Dental topography and the diet of *Homo naledi*

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**Abstract**

Though late Middle Pleistocene in age, *Homo naledi* is characterized by a mosaic of *Australopithecus*-like (e.g., curved fingers, small brains) and *Homo*-like (e.g., elongated lower limbs) traits, which may suggest it occupied a unique ecological niche. Ecological reconstructions inform on niche occupation, and are particularly successful when using dental material. Tooth shape (via dental topography) and size were quantified for four groups of South African Plio-Pleistocene hominins (specimens of *Australopithecus africanus*, *Paranthropus robustus*, *H. naledi*, and *Homo sp.*) on relatively unworn M2s to investigate possible ecological differentiation in *H. naledi* relative to taxa with similar geographical ranges. *H. naledi* has smaller, but higher-crowned and more wear resistant teeth than *Australopithecus* and *Paranthropus*. These results are found in both lightly and moderately worn teeth. There are no differences in tooth sharpness or complexity. Combined with the high level of dental chipping in *H. naledi*, this suggests that, relative to *Australopithecus* and *Paranthropus*, *H. naledi* consumed foods with similar fracture mechanics properties but more abrasive particles (e.g., dust, grit), which could be due to a dietary and/or environmental shift(s). The same factors that differentiate *H. naledi* from *Australopithecus* and *Paranthropus* may also differentiate it from *Homo sp.*, which geologically predates it, in the same way. Compared to the great apes, all hominins have sharper teeth, indicating they consumed foods requiring higher shear forces during mastication. Despite some anatomical similarities, *H. naledi* likely occupied a distinct ecological niche from the South African hominins that predate it.

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1. Introduction

Ecological reconstructions help clarify niche partitioning, and some of the most successful hominin reconstructions have relied on dental remains (e.g., Grine et al., 2012; Henry et al., 2012; Sponheimer et al., 2013). Dental differences (e.g., absolute and relative tooth size, dental proportions, dental topography, absolute and relative enamel thickness) among hominin taxa are often cited to reflect dietary shifts, but can also reflect environmental or a combination of environmental and dietary shifts (Lucas et al., 2008; Ungar and Sponheimer, 2011). For example, increases in aridity can lead to a decrease in fruit availability, a change in food mechanical properties, and/or an increase in dust/grit consumption (Onoda et al., 2011).

Little is known about the ecology of the recently discovered hominin *Homo naledi* (Berger et al., 2015, 2017; Hawks et al., 2017). Though Middle Pleistocene (236–335 ka) in age (Dirks et al., 2017), it resembles species of *Australopithecus* by evincing a short stature, small body mass, and small brain, both absolutely and relative to body size (Garvin et al., 2017). Small brains and bodies indicate differing energetic requirements and home ranges compared to other species of Middle Pleistocene Homo (Antón et al., 2014). Further, curved fingers and aspects of shoulder morphology suggest significant levels of climbing (Kivell et al., 2015; Feuerriegel et al., 2017), which could point towards an *Australopithecus*-like pattern of resource exploitation (Pérez-Pérez, 1988; Pruett, 2006) for *H. naledi*. Yet, similar to *Homo* and unlike *Australopithecus*, the lower limb is elongated (Marchi et al., 2017), sexual size dimorphism is minimal (Garvin et al., 2017), and the postcanine teeth are absolutely small (Berger et al., 2015; Hawks et al., 2017). In these regards, *H. naledi* appears to be a late surviving member of the genus *Homo*. This begs the question of whether *H. naledi* occupied...
an ecological niche more like *Australopithecus*, other species of Middle Pleistocene *Homo*, or neither. Resolving this issue is complicated due to the minimal faunal remains associated with the more than 1550 and 131 *H. naledi* fossils from the Dinaledi and Lesedi chambers, respectively, and the lack of tools associated with this species (Berger et al., 2015; Dirks et al., 2015, 2017; Hawks et al., 2017). The paucity of these data inhibits robust reconstructions of the *H. naledi* paleoenvironment and its pattern of resource exploitation. In this paper, we investigate the dietary ecology of *H. naledi* by quantifying tooth shape and contextualize the results by comparing them to three other groups of South African hominins: *Australopithecus africanus*, *Paranthropus robustus*, and *Homo* sp. (i.e., Swt 80, SK 15, Cave of Hearths mandible), all of which are presumed to predate the remains of *H. naledi* from Rising Star.

