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 known geographical ranges. *Homo 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 South African hominins that predate it.

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; Pruetz, 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., Stw 80, SK 15, Cave of Hearths mandible), all of which are presumed to predate the remains of *H. naledi* from Rising Star.

**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*, *A. 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 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 (ePLsar₁₄) 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’, mechanically 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.

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1 The definitions of ‘tough’ and ‘hard’ foods do not always align with those in engineering/materials science, where tough items absorb large amounts of energy per unit volume, and hard ones resist plastic deformation at their surface (Berthaume, 2016b).
Dental topography

A popular method for quantifying tooth shape, dental topographic analysis, is used here to contextualize potential ecological differentiation in *H. naledi* (Zuccotti 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: p. 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 (Zuccotti 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
ing 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.

**Materials and methods**

**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. africanus = 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 $M_2$ 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/H. 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/H. heidelbergensis (e.g., Tobias, 1971; Kuman and Clarke, 2000; Herries and Shaw, 2011). Due to small sample size, 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. africanus* or *P. robustus*, and no antimeres were present for *Homo* sp.

**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 Avizo 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, 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 (Zuccotti 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 teeth 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 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 (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.

Calculating shape and size
DNE, RFI, OPCR, and tooth size were calculated using Morphotester (Winchester, 2016). Two values
were reported for DNE, removing the top 1% (DNE 99%) and 5% (DNE 95%) energy*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 (RFI = ln
(sqrt(SA/CA)); Boyer, 2008). 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, 2008; 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 EEC 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.

**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 0–10, 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.

**Statistical analyses**

Statistical analyses were run in RStudio using R v3.2.3 on the 10,000 EEC, 20,000 EEC, 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- 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.

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.

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 taxon, but not the interaction variable between wear and taxon (Table 4). Additional two-way ANOVAs for different triangle counts and cropping methods are found in SOM Tables S6 to S8. Taxon is important for DNE 99%, but not DNE 95%—this difference is due to the top 5% of the ‘curviest’ parts of the surface being disregarded in DNE 95% compared to the top 1% in DNE 99%. 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.

**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.

**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. africanus*. Significant differences exist between *H. naledi* and *P.*
rostus/A. africanus in tooth size, but no difference in tooth size existed between A. africanus and P. robustus. Boxplots of shape and size values are shown in Figure 3 for lightly worn teeth. Descriptive statistics and additional boxplots, ANOVAs, and Tukey HSD tests for moderately worn teeth, and different cropping methods and triangle counts, which produced the same pattern of results, can be found in SOM Tables S19 to S25.

Although the small sample size for Homo sp. prohibits statistical analyses, it appears H. naledi differs from Homo sp. in the same direction that it differs from A. africanus and P. robustus (Figs. 2 and 3). Additionally, H. naledi may differ from Homo sp. in DNE 99% and DNE 95%. Compared to Homo sp., H. naledi has relatively larger teeth when in the lightly worn sample, but smaller teeth in the moderately worn sample. This discrepancy is likely due to a small sample in Homo sp. (Fig. 3; SOM Table S2). Compared to the great apes, all hominins had curvier, sharper teeth (Fig. 4, Table 8).

To further contextualize the results, they were compared to published great ape data (Berthaume and Schroer, 2017; Fig. 4). For the sake of comparison, DNE99% was performed on teeth with the basin cut off (BCO) cropping method with Laplacian smoothing (Spradley et al., 2017). One-way ANOVA and Tukey HSD tests reveal that P. robustus and H. naledi have curvier teeth than all great apes \( p < 0.0005-0.02; \) Table 8). Australopithecus africanus has curvier teeth than Pan, but no differences exist between A. africanus and Gorilla or Pongo. Processing the teeth in this manner also caused a difference in DNE to develop between A. africanus and H. naledi \( p < 0.001 \), indicating significant differences in DNE 99%. The \( M_2 \) of the Cave of Hearths Homo mandible falls within the DNE range of all apes except for Pan troglodytes troglodytes.

