to chipping, due to noneruption or limited occlusion (based on negligible or no crown wear), were not recorded. Thus, data in 126 teeth were employed for comparison with the other samples (Table 1). The same criteria for tooth exclusion were followed when recording chipping in *A. africanus* (n= 265 teeth) and *P. robustus* (n= 235) from South Africa, and three extant primate species: chimpanzees (n= 1,991), gorillas (n= 1,518), and hamadryas and olive baboons (n= 760). To assess the level of intraobserver error, 218 baboon teeth were recorded on two separate occasions; no significant difference was detected ($\chi2=0.008$, 1 df, $p=0.927$). Analogous data in seven additional samples of recent humans were derived from the literature (refer to list in Table 2, below); of course, interobserver error could not be determined in these cases.

Chipping frequencies are displayed by tooth rather than by individual. As well as presenting overall frequencies, teeth are subdivided according to the severity of occlusal wear. Extensively worn teeth are often excluded from study over concerns that previous chips have worn away or the enamel has become more susceptible to chipping (Bonfiglioli et al., 2004; Scott & Winn, 2011). However, this strategy can omit important dietary trends, particularly when comparing species. Occlusal wear is a normal part of the masticatory process, so eliminating from consideration data on teeth worn past a certain point may mask dietary differences.

Wear data for molars were scored in accordance with the method of Scott (1979), and for all other teeth the method of Smith (1984). This approach was employed to determine whether dental attrition is related to chipping frequencies. Scott's (1979) method divides teeth into quadrants, where each quadrant is given a score from 1 to 10. The former value refers to a tooth that is unworn or has very small wear facets, while the latter describes complete loss of the enamel. Smith's (1984) method is similar, but uses a scale of 1 to 8. In this study, molars are separated from the other teeth based on the total of their four quadrants into categories of high (i.e., 20+), medium (13-19), and low wear (5-12). Anterior teeth, here including premolars, are divided into high (5+), and medium-to-low wear (2-4) categories. If a tooth is listed as grade 1 for either method, it was not included in the analysis due to the likelihood it was not in occlusion. Statistical significance was tested between tooth groups using a chi-square test of homogeneity, with significance set at the 0.05 alpha level.

Teeth were observed macroscopically with a 10x hand lens to determine whether a chip occurred ante- or post-mortem. Distinguishing between post and ante-mortem fractures was based on criteria of Scott & Winn (2011), where only chips evidencing subsequent attrition were included in the latter category. The severity, position, and number of chips were also recorded. Severity is based on the three-point scale of Bonfiglioli et al. (2004): 1) slight crack or fracture up to 0.5 mm in width or larger, but with only superficial enamel loss, 2) larger irregular fracture up to 1 mm with the enamel more deeply involved, and 3) chip larger than 1 mm involving both enamel and dentine. The number of chips per tooth was recorded following Belcastro et al. (2007). Position was recorded as buccal, lingual, mesial, and distal. If multiple chips are present then the tooth surface with the most fractures was recorded, whereas if the number is equal between two or more sides then the surface with the largest chip was recorded. *Homo naledi* individuals referred to in the original publication (Berger et. al., 2015) and those defined as likely individuals at the time of data collection were included.

2. Results

With 44.4% of permanent teeth affected (Table 1), *H, naledi* exhibits a far higher chipping rate than the other South African samples (Table 2). Specifically, 53.7% of molars, 44.4% of premolars, 25% of canines, and 33.3% of incisors have at least one chip; of these, 50% display two or more chips (Fig. 1 and Table 3). Only 13.6% of primary teeth are affected. Most chips are small, i.e., severity 1 (n=51), with only six recorded as 2 or 3. Over 73% of those on the molars are located interproximally. Particularly common are several small chips above the wear facets of posterior teeth (Fig. 2).

[Figure 1 here]

[Table 1 here]

[Figure 2 here]

Chipping frequencies are presented by wear score and side in Table 1. Among other variation evident in these categories, it can be seen that right teeth are affected slightly more often than left, with rates of 50% and 37.7%, respectively, having at least one chip. The average affected right molar has 2.37 chips and the left 2.06, with medians of 2 and 1 in these non-normally distributed data (Shapiro-Wilk, p=0.000). However, differences by side are not statistically significant (X^2= 1.945, 1 df, p= 0.16). Of the 12 individuals represented by dental remains, nine have at least one chipped tooth; two of the remaining three are represented by only one tooth, and the third has minimally worn teeth (i.e., scores of <2).