1.1. Dental paleoecological evidence for Plio-Pleistocene hominins in South Africa

Between 3.0 and 1.5 Ma, there were at least four hominin taxa in South Africa, and ecological reconstructions for *A. africanus*, *P. robustus*, *Australopithecus sediba*, and *Homo* sp. indicate some niche partitioning (Grine et al., 2012; Henry et al., 2012). During this time, the environment in South Africa changed from more closed and mosaic to more open and arid (e.g., Vrba, 1975, 1985; Reed, 1997; Lee-Thorp et al., 2007). Carbon isotope data from dental and mosaic to more open and arid (e.g., Vrba, 1975, 1985; Reed, 1997; Lee-Thorp et al., 2007). Carbon isotope data from dental enamel reveal dietary overlap in these hominins and consumption of C4 resources (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999; Sponheimer et al., 2005, 2013; Grine et al., 2012), with the exception of *A. sediba* (see Henry et al., 2012). In *A. africanus* and *Homo* sp., dental microwear textures show a large range in anisotropy (eplسار1.8) and low range in complexity (Asfc) due to a high density of scratches and a low density of pits. This has been interpreted as indicating consumption of ‘tough’, challenging foods. The opposite is found in *A. sediba* and some specimens of *P. robustus*, indicating occasional consumption of ‘hard’ foods (Scott et al., 2005; Ungar and Scott, 2009; Ungar and Sponheimer, 2011; Henry et al., 2012; Ungar et al., 2012). It has been argued that more complex microwear textures could also be a product of increased quartz consumption, due to living in a more arid environment (Lucas et al., 2013; Schulz et al., 2013; Merceron et al., 2016)—meaning that the observed differences between *A. africanus* and *P. robustus* could be due to greater dust or grit consumption, as a result of increased aridity (Vrba, 1975, 1985; Reed, 1997; Lee-Thorp et al., 2007). However, a broad analysis of extinct hominins and bovids and experimental work on dust suggests that increasing dust and/or grit in the diet is unlikely to explain the interspecific and regional differences observed in hominin microwear (Merceron et al., 2016; Ungar et al., 2016). As *P. robustus* and *Homo* sp. fossils have been recovered from the same stratigraphic units at Swartkrans and Drimolen (e.g., Grine et al., 2009; Moggi-Cecchi et al., 2010), differences in dental microwear between them are likely due to diet.

Assessing tooth size and structure, *P. robustus* has relatively larger molars with thicker enamel than many other hominins, possibly indicating an adaptation towards bulk feeding (i.e., the consumption of large amounts of poor quality foods), high bite force production, and/or consumption of more dietary abrasives (McHenry, 1984; Madden, 2015; Skinner et al., 2015; Ruiz and Arsuaga, 2017). The C4 and dental microwear signatures make a shift towards bulk feeding less likely, as bulk feeding tends to manifest in higher C4 values and more scratches/less pits. Compared to *P. robustus*, *Homo* sp. has smaller teeth with absolutely and relatively thinner enamel (Skinner et al., 2015), which, given that the two taxa lived in the same environment, points towards dietary differentiation, possibly due to different food processing methods (e.g., extraoral food processing with tools and/or cooking foods in *Homo*; Wrangham, 2009; Zink et al., 2014). Functional studies have produced contradictory results, suggesting that *A. africanaus* was both better and worse adapted for consuming hard, brittle food items than *P. robustus* (Spears and Crompton, 1994; Berthaume et al., 2010). Although disparities can arise depending on the method used and how the results are interpreted, all studies point toward ecological differentiation among South African taxa.

1.2. Dental topography

A popular method for quantifying tooth shape, dental topographic analysis, is used here to contextualize potential ecological differentiation in *H. naledi* (Zucchini et al., 1998; Evans, 2013). Dental topography is “a method of quantifying and representing 2.5 or 3D whole tooth shape with a single metric” (Berthaume, 2016a:680), and has successfully been used to correlate tooth shape to diet (Ungar, 2004; King et al., 2005; Godfrey et al., 2012; Ledogar et al., 2013; Winchester et al., 2014; Berthaume and Schroer, 2017). Originally developed using geographic information systems (GIS) technology (Zucchini et al., 1998; Ungar and Williamson, 2000), it has since come to encompass several non-GIS specific methods (Evans, 2013). Besides inferring dietary ecology, dental topography has also been used to predict enamel surface morphology from the shape of the enamel-dentine junction (Skinner et al., 2010; Guy et al., 2015), to investigate evolutionary pressures, such as niche partitioning (Boyer et al., 2012; Godfrey et al., 2012; Berthaume and Schroer, 2017), and to describe and assign a primate fossil to a new species (Boyer et al., 2012). The relationship between tooth shape and food item breakdown have additionally been investigated (Thiery et al., 2017a, 2017b), but how foods break down during mastication is not yet fully understood, and the proposed categories (e.g., crushing, grinding) need to be better defined from a fracture mechanics standpoint before this classification system can be used (Berthaume, 2016b; Thiery et al., 2017b).