**Discussion**

It has been observed that there is very low variation in tooth shape in H. naledi when compared to other hominins (Skinner et al., 2016; Delezene et al., 2017). For lightly worn teeth in this study, H. naledi has the lowest level of coefficient of variation for five of the six shape and size variables (Homo sp. was excluded because of sample size; Table 9). Overall, it appears that there is less variation in tooth shape in H. naledi than in A. africanus or P. robustus, which could be due to a) low variation within the species, b) the
*H. naledi* sample in this study being from a single chamber (i.e., the Dinaledi chamber), whereas both *A. africanus* and *P. robustus* are represented from several sites spanning a larger temporal and geographical range, or c) chance sampling and low sample sizes.

As in previous studies (e.g., M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; King et al., 2005; Glowacka et al., 2016; Pampush et al., 2016), tooth wear played a significant role in some of the dental topographic metrics. As expected, wear caused DNE 99%, DNE 95% and RFI to decrease, indicating the teeth were becoming duller and lower crowned (Figs. 2 and 3). Wear caused PCV to increase, indicating teeth became less wear resistant as they became more worn. OPCR was uncorrelated to tooth wear, which initially seemed counterintuitive as teeth lose ‘tools’ (e.g., crenulations) as they wear. However, in the initial stages of wear, the 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 cusps 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 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.

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, P. robustus*, and *H. naledi*, temporal increases in relative crown height (RFI) and wear resistance (PCV) are coincident with an increasingly dry and arid environment (Vrba, 1975, 1985; Lee-Thorp et al., 2007). Therefore, it is possible that the foods being consumed by *H. naledi* had more inorganic abrasives on them, which required more wear-resistant molars. A recent study reported an extremely high level of dental chipping in *H. naledi* (Towle et al., 2017), suggesting the increase in dental longevity could be an adaptation to offset high levels of wear due to accidental grit consumption. It is not possible from our data to discern whether this is because of a dietary (e.g., underground storage organs, USOs) or an environmental shift. Data from stable carbon isotope and dental microwear analyses for *H. naledi* (e.g., Henry et al., 2012) will shed light on this issue.

The great apes were found to have duller, less curvy teeth than hominins in some analyses (Fig. 4). This may seem odd that, given their generally taller cusps generate relatively longer shearing crests that would, presumably, increase tooth sharpness. However, it appears that the extremely crenulated surfaces of some hominin teeth (i.e., *A. africanus* and *P. robustus*) may be making their occlusal surfaces, overall, sharper: but this cannot be the case for *H. naledi*, which lacks crenulations (L.K.D., pers. obs.). The relatively higher DNE values in *H. naledi*, *A. africanus*, and *P. robustus* imply their diets required higher shear forces, for eating substances such as plant fiber and/or muscle fiber, 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 fibers; this is the reason primates that consume more plant fiber have higher DNE values (Godfrey et al., 2012; Winchester et al., 2014; Berthaume and Schroer, 2017). Foods high in structural fiber can be low (e.g., grasses, sedges, bark, and leaves) or high (e.g., USOs, animal muscle
fascicles and fibers) quality. Therefore, from a fracture mechanics perspective, the higher DNE in \textit{A. africanus}, \textit{P. robustus}, and \textit{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 \textit{Homo} sp. could have occurred due to a dietary shift towards 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.

Previous hominin dental topographic studies (Ungar, 2004, 2007) have reported that \textit{Homo} sp. had molar cusps with steeper slopes and higher relief than \textit{A. afarensis}, and that \textit{A. africanus} had molar cusps with steeper slopes compared to \textit{P. robustus}. However, Ungar (2004, 2007) did not calculate RFI for the South African sample. The reported difference in RFI in this study show \textit{A. africanus} to have lower relief than \textit{P. robustus} (Fig. 3, Table 7), which is the opposite of what is expected given the correlation between slope and RFI in the east African hominins and great apes reported in Ungar (2004, 2007), although this could be due to differences in cropping methods (EEC vs. BCO). To investigate if this was the case, we used the same cropping method as Ungar (2004, 2007) to make our results comparable. Using the BCO cropping method produced the same results as using the EEC: the molar cusps of \textit{A. africanus} still had lower relief than \textit{P. robustus}, although the difference was no longer statistically significant ($p = 0.122–0.133$; SOM Figs. S1 to S7 and Tables S3 to S5). This suggests there is some discordance among the hominin dental topographic results, where it may be possible for some hominins to have cusps with steeper slopes and higher relief, and others to have steeper slopes and lower relief—a discordance that must be remedied to provide better dietary reconstructions through dental topographic analyses using these methods.