The posterior teeth of *H. naledi* have more chips than the anterior teeth, and the average difference in overall frequency is statistically significant (χ^2=3.938, 1 df, p=0.047). Posterior teeth are also more likely to exhibit multiple chips than anterior teeth; to test this, a chi-square test was again used, though with Yates' continuity correction because expected cell size for anterior teeth with multiple chips is $\leq$5. The difference is significant (χ^2_c = 7.240, 1 df, p= 0.007).

[Table 2 here]

Lastly, Tables 2 and 3 compare *H. naledi* with samples of other South African hominins, extant primates, and recent humans. Overall chipping rates, as well as ratios comparing chip frequency are provided for maxillary vs. mandibular teeth, posterior vs. anterior teeth, and small vs. large chips (Table 2). *Homo naledi* has a higher rate of chipping than other South African hominins and extant non-human primates (Table 3). The rate is more comparable to several of the recent human samples. However, many of the latter differ in chipping ratios compared to *H. naledi*; particularly noticeable is the preponderance of small chips vs. large (i.e., ratio of 8.33:1) and fewer affected anterior vs. posterior teeth (0.61:1). Although the overall rate of chipping in *H. naledi* is more similar to these recent human groups, the nature of the chipping with regard to size and location within the dental arcade is more like that observed in *A. africanus* and in baboons.

[Table 3 here]

3. Discussion

The *H. naledi* sample appears quite homogeneous with regard to the location, number, and severity of chipping across individuals, not unlike that of the species' developmental attributes, such as uniformly simple crown morphology on relatively small, thick-enameled teeth (Berger et. al., 2015; Cofran et al., 2016; Skinner et al., 2016). The amount of ante-mortem dental chipping across the sample, including multiple instances in individuals with greater attrition, indicates that the teeth were exposed to acute trauma on a regular basis. Interproximal surfaces are more affected than buccal surfaces and posterior teeth more than anterior teeth, which is suggestive of a dietary rather than a non-masticatory cause (Belcastro et al., 2007). This patterning can result from contaminants in the diet, like grit when consuming such foods as roots and tubers (Belcastro et al., 2007; Robinson, 1963; Stojanowski et al., 2015).

Clearly, there will be a point when an object is too small to create a visible chip and instead results in enamel microwear. The point at which this occurs likely varies, depending on the properties and shape of both the enamel and the object (Daegling et al., 2013). The contaminants consumed by *H. naledi* would have had to at least occasionally been above this size threshold. Certain environments make contaminants more likely to be consumed, such as dry and arid conditions or areas affected by such phenomena as ash clouds following a volcanic eruption (Belcastro et al., 2007; Riede & Wheeler, 2009; Spradley, Glander, & Kay, 2016). It will therefore be useful to incorporate data about the environment in which *H. naledi* lived.

As mentioned in the introduction, the effects of enamel thickness, occlusal wear, and enamel microstructure on chipping frequencies are not well understood at present. It has been suggested that thickness is not important in terms of chip number (Constantino et al., 2012). Nevertheless, thicker enamel can accommodate larger chips and hence may skew inferences drawn from assessments of chip size. Severe wear will have a similar effect on frequencies, with chip size being limited. These factors do not seem to be responsible for small chips in this sample, because chip size is consistently small regardless of wear and despite the presence of thick enamel (Skinner et al., 2016). It is also unlikely that *H. naledi* has significantly different enamel microstructural properties than other hominin species, given their presumed phylogenetic relationship. Additional research on masticatory and enamel properties should offer further insight into the susceptibility of these individuals to dental fractures. Chipping rates clearly increase with wear, due to enamel properties or, more likely, time in occlusion. However, it is clear that the high rate in this sample is not simply a consequence of heavy wear, for even lightly worn teeth have far higher rates of chipping than that observed in the other hominin samples. It seems probable that the objects responsible for this chipping were consumed regularly, especially given that small chips should wear away more quickly than large chips.