The first metrics to reliably quantify tooth shape and relate it to dietary ecology, shearing ratio and shearing quotient, established that teeth with relatively longer shearing crests were more efficient at masticating fibrous and chitinous foods in small mammals (Sheine and Kay, 1977, 1982). A major drawback of this approach is that shearing crests can be measured only on unworn teeth with defined shearing crests. Dental topography overcomes these limitations and can be used to quantify dental morphologies at all wear stages (Ungar and M’Kirera, 2003; Winchester et al., 2014). We employ four dental topographic metrics in the South African hominins: orientation patch count rotated (OPCR), Dirichlet normal energy (DNE), relief index (RFI) and ambient occlusion (PCV, portion de ciel visible or ‘portion of visible sky’). Orientation patch count rotated is used to quantify occlusal complexity (Evans et al., 2007). From a functional perspective, it quantifies the number of ‘tools’ (e.g., cusps, crests, crenulations, and cutting edges) on the tooth’s surface: a tooth with more tools is more efficient at chewing foods with structural fibers and has a higher OPCR value. Dirichlet normal energy is a measure of surface curvature, and is used to quantify tooth sharpness, with sharper teeth having higher DNE values (Bunn et al., 2011). Unlike other measures of curvature (e.g., curvature in Guy et al., 2013), DNE does not differentiate between convexities and concavities (i.e., positive and negative curvatures).
However, it is strongly positively correlated to shearing quotient and shearing ratio in unworn teeth, indicating that it is a good measure of positive tooth curvature (Bunn et al., 2011; Winchester et al., 2014). Unlike shearing quotient and shearing ratio, DNE can be used for teeth with a variety of morphologies in a variety of wear stages (Pampush et al., 2016). Depending on the surface cropping method used (i.e., the entire crown or just the portion of the crown superior to the lowest point on the talonid basin), relief index (RFI) quantifies relative crown and/or cusp height. High-crowned/cusped teeth have higher RFI values, while teeth with lower crowns/cusps have lower RFI values (Ungar and M’Kirera, 2003; Boyer, 2008). Finally, ambient occlusion, a relatively new dental topographic metric, quantifies the likelihood of tooth wear (Berthaume, 2016a). Ambient occlusion is a method for making 3D images appear more realistic by approximating the amount of ambient lighting that would be shining across the surface. Measured from above the occlusal surface, a point with higher ambient occlusion, or PCV, will be more likely to contact a food item/opposing tooth during a masticatory cycle than a point with lower PCV. Consequently, areas of the tooth with higher PCV values have an increased probability of wearing during a masticatory cycle. Portions of the tooth responsible for food item fracture (e.g., cusps and crests) tend to have higher PCV values, while areas responsible for trapping/stabilizing the food item and increasing dental longevity (e.g., basins, and the sides of the crown, respectively) tend to have lower values (Fig. 1; Berthaume, 2016a). When all PCV values are averaged over the surface, teeth with lower mean PCV values are less likely to experience large levels of wear during mastication and are, therefore, more wear resistant. In addition to the dental topographic metrics, tooth size, measured via projected cross-sectional area (Boyer, 2008), was quantified, as this measure is correlated to diet in primates.

2. Materials and methods

2.1. Sample

Out of a total of 102 mandibular second molars available from eight South African fossil hominin-bearing sites, 43 relatively unworn teeth with well-preserved enamel caps were selected for analysis (A. africanaus = 16, P. robustus = 16, H. naledi = 8, Homo sp. = 3; see Supplementary Online Material [SOM] Tables S1 and S2 for accession numbers). Lower second molars were chosen because: 1) they are morphologically highly (although not exclusively) representative of the postcanine dentition (Kay, 1975; Sheine and Kay, 1977); 2) the relationship between M2 shape and diet in primates is well established (e.g., Boyer, 2008; Godfrey et al., 2012; Ledogar et al., 2013; Winchester et al., 2014); and 3) dietary signatures are stronger in mandibular than maxillary teeth in dental topographic analyses (Allen et al., 2015). This does not imply other postcanine teeth hold no dietary signatures (e.g., Kay, 1975, 1981; Sheine and Kay, 1977, 1982; Berthaume, 2014; Winchester et al., 2014; Allen et al., 2015). The sample of Homo sp. includes fossils from Swartkrans (i.e., SK 15), Sterkfontein Member 5 West (i.e., Stw 80), and the mandible from the Cave of Hearths that have been referred to as Homo ergaster/Homo erectus. The Cave of Hearths mandible is poorly dated, but recovered from Acheulean levels (Herries, 2011). It was suggested that this mandible could belong to H. naledi (Berger et al., 2017), but it differs from H. naledi in premolar and molar crown morphology (L.K.D., pers. obs.), and plots out separately from H. naledi in most of our analyses. It is likely younger than either the Swartkrans or Sterkfontein Homo material included in this study and may represent Homo rhodesiensis/Homo heidelbergensis (e.g., Tobias, 1971; Kuman and Clarke, 2000; Torley and Shwadron, 2014). During sample preparation, two possible antimeres were included for H. naledi; in particular, U.W. 101–507 and U.W. 101–145 are likely antimeres, and U.W. 101–377 and U.W. 101–789 have been suggested to be antimeres (L.K.D., pers. obs.), although the former is 12.67% smaller than the latter (128.334 mm² vs. 146.955 mm², quantified through outline area; Boyer, 2008). No antimeres were used for A. africanaus or P. robustus, and no antimeres were present for Homo sp.