Ungar (2004, 2007) reported on differences in hominin cusp slope that mirrored those found in chimpanzees and gorillas. Based on similarities in primary diet in \textit{Pan troglodytes} and \textit{Gorilla gorilla}, but

\footnotetext{2}{Foods high in structural fiber 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 and tensile fracture with variable levels of efficiency. In plants, energy release rate and fiber 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.}
differences in fallback foods, Ungar (2004, 2007) concluded that differences in tooth shape reflected differences in fallback foods, and that the hominins, *Homo* sp. and *A. africanus*, fell back on ‘tougher’ foods than *A. afarensis* and *P. robustus*, respectively. Since these pioneering studies, research has shown that dental topography frequently reflects primary diet in primates (e.g., Winchester et al., 2014; Berthaume and Schroer, 2017), so differences in tooth shape may reflect differences in preferred, not fallback, foods. It appears that, from a topographic perspective, the relationship between tooth form and preferred vs. fallback food is not straightforward. A recent study on great apes additionally showed that comparing allopatric hominoids must be done carefully, as character displacement has occurred in great ape tooth shape due to indirect competition over dietary resources (Berthaume and Schroer, 2017), although, fortunately, the signature for relative fiber content appears to be unaffected by this evolutionary phenomenon. The fact that *H. naledi* was temporally separated, and therefore allochronic from the other hominins in our sample (Dirks et al., 2015), hinders an easy interpretation of the results of this study.

Without more associated faunal material, or other information on the paleoenvironment of *H. naledi* (see Dirks et al., 2015), it is currently impossible to determine if the competitive environment in South Africa was similar from the early to the late Middle Pleistocene, the time interval in which *A. africanus*, *P. robustus*, *Homo* sp., and *H. naledi* existed. However, from a perspective of the functional morphology of the molars, *H. naledi* seems unlikely to have had an *Australopithecus*-like pattern of resource exploitation, despite sharing similarities in brain size, body size, and hand and shoulder morphology (Berger et al., 2017).

It could be argued that a drawback of this study comes from the potential decoupling between morphology and diet. Dietary signatures drawn from morphology do not always match dietary signatures from other methods, such as stable carbon isotope or dental microwear analyses. This was thought to be the case with *Paranthropus boisei*, which has large teeth and a powerfully-built skull coupled with large chewing muscles, leading many to expect that it consumed hard foods, such as nuts or seeds (Jolly, 1970; Rak, 1983; Demes and Creel, 1988; Dzialo et al., 2013; Smith et al., 2015). However, more recent isotope and microwear 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).

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 RFI 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.
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**Figure Captions**

**Figure 1.** 2D 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.

**Figure 2.** Lightly worn (gray background) and moderately worn M₂ for *Australopithecus africanus* (STW 560E and 109), *Paranthropus robustus* (DNH 60c, SK 858), *Homo naledi* (U.W. 101-307 and U.W. 101-1261),
and South African Homo sp. (Cave of Hearths and STW 80) with dental topographic scores approaching the average for each species. Dark blue triangles along the cervical margin and at the intersections of the cusps in the DNE 99% pictures represent triangles discarded using 1% outlier removal (energy*area). Note that STW 80 is mirrored to make it comparable to the other teeth in the 3D views. Teeth are not to scale.

**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.

**Figure 4.** Ape vs. hominin DNE using published ape data (20,000 triangles, DNE 99%, BCO, lightly worn, Laplacian smoothing = 2; Berthaume and Schroer, 2017). As in a previous study (Spradley et al., 2017), Laplacian smoothing caused DNE to decrease from 3.62 to 23.67% for all teeth (except SKX 4446, which has a 40% increase), but was necessary to make the hominin data comparable to the ape data. Hominin data was recalculated with the BCO to make it comparable to the great ape data. All comparisons without the apes were done using the entire enamel cap (EEC) without Laplacian smoothing. Abbreviations: Ptt = *Pan troglodytes* troglodytes; Ppa = *Pan paniscus*; Pts = *Pan troglodytes schweinfurthii*; Ppy = *Pongo pygmaeus*; Ggg = *Gorilla gorilla gorilla*; Gbb = *Gorilla beringei beringei*; Gbg = *Gorilla beringei graueri*; Aa = *Australopithecus africanus*; Pr = *Paranthropus robustus*; Hn = *Homo naledi*; Hsp = *Homo sp.*