Dental chipping in *H. naledi* differs notably from the other fossil hominin samples examined for this study. The rate is roughly twice that of *A. africanus* (44.44% vs. 21.13%) and more than three times that of *P. robustus*, among whom only 12.77% of teeth are affected. The patterning of chipping differs as well, particularly relative to *P. robustus* (see ratios in Table 2). The low rate of chipping in *P. robustus*, with comparable rates to gorillas, suggests they did not specialize in hard object feeding. Although the chipping rate for *A. africanus* is substantially lower than in *H. naledi*, it is higher than that for extant great apes and *P. robustus*. Interestingly, the premolars of *A. africanus* are the most affected teeth, supporting recent biomechanical analyses (Strait et al., 2009; 2012), with this pattern not observed in the other hominins studied.

The extant primate samples may offer more useful comparisons for *H. naledi*. For example, in a microwear study by Nystrom et al. (2004), baboons in dry environments were reported to consume large amounts of grit. In the present, combined sample of hamadryas and olive baboons, we found similarities to *H. naledi*, with frequent small chips and a higher rate of chipping among posterior teeth relative to anterior teeth.

Recent human samples with comparably high rates, such as the Inuit and medieval Italian Quadrella (Table 2), have different patterns of chipping than observed in *H. naledi*; either their anterior teeth are more affected from extra-masticatory activity, or all teeth evidence severe chipping as a result of dietary and cultural behaviors (Belcastro et al., 2007; Scott & Winn, 2011; Turner & Cadien, 1969). However, there are some human parallels. A Late Woodland sample from Cape Cod in the U.S.A. has a pattern like *H. naledi* in terms of frequency and position (McManamon, Bradley, & Magennis, 1986). The overall frequency is 43% and molars are reported as the tooth type most prone to chipping, with interproximal surfaces most affected. Unfortunately, frequencies for tooth types and positions in that study are not reported. McManamon et al. (1986) suggest that the cause of this patterning was the incorporation of sand, gravel, and/or shell fragment contaminants into the food. Another sample with somewhat similar frequencies to *H. naledi* is from the site of Taforalt. Bonfiglioli et al. (2004) concluded that the frequent interproximal chipping in these epipalaeolithic Moroccans was due to chewing hard, abrasive snail shells and fruit stones. Many seeds and nuts were also consumed (Humphrey et al., 2014). Dietary contaminants may have been a factor as well, given the environmental conditions and presence of grindstones (Humphrey et al., 2014). However, direct comparison is confounded, because these peoples practiced maxillary incisor avulsion (De Groote & Humphrey, 2016). Lastly, the medieval Vicenne-Campochiaro sample exhibits a chipping pattern similar to *H.naledi*; it has high rates of interproximal chipping on posterior teeth, especially in females. Belcastro and coworkers (2007) suggest the cause was grit incorporated into the diet.

If a specific food item is responsible for chipping in *H. naledi*, then these individuals must have specialized in the consumption of a particular type of very small hard object. Additional evidence, to be detailed in separate study, includes steeply-angled wear and slight cupped, i.e., scooped-out, wear of dentine on several posterior teeth in *H. naledi* – both of which can result from consumption of grit, generally in conjunction with softer foods (Brace, 1962; Hinton, 1981; Smith, 1984; Fig. 3). It also cannot be ruled out that these individuals were processing foods, at least to the extent seen in chimpanzees who dismantle seeds and nuts before ingestion (Boesch & Boesch, 1982; Daegling et al., 2013; Wrangham & Conklin-Brittain, 2003). So, potentially, only small hard objects were masticated in the mouth, with larger hard items processed to some extent prior to mastication. That said, other evidence for this hypothesis is lacking. Moreover, although conjectural, perhaps the higher rate of chipping in the right teeth of *H. naledi* resulted from preferential placement of the food or objects (and contaminants) in this side of the mouth. Greater wear on right relative to left teeth has been reported in several fossil *Homo* specimens and has been attributed to right hand dominance in the manipulation of objects during oral processing (Estalrrich & Rosas, 2013; Fiore, Bondioli, Radovcic, & Frayer, 2015; Frayer et al., 2016). Yet, as noted, side differences in chipping in *H. naledi* were found to be non-significant; recovery of additional specimens may provide clarification, while micro- and macrowear analyses by side should provide interesting comparisons.