2.2. Surface digitization

Digital representations of the teeth were created using a BIR Actis 300/255 FP, SkyScan 1172, or a Nikon Metrology XTH 225/320 microtomography (microCT) scanner at resolutions of 14–91 µm (only four teeth are at a resolution of 91 µm, all other teeth are at resolutions of 14–36 µm; see SOM Table S2 for resolutions). CT scans were processed in Aivoz 8.1 (FEI, Hillsborough, USA) by thresholding, removing any matrix or bone touching the outer surface of the enamel cap, using the ‘smooth labels’ command (size = 3, 3D volume), and generating surfaces (smoothing type: existing weights). Surfaces files were imported into Geomagic Studio 2013 (3D Systems, Morrisville, USA), where the outer surface of the enamel cap was isolated and edited (e.g., smoothed, reconstructed, and/or erasing cracks; SOM Table S2). When necessary and possible, portions of missing enamel along the cervical margin were repaired, and teeth were cropped.

Two surface cropping methods are commonly used for dental topography, using the entire enamel cap (EEC) or the portion of the enamel cap superior to the lowest point on the occlusal basin (BCO). BCO is popular because it is not always possible to mold or scan the entire tooth or because of enamel chipping along the cervical margin (Zucconi et al., 1998; Ungar and Williamson, 2000; M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Dennis et al., 2004; King et al., 2005; Evans et al., 2007; Godfrey et al., 2012; Berthaume and Schroer, 2017). Entire enamel cap was introduced in Boyer (2008) because there were taxa for which the BCO could not be reliably employed. The EEC method is advantageous as it considers whole tooth shape, providing information about tooth shape not responsible for food item breakdown that is related to diet (e.g., relative crown height), but requires 3D scans. The BCO method is advantageous as it attempts to isolate portions of the tooth responsible for food item breakdown and can be done with both 2.5 and 3D scans, as the cervix is not always imaged in 2.5D.

Figure 1. 3D image of light shining from the superior direction onto the occlusal surface of the tooth. Portions of the tooth that are more exposed to ambient light (i.e., high exposure) are more likely to come in contact with food, grit, and/or an opposing tooth during mastication, making them more likely to experience wear than areas less exposed to ambient light (i.e., low exposure). Teeth that are less exposed to ambient light have a lower PCV score and are more wear resistant.
scans. Previous studies have reported no significant differences in dental topographic values due to cropping method (Bunn et al., 2011; Godfrey et al., 2012; Prufrock et al., 2016), but have suffered from small sample sizes. All teeth were subjected to both the ECC and BCO to determine if the two cropping methods produced statistically different results.

Edited tooth surfaces were reimported into Avizo, simplified down to 10,000 and 20,000 triangles, and smoothed (100 iterations, lambda = 0.6; Boyer, 2008; Bunn et al., 2011; Winchester et al., 2014). Triangle counts of 10,000 are standard for DNE studies (Bunn et al., 2011; Winchester et al., 2014), but tend to oversimplify large and complex teeth (Berthaume and Schroer, 2017). A triangle count of 20,000 was suggested by Berthaume and Schroer (2017), but higher triangle counts have been recommended for other dental topographic metrics (e.g., 22,000 and 55,000; Guy et al., 2013, 2015; Lazzari and Guy, 2014; Thiery et al., 2017a). Simplified and full versions of the teeth were imported into CloudCompare (2017) and oriented into anatomically correct position, using fossils with portions of the mandible preserved as guides. Specimen specific deviations from the procedure detailed in this section can be found in the SOM Table S2.