[Figure 3 here]

4. Summary and Conclusion

Homo naledi exhibits high rates of ante-mortem enamel chipping, particularly on the posterior teeth and interproximal areas. These chips are predominately small and all individuals are affected. These characteristics are suggestive of a dietary etiology rather than a non-masticatory cause. Once microwear analysis of the teeth by other researchers is completed, further support may be provided for the possibility that grit underlies the patterns of macroscopic chipping reported here. In addition, alternative forms of analyses of *H. naledi* specimens (e.g., photolith analyses, etc.), along with chipping research on additional primates, particularly hominins, can help further elucidate whether *H. naledi* regularly ate foods that contained contaminants. Environmental data will be of interest to integrate. However, at present, results from this chipping study highlight the fact that *H. naledi* differed noticeably from species comprising the comparative samples studied here – in terms of diet, behavior, and/or the environment in which they lived.

Acknowledgements

We thank L. Berger and B. Zipfel for access to the collections at the University of the Witwatersrand, and J. Hawks and L. Delezene for their help and advice during data collection. We also thank I. Livne from the Powell-Cotton museum and S. Potze from the Ditsong Museum of South Africa for access to their collections. This research was supported by a studentship to the first author from Liverpool John Moores University.

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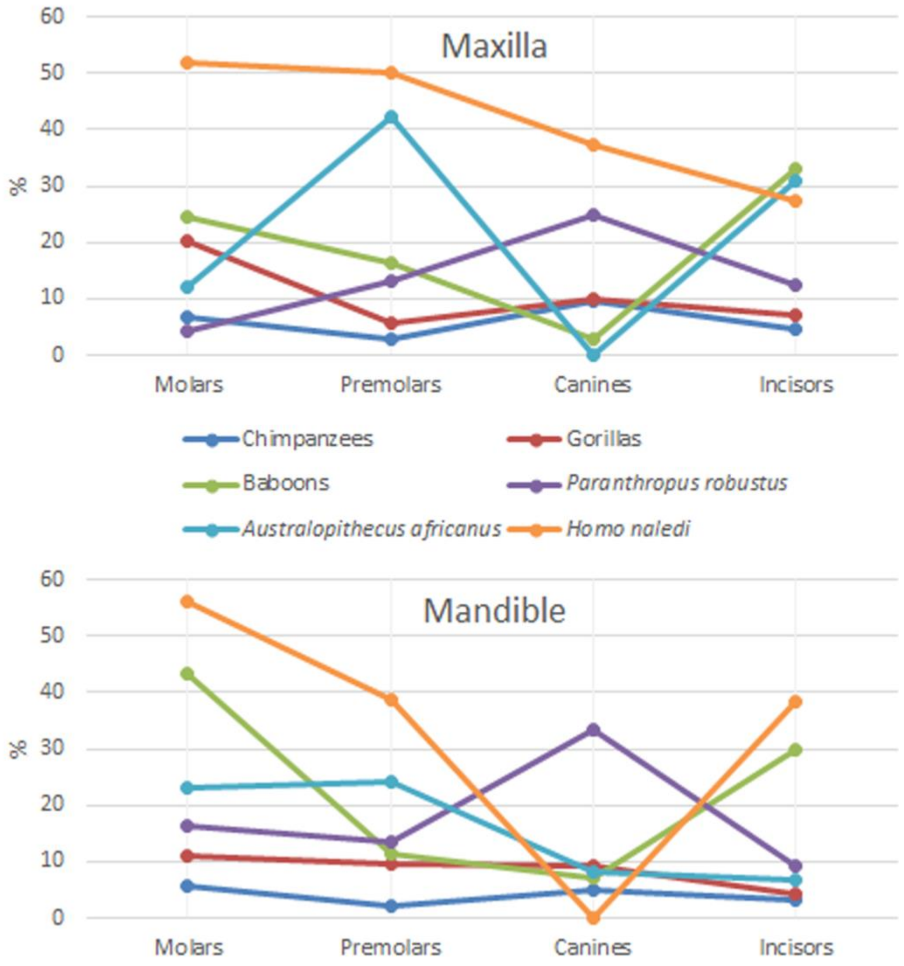

Figure 1. Chipping rates (%) for extant primates and fossil hominins, divided by jaw and tooth type.

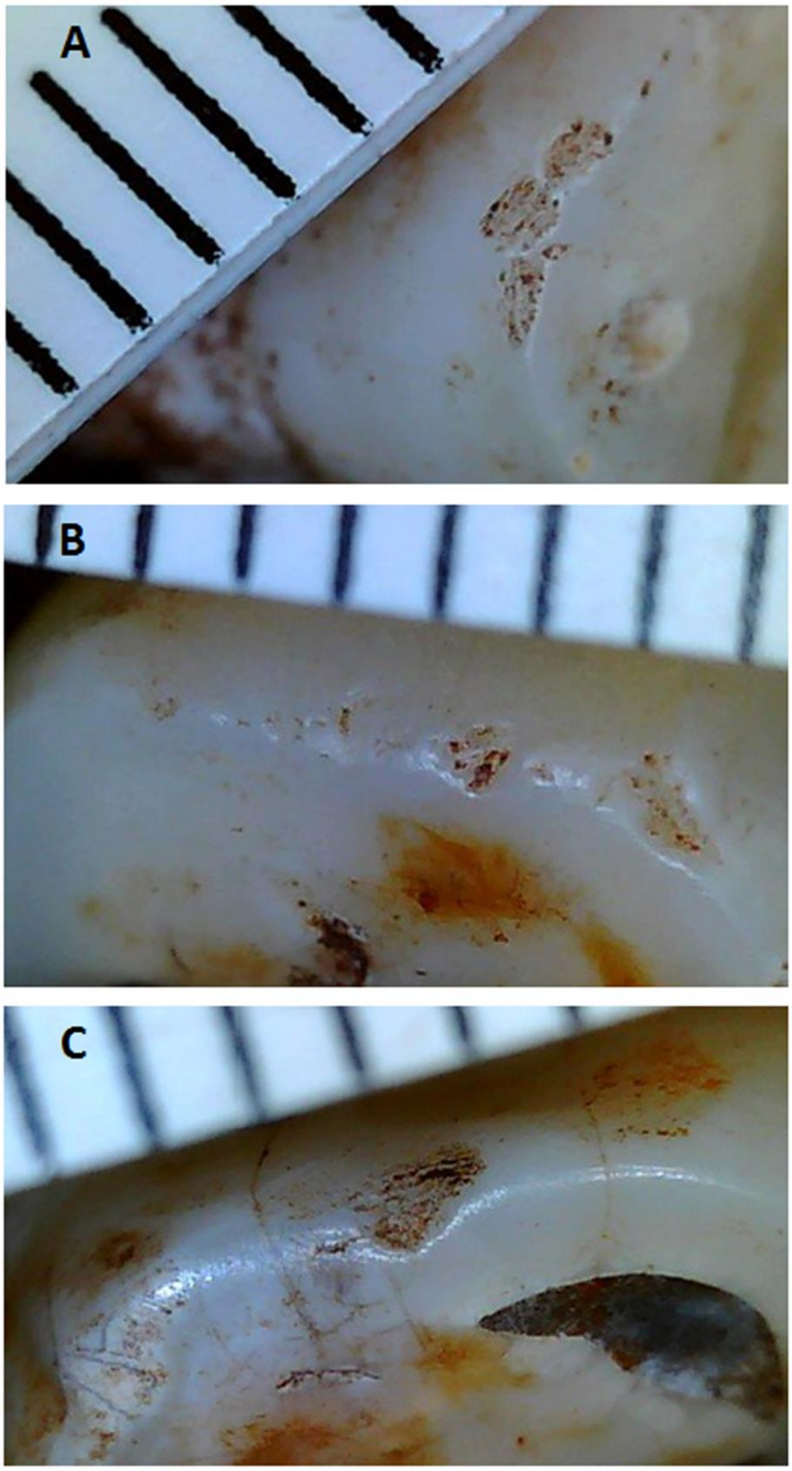

Figure 2. Chipping examples: a) U.W. 101-525 upper right first molar, three chips on mesial surface; b) U.W. 101-1401 upper right second premolar, multiple small chips on distal surface; c) U.W. 101-1402 upper right first premolar, mesial chip. Scale is in mm.