2.3. Calculating shape and size

DNE, RFI, OPCR, and tooth size were calculated using Morpho-tester (Winchester, 2016). Two values were reported for DNE, removing the top 1% (DNE 99%) and 5% (DNE 95%) energy \times area values, as taphonomic processes can cause an unusually high number of sharp edges at fissures on the occlusal surface. This causes artificial inflations in DNE scores when 1% outlier removal was used; 5% outlier removal discarded these artifacts. RFI is a function of surface and cross-sectional areas (Boyer, 2008): RFI = ln (sqrt(SA/CA)). Cross-sectional area is also the measure of tooth size. OPCR here is not directly comparable to OPCR calculated using 2.5D surfaces with regular grids (Evans et al., 2007; Wilson et al., 2012; Evans, 2013; Winchester, 2016), but is correlated. PCV was calculated in CloudCompare using the ‘PCV’ function, with the ‘fits a statistical model on the active scalar field’ command, which reports on an average PCV value (Berthaume, 2016a). Dental topography was performed on surfaces simplified to 10,000 triangles, as is typical in dental topographic studies (e.g., Godfrey et al., 2012; Winchester et al., 2014) and 20,000 triangles, as occlusal features were better preserved at 20,000 triangles. It is important to keep triangle count constant, as some dental topographic metrics are sensitive to triangle count (e.g., DNE and OPCR; Bunn et al., 2011; Evans and Janis, 2014).

To contextualize the hominin DNE results, they are compared to published DNE results on great apes (Berthaume and Schroer, 2017). As the great ape data were collected with the BCO cropping method, we employed both the ECC and BCO and investigated the effect of cropping method on our results. Finally, as great ape data used Laplacian smoothing, which affects DNE results (Spradley et al., 2017), hominin teeth had Laplacian smoothing applied when compared to the great ape data.

2.4. Tooth wear

As in previous studies (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003), tooth wear was scored using Scott’s (1979) dental scoring technique. However, it was modified, where the entoconid, metaconid, protoconid, hypoconid, and hypoconulid were each scored from 0 to 10, where a score of 3 indicates cusps had significant wear, but no dentin was exposed and cusps retained their relative curvature (Scott, 1979). When additional cusps were present, they were not scored. A final wear score was calculated by averaging the scores from across the five cusps. Tooth wear was scored using a combination of photographs of the fossils and the surface files of the teeth.

2.5. Statistical analyses

Statistical analyses were run in RStudio using R v3.2.3 on the 10,000 ECC, 20,000 ECC, 10,000 BCO, and the 20,000 BCO separately (R Development Core Team, 2015). A two-way ANOVA was run to determine if species and/or wear stage had a significant effect on dental topographic results. Tooth size was analyzed with dental topographic results as topographic scores can predict diet more efficiently when tooth size is included (Bunn et al., 2011; Winchester et al., 2014). Kendall’s and Pearson’s correlations were used to evaluate the strength of the relationship between shape (DNE, OPCR, RFI, and PCV) and size and wear scores within each species. Exact p-values were calculated for Pearson’s correlation, but not Kendall’s due to ties. Pearson’s pairwise correlations were run between shape and size values to determine if any relationship existed among these metrics. Dental topographic variables were analyzed separately.

As wear had a significant effect on some shape and size values, one-way ANOVAs were run on moderate and lightly worn teeth separately to determine if there was any difference in shape and size values between species in R and RStudio (R Development Core Team, 2015; RStudio Team, 2016). Tukey’s honestly significant difference (HSD) tests were run to determine where significant differences occurred between species. Mann-Whitney U-tests and Student’s t-tests were run to determine if there was any difference in cropping methods. Although previous studies have shown there is a phylogenetic signal in tooth shape and size (Winchester et al., 2014), it is not possible for us to run phylogenetically corrected analyses as there is no secure, agreed, or well-quantified phylogeny for these taxa.

3. Results

Forty-three hominin M2 from eight sites were included in the dental topographic analysis (Table 1; SOM Table S2). Descriptive dental topographic statistics can be found in Table 2. Additional descriptive statistics for different triangle counts and cropping methods can be found in the SOM Tables S3 to S5. As in previous studies, significant relationships exist between many shape and size variables (Table 3). Relationships between shape and size variables for different triangle counts and cropping methods are found in SOM Tables S16 to S18. DNE 95% and DNE 99% are correlated to all other metrics (positively with each other, OPCR and RFI, negatively with PCV), and a negative correlation exists between RFI and PCV. Tooth size is correlated to PCV and RFI. Given the low sample of Homo sp. (n = 3), it was excluded from statistical analyses but compared to the range of values for the other taxa.

3.1. Wear

Similar to previous studies (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003), a two-way ANOVA showed many topographic metrics were significantly affected by occlusal wear and

Table 1

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Lightly worn</th>
<th>Moderately worn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australopithecus aficanus</td>
<td>10</td>
<td>7</td>
</tr>
<tr>
<td>Paranthropus robustus</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Homo naledi</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Homo sp.</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>
Results of two-way ANOVA investigating the effect of wear stage and taxon on dental topographic results. Significant p-values (p < 0.05) are in bold. The drastic change in results is due to a large number of highly curvy singularities on the surface of the tooth, usually located at the fissures that form at the intersection of the cusps. Differences in DNE, OPCR, and PCV due to wear are easily visible for each taxon (Fig. 2; note that RFI is a ratio and cannot be visualized). Kendall’s correlations between wear and shape and size metrics within each taxon revealed significant correlations between tooth wear and a) DNE 99% and DNE 95% in all taxa (p < 0.001 – 0.034); b) PCV in P. robustus and H. naledi (p < 0.001); c) RFI in P. robustus (p < 0.001); and d) OPCR in A. africanus (p = 0.044; Table 5). Wear was never significantly correlated to tooth size (p = 0.111–0.618), despite the presence of interproximal wear, which can significantly affect tooth size (Wood and Abbott, 1983). This could be because we did not include heavily worn teeth in our analysis. Kendall’s correlations for other triangle counts and cropping methods are found in SOM Tables S9 to S11. Pearson’s correlations revealed nearly identical results (SOM Tables S12 to S15), and, as such, are not reported here. We therefore analyzed lightly worn (Scott score < 3) and moderately worn (Scott score 3+) teeth separately.

### Table 2
Descriptive statistics for more lightly and moderately worn lower second molars.

| Tooth size | A. africanus | Moderate (10) | 168.388 | 158.5 | 4.132 | 180.297 | 170.592 | 4.702 |
| Tooth size | Moderate (7) | 123.5 | 112.1 | 2.267 | 0.614 | 0.506 | 0.003 | 187.529 | 184.391 |
| Tooth size | P. robustus | Light (7) | 148.096 | 142 | 5.463 | 0.556 | 0.552 | 0.002 | 205.045 | 208.778 |
| Tooth size | Moderate (8) | 161.594 | 155.875 | 5.617 | 0.601 | 0.6 | 0.004 | 203.794 | 194.643 |
| Tooth size | H. naledi | Light (5) | 143.625 | 143.625 | 1.787 | 0.513 | 0.506 | 0.003 | 133.227 | 131.926 |
| Tooth size | Moderate (3) | 148.083 | 148.5 | 2.336 | 0.536 | 0.542 | 0.006 | 134.689 | 134.145 |
| Tooth size | Homo sp. | Light (1) | 148.5 | 148.5 | 2.336 | 0.536 | 0.542 | 0.006 | 134.145 | 134.145 |
| Tooth size | Moderate (2) | 153.625 | 193.625 | 2.336 | 0.536 | 0.542 | 0.006 | 134.145 | 134.145 |

### Table 3
Coefficient of correlation (R), followed by p-values in parentheses for Pearson’s pairwise comparisons between form variables. Significant correlations (p < 0.05) are in bold.

| Tooth size | A. africanus | Moderate (10) | 0.819 (0) | 0.504 (0.001) | -0.102 (0.532) | 0.102 (0.532) |
| Tooth size | Moderate (7) | 0.654 (0.001) | 0.465 (0.002) | -0.125 (0.444) | 0.125 (0.444) |
| Tooth size | P. robustus | Light (7) | -0.702 (0) | -0.527 (0) | -0.527 (0) | 0.527 (0) |
| Tooth size | Moderate (8) | 0.355 (0.025) | 0.465 (0.002) | 0.061 (0.707) | 0.614 (0.003) |

### Table 4
Results of two-way ANOVA investigating the effect of wear stage and taxon on dental topographic results. Significant p-values (p < 0.05) are in bold.

### 3.2. Cropping method
Both Mann-Whitney U-tests and Student’s t-tests yielded identical results: regardless of triangle count or shape/size metric, cropping method caused a statistically significant difference in dental topographic values (p < 0.001–0.006; Table 6 and SOM Table S26). Since EEC provides information about relative crown height, EEC results were used to compare the hominins to each other; however, as the ape teeth were analyzed using BCO (due to differences in data acquisition which prevent EEC from being used), BCO was used to compare the hominin and ape data.
3.3. Taxonomic differences

One-way ANOVAs revealed taxonomic differences in RFI, PCV, and tooth size in lightly worn teeth ($p < 0.001$). The small sample size of moderately worn *H. naledi* teeth ($n = 3$; Table 1) prevented their inclusion in these statistical analyses. No differences existed between *A. africanus* and *P. robustus* in moderately worn teeth (SOM Tables S19 to S22). In lightly worn teeth, a Tukey HSD test revealed taxonomic differences in RFI and PCV, with *H. naledi* having the highest RFI, followed by *P. robustus*, then *A. africanus* (Table 7). The opposite trend is found with PCV, indicating *H. naledi* had the most wear resistant teeth, followed by *P. robustus*, then *A..
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toe when in the lightly worn sample, but smaller teeth in the
\( \text{Homo} \) sp. prohibits statistical
\( \text{significan} \) differences exist between
\( \text{P. robustus} \) and \( \text{A. africanus} \).