Figure 3. Steeply-angled wear on an upper left second molar (U.W. 101-528).

Table 1 Chipping frequencies for different tooth types in *H. naledi*.

Sample	Total Teeth	With Chipping	%
All teeth	126	56	44.44
Left teeth	61	23	37.70
Right teeth	66	33	50.00
Primary teeth	22	3	13.64
Molar wear stage[1]			
All molars	54	29	53.70
Light wear (5 to 12)	19	4	21.05
Medium wear (13 to 19)	21	12	57.14
High wear (20+)	14	13	92.86
PM's, C's and I's wear stage[1]			
All anterior and premolar teeth	72	27	37.50
Light wear (2 to 4)	46	15	32.61
Heavy wear (5+)	26	12	46.15

[1] Molar wear is calculated following Scott (1979) with all other teeth using Smith (1984)

Table 2 Per-tooth chipping frequencies and ratios of dentition affected for *H. naledi* and comparative samples.

Sample/Location	Chipping rate %	Multiple chipped teeth %	Small:Large[1] chip ratio	Maxilla:Mandible ratio	Anterior:Posterior ratio	Time period	Reference
Fossil hominins							
H. naledi	44.44	50.00	8.33:1**	1.05:1	0.61:1**	Not yet known	This study
A. africanus	21.13	16.07	10.20:1**	1.04:1	0.54:1	Plio-Pleistocene	This study
P. robustus	12.77	6.67	1.73:1	0.66:1	1.25:1	Plio-Pleistocene	This study
Extant primates							
Baboons	25.26	18.75	5.40:1**	0.79:1	0.93:1	19th/20th cent CE	This study
Gorillas	11.13	4.14	10.27:1**	1.48:1**	0.51:1**	19th/20th cent CE	This study
Chimpanzees	4.92	2.04	2.27:1**	1.73:1	0.95:1	19th/20th cent CE	This study
Recent humans							
St. Lawrence Island Inuit	66.40	*	*	1.04:1	0.77:1**	2nd–17th cent CE	Scott & Winn (2011)
Quadrella (Italy)	48.40	*	0.70:1	1.14:1	1.50:1**	2nd–3rd cent BCE	Belcastro et al. (2007)
Vicenne-Campochiaro (Italy)	38.90	*	1.12:1	1.17:1	1.68:1**	4th–10th cent CE	Belcastro et al. (2007)
Taforalt (Morocco)	29.20	*	*	*	0.64:1**	11,000–12,000 BP	Bonfiglioli et al. (2004)
Norway	21.90	*	*	1.24:1**	3.40:1**	11th- 14th cent CE	Scott & Winn (2011)
Spain	5.90	*	*	1.73:1	3.10:1**	11th– 18th cent CE	Scott & Winn (2011)
Cape Cod Woodland (USA)	43.40	*	*	0.79:1	*	5th–10th cent CE	McManamon et al. (1986)

[1] Small chips are those recorded as severity grade 1 and large as grades 2-3, according to Bonfiglioli et al. (2004)

*Data not reported in publication

**Chi-square significant at 0.05 level

Table 3 Chipping presence, absence, and severity for upper molars (UM), upper premolars (UP), upper canines (UC), upper incisors (UI), lower molars (LM), lower premolars (LP), lower canines (LC), lower incisors (LI), and all teeth (All).