\( \text{Regardless of wear stage, triangle count, or form metric, results are always sensitive} \)
\( \text{Table 6} \)
\( \text{Mann-Whitney U-test results, testing the effect of cropping method (EEC vs. BCO).} \)

\( \text{Regardless of wear stage, triangle count, or form metric, results are always sensitive to cropping method.} \)

<table>
<thead>
<tr>
<th>Wear stage</th>
<th>Triangle count</th>
<th>Variable</th>
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\( a \) Cropping method – EEC. Triangle count – 20,000. \( p \)-values of 0 are less than 0.0005.

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cusps and crests are all still essentially salient, which may be why OPCR was not related to wear. It may only be in later stages of wear, when crests and cusps are obliterated and large dentin pools begin to form, that OPCR is significantly correlated to wear in hominins. Although changes in tooth size occur due to interproximal wear (Wood and Abbott, 1983), intraspecific variation plays a larger role in variation in M2 size in this study. 

Homo naledi displays a unique combination of dental topographic traits relative to other South African hominins, suggesting that this taxon could have occupied its own ecological niche. Within lightly worn teeth, H. naledi had the highest crowned (RFI) and most wear resistant (PCV) molars, indicating an adaptation for tooth longevity. The lack of differences in tooth sharpness (DNE) and the number of ‘tools’ on the occlusal surface (dental complexity, OPCR) of P. robustus, A. africanus, and H. naledi suggests that the teeth of H. naledi are no more or less efficient at chewing foods with structural fibers than are those of A. africanus and P. robustus. In other words, the differences in dental topography among the hominin samples may not reflect a shift towards lower quality foods such as grasses or sedges in H. naledi. Instead, the increases in dental longevity could be due to consuming foods with similar mechanical properties but different phytolith loads, or increased dust/ grit consumption (Lucas et al., 2013; Kaiser et al., 2015; Madden, 2015; Xia et al., 2015). The absolutely smaller molars in H. naledi relative to A. africanus and P. robustus suggest that the former was not consuming more mechanically challenging foods and further support the conclusion that H. naledi was not consuming foods that require bulk processing, such as grasses or sedges.

Figure 3. Dental topographic and tooth size results, per species, for lightly worn teeth (average Scott score < 3). Triangle count ~ 20,000. Cropping method – EEC.
There are two probable adaptive scenarios for an increase in dental longevity in H. naledi. The first is a dietary shift towards foods with a higher abrasive load, such as phytoliths, dust, or grit. A probable candidate for such foods would be underground storage organs, which, if unwashed, would transfer large amounts of grit to the oral cavity. The second is an environmental (climatic) shift towards increased aridity led to an incidental increase in dust and/or grit consumption, affecting all food sources. Among A. africanus,

<table>
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<tr>
<th>Pa. t. troglodytes</th>
<th>Pa. paniscus</th>
<th>Pa. t. schweinfurthii</th>
<th>Po. pygmaneus</th>
<th>G. g. gorilla</th>
<th>G. b. beringei</th>
<th>G. b. graueri</th>
<th>A. africanus</th>
<th>P. robustus</th>
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<tr>
<td>Pa. paniscus</td>
<td>99.107 (0.905)</td>
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<td>Pa. t. schweinfurthii</td>
<td>86.446 (0.965)</td>
<td>12.661 (1)</td>
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<td>Po. pygmaneus</td>
<td>188.431 (0.141)</td>
<td>89.323 (0.939)</td>
<td>101.985 (0.892)</td>
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<td>G. g. gorilla</td>
<td>110.255 (0.857)</td>
<td>11.148 (1)</td>
<td>23.809 (1)</td>
<td>78.176 (0.979)</td>
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<tr>
<td>G. b. beringei</td>
<td>132.533 (0.637)</td>
<td>33.425 (1)</td>
<td>46.087 (1)</td>
<td>55.898 (0.998)</td>
<td>22.278 (1)</td>
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<td>G. b. graueri</td>
<td>231.652 (0.041)</td>
<td>134.545 (0.657)</td>
<td>147.206 (0.575)</td>
<td>45.221 (1)</td>
<td>123.397 (0.787)</td>
<td>101.119 (0.91)</td>
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<td>A. africanus</td>
<td>306.926 (0)</td>
<td>207.819 (0.037)</td>
<td>220.48 (0.03)</td>
<td>118.495 (0.614)</td>
<td>196.671 (0.081)</td>
<td>174.393 (0.146)</td>
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<td>P. robustus</td>
<td>500.758 (0)</td>
<td>401.651 (0)</td>
<td>414.312 (0)</td>
<td>312.327 (0.001)</td>
<td>390.503 (0)</td>
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<td>267.106 (0.02)</td>
<td>193.832 (0.123)</td>
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<td>H. naledi</td>
<td>735.098 (0)</td>
<td>635.99 (0)</td>
<td>648.651 (0)</td>
<td>546.667 (0)</td>
<td>624.843 (0)</td>
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<td>501.446 (0)</td>
<td>428.171 (0)</td>
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a Great ape data are from Berthaume and Schroer (2017).
b p-values of 0 are less than 0.0005.
A. africanus (EEC, 20,000, lightly worn teeth). Coef
dust consumption and/or tooth longevity. Differences in DNE have not been shown to be correlated with grit/
function of cooking and/or food processing relaxed the selective forces
acting on tooth sharpness (Wrangham, 2009; Zink et al., 2014), or
der the selective forces that generated the high levels of shear forces. Relative
imply their diets required higher shear forces, for eating substances such as plant
fibre, compared to the great apes. Sharper teeth are more efficient at producing high shear forces during mastication,
which is advantageous for processing foods high in structural
fibres; this is the reason primates that consume more plant fibre have higher DNE values (Godfrey et al., 2012; Winchester et al.,
2014; Berthaume and Schroer, 2017). Foods high in structural
fibres can be low (e.g., grasses, sedges, bark, and leaves) or high (e.g.,
USOs, animal muscle fascics and fibres) quality.2 Therefore, from a
fracture mechanics perspective, the higher DNE in A. africanaus, P. robustus, and H. naledi could be an adaptation towards consuming
a large range of resources requiring shear forces to process. Relative
to the great apes and the other hominins, the apparent reversion in DNE with Homo sp. could have occurred due to a dietary shift to-
wards foods requiring lower shear forces, because the introduction of
cooking and/or food processing relaxed the selective forces
acting on tooth sharpness (Wrangham, 2009; Zink et al., 2014), or
because their diet did not require high shear forces to process. It is
unlikely that differences in DNE are environmentally driven, as differences in DNE have not been shown to be correlated with grit/ dust consumption and/or tooth longevity.