Sample	UM	%	UP	%	UC	%	UI	%	LM	%	LP	%	LC	%	LI	%	All	%
Chimpanzees																		
Total number of teeth[1]	501		292		136		315		497		300		140		320		2501	
Complete teeth with chip(s)	29		6		9		11		25		5		5		8		98	
Complete teeth with no chips	415		248		107		261		432		279		121		278		2141	
Damaged/incomplete teeth	57		38		20		43		40		16		14		34		262	
Teeth with a wear score of 1	24		51		23		26		17		51		24		32		248	
Small chips[2]	19	66	5	83	6	67	9	82	16	64	3	60	2	40	8	100	68	69
Medium chips[2]	10	34	1	17	2	22	2	18	9	36	2	40	3	60	0	0	29	30
Large chips[2]	0	0	0	0	1	11	0	0	0	0	0	0	0	0	0	0	1	1
Chipping frequency %	7		3		10		4		6		2		5		3		5	
Gorillas																		
Total number of teeth[1]	409		247		110		271		411		241		113		288		2090	
Complete teeth with chip(s)	72		9		6		12		37		19		6		8		169	
Complete teeth with no chips	301		201		78		200		332		200		83		217		1612	
Damaged/incomplete teeth	36		37		26		59		42		22		24		63		309	
Teeth with a wear score of 1	17		54		23		43		32		24		25		45		263	
Small chips[2]	68	94	7	78	6	100	8	67	33	89	18	95	6	100	8	100	154	91
Medium chips[2]	4	6	1	11	0	0	4	33	4	11	1	5	0	0	0	0	14	8
Large chips[2]	0	0	1	11	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Chipping frequency %	20		6		10		7		11		10		9		4		11	
Baboons																		
Total number of teeth[1]	174		116		49		107		166		110		49		112		883	
Complete teeth with chip(s)	38		16		1		29		62		10		3		33		192	
Complete teeth with no chips	123		90		41		59		85		80		43		77		598	

Damaged/incomplete teeth	13		10		7		19		19		20		3		2		93	
Teeth with a wear score of 1	5		8		8		0		4		1		4		0		30	
Small chips[2]	31	82	13	81	1	100	27	93	49	79	9	90	3	100	29	88	162	84
Medium chips[2]	7	18	3	19	0	0	2	7	13	21	1	10	0	0	4	12	30	16
Large chips[2]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chipping frequency %	24		16		3		33		43		11		7		30		25	
Paranthropus robustus																		
Total number of teeth[1]	78		63		15		38		117		58		10		23		402	
Complete teeth with chip(s)	2		4		2		3		12		5		1		1		30	
Complete teeth with no chips	50		30		7		26		74		34		4		15		240	
Damaged/incomplete teeth	26		29		6		9		31		19		5		7		132	
Teeth with a wear score of 1	4		4		1		5		12		2		2		5		35	
Small chips[2]	2	100	1	25	0	0	1	33	10	83	4	80	0	0	1	100	19	63
Medium chips[2]	0	0	3	75	1	50	2	67	2	17	1	20	1	100	0	0	10	33
Large chips[2]	0	0	0	0	1	50	0	0	0	0	0	0	0	0	0	0	1	3
Chipping frequency %	4		13		25		13		16		14		33		9		13	
Australopithecus africanus																		
Total number of teeth[1]	81		55		20		31		153		65		36		36		477	
Complete teeth with chip(s)	6		11		0		4		24		9		1		1		56	
Complete teeth with no chips	48		24		16		19		90		36		19		22		274	
Damaged/incomplete teeth	27		20		4		8		39		20		16		13		147	
Teeth with a wear score of 1	4		9		8		10		10		8		8		8		65	
Small chips[2]	6	100	10	91	0	0	4	100	22	92	8	89	0	0	1	100	51	91
Medium chips[2]	0	0	1	9	0	0	0	0	1	4	1	11	1	100	0	0	4	7
Large chips[2]	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0	1	2
Chipping frequency %	12		42		0		31		23		24		8		7		21	
Homo naledi																		
Total number of teeth[1]	31		21		13		14		28		19		11		19		156	
Complete teeth with chip(s)	15		9		3		3		14		7		0		5		56	
Complete teeth with no chips	16		11		9		11		14		11		10		12		94	
Damaged/incomplete teeth	0		1		1		0		0		1		1		2		6	
Teeth with a wear score of 1	2		2		4		3		3		0		6		4		24	
Small chips[2]	13	87	9	100	3	100	3	100	11	79	6	86	0	0	5	100	50	89

Medium chips[2]	2	13	0	0	0	0	0	0	3	21	0	0	0	0	0	0	5	9
Large chips[2]	0	0	0	0	0	0	0	0	0	0	1	14	0	0	0	0	1	2
Chipping frequency %	52		50		38		27		56		39		0		38		44	

[1] Damaged/incomplete teeth and teeth with a wear score of 1 dropped from the total number of teeth before chipping frequency is calculated.

[2] Small, medium, and large chips are scored according to Bonfiglioli et al. (2004) with three-point severity scale