2 Foods high in structural fibre have traditionally been classified as 'tough,' but it is
recommended that this term not be used, as toughness has more than one
definition in materials science (Berthaume, 2016b). Toughness, as used by Lucas
(2004), is energy release rate. Objects with high energy release rates resist shear
tensile fracture with variable levels of efficiency. In plants, energy release rate and
fibre content are correlated (Lucas et al., 2000; Westbrook et al., 2011), and
plants with high energy release rates are most efficiently processed with shear
forces.
work has suggested it ate larger amounts of low quality, mechanically challenging foods, such as grasses, sedges, or underground storage organs (Ungar et al., 2008; Cerling et al., 2011; Grine et al., 2012). This and other discrepancies between morphology and isotopes/microwear have led some researchers to question whether morphology can be used to predict diet (Strait et al., 2009, 2012, 2013; Grine et al., 2010; Daegling et al., 2013). This debate was further fueled by observed discrepancies between morphology and diet in extant taxa (e.g., King et al., 2005). But this need not be the case, as isotope/microwear analyses can be used in conjunction with morphological analyses to produce new hypotheses about the diets of extinct taxa (Dominy et al., 2008; Macho, 2014).

5. Conclusions

Overall, *H. naledi* has smaller, higher-crowned and wear resistant teeth than *A. africanus* and *P. robustus*. Thus, despite similarities in brain size, body size, and hand and shoulder anatomy suggesting ecological constraints and environmental exploitation similar to *Australopithecus* (Kivell et al., 2015; Feuerriegel et al., 2017; Garvin et al., 2017), the results of this study suggest that *H. naledi* teeth are distinct in functional anatomy from those of *Australopithecus* and *Paranthropus*. In conjunction with the apparent difference in DNE and PCV between *H. naledi* and *Homo* sp., it appears *H. naledi* carved out an ecological niche in southern Africa that required it to have more wear resistant, tall crowned teeth than any other hominin measured in this study. Several dental traits that distinguish *H. naledi* from *A. africanus* and *P. robustus* also distinguish it from *Homo* sp., both the older material from Swartkrans and Sterkfontein and the younger specimen from the Cave of Hearths. These differences in dental morphology, in conjunction with differences in DNE 99% and DNE 95%, suggest the potential for ecological differentiation between *H. naledi* and other South African *Homo* as well. The results of this study are thus inconsistent with the simple notion that *H. naledi* represents a hominin in the Middle Pleistocene with an *Australopithecus*-like ecology, or that African Middle Pleistocene *Homo* were adaptively and ecologically uniform. Whether differences in dental shape and size reflect adaptations to dietary or environmental (e.g., grit loads) factors, we cannot say now. However, these differences do provide context for interpreting future microwear and isotopic studies of the taxa (e.g., Henry et al., 2012) and highlight the need for paleoenvironmental reconstructions for the Rising Star hominin sites.

Acknowledgements

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Supplementary Online Material

Supplementary online material related to this article can be found at https://doi.org/10.1016/j.jhevol.2018.02.006.

References


