

1 Dental topography and the diet of *Homo naledi*

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3 Michael A. Berthaume^{a,b,*}, Lucas K. Delezene^{c,d}, Kornelius Kupczik^a

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5 ^a *Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Max Planck Institute for*
6 *Evolutionary Anthropology, Deutscher Platz 6, Leipzig, 04103, Germany*

7 ^b *Department of Anthropology, Durham University, Dawson Building, South Road, Durham, DH1 3LE, United*
8 *Kingdom*

9 ^c *Department of Anthropology, University of Arkansas, 330 Old Main, Fayetteville, Arkansas, 72701, United*
10 *States of America*

11 ^d *Evolutionary Studies Institute, University of the Witwatersrand, 1 Jan Smuts Avenue, Braamfontein 2000,*
12 *Johannesburg, South Africa*

13

14 *Corresponding author.

15 *E-mail address:* michael.a.berthaume@durham.ac.uk (M.A. Berthaume).

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20

21 **Abstract**

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

39

40 **Introduction**

41 Ecological reconstructions help clarify niche partitioning, and some of the most successful hominin
42 reconstructions have relied on dental remains (e.g., Grine et al., 2012; Henry et al., 2012; Sponheimer et al.,
43 2013). Dental differences (e.g., absolute and relative tooth size, dental proportions, dental topography,
44 absolute and relative enamel thickness) among hominin taxa are often cited to reflect dietary shifts, but
45 can also reflect environmental or a combination of environmental and dietary shifts (Lucas et al., 2008;
46 Ungar and Sponheimer, 2011). For example, increases in aridity can lead to a decrease in fruit availability, a
47 change in food mechanical properties, and/or an increase in dust/grit consumption (Onoda et al., 2011).

48 Little is known about the ecology of the recently discovered hominin *Homo naledi* (Berger et al., 2015,
49 2017; Hawks et al., 2017). Though Middle Pleistocene (236–335 ka) in age (Dirks et al., 2017), it resembles
50 species of *Australopithecus* by evincing a short stature, small body mass, and small brain, both absolutely
51 and relative to body size (Garvin et al., 2017). Small brains and bodies indicate differing energetic
52 requirements and home ranges compared to other species of Middle Pleistocene *Homo* (Antón et al.,
53 2014). Further, curved fingers and aspects of shoulder morphology suggest significant levels of climbing (
54 Kivell et al., 2015; Feuerriegel et al., 2017), which could point towards an *Australopithecus*-like pattern of
55 resource exploitation (Pérez-Pérez, 1988; Pruetz, 2006) for *H. naledi*. Yet, similar to *Homo* and unlike
56 *Australopithecus*, the lower limb is elongated (Marchi et al., 2017), sexual size dimorphism is minimal
57 (Garvin et al., 2017), and the postcanine teeth are absolutely small (Berger et al., 2015; Hawks et al., 2017).
58 In these regards, *H. naledi* appears to be a late surviving member of the genus *Homo*. This begs the
59 question of whether *H. naledi* occupied an ecological niche more like *Australopithecus*, other species of
60 Middle Pleistocene *Homo*, or neither.

61 Resolving this issue is complicated due to the minimal faunal remains associated with the more
62 than 1550 and 131 *H. naledi* fossils from the Dinaledi and Lesedi chambers, respectively, and the lack of
63 tools associated with this species (Berger et al., 2015; Dirks et al., 2015, 2017; Hawks et al., 2017). The
64 paucity of these data inhibits robust reconstructions of the *H. naledi* paleoenvironment and its pattern of
65 resource exploitation. In this paper, we investigate the dietary ecology of *H. naledi* by quantifying tooth
66 shape and contextualize the results by comparing them to three other groups of South African hominins:
67 *Australopithecus africanus*, *Paranthropus robustus*, and *Homo* sp. (i.e., Stw 80, SK 15, Cave of Hearths
68 mandible), all of which are presumed to predate the remains of *H. naledi* from Rising Star.

69 70 *Dental paleoecological evidence for Plio-Pleistocene hominins in South Africa*

71 Between 3.0 and 1.5 Ma, there were at least four hominin taxa in South Africa, and ecological
72 reconstructions for *A. africanus*, *P. robustus*, *A. sediba*, and *Homo* sp. indicate some niche partitioning
73 (Grine et al., 2012; Henry et al., 2012). During this time, the environment in South Africa changed from
74 more closed and mosaic to more open and arid (e.g., Vrba, 1975, 1985; Reed, 1997; Lee-Thorp et al., 2007).

75 Carbon isotope data from dental enamel reveal dietary overlap in these hominins and consumption of C₄
76 resources (Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999; Sponheimer et al., 2005, 2013; Grine
77 et al., 2012), with the exception of *A. sediba* (see Henry et al., 2012). In *A. africanus* and *Homo* sp., dental
78 microwear textures show a large range in anisotropy (epLsar_{1.8}) and low range in complexity (Asfc) due to a
79 high density of scratches and a low density of pits. This has been interpreted as indicating consumption of
80 ‘tough’, mechanically challenging foods. The opposite is found in *A. sediba* and some specimens of *P.*
81 *robustus*, indicating occasional consumption of ‘hard’ foods (Scott et al., 2005; Ungar and Scott, 2009;
82 Ungar and Sponheimer, 2011; Henry et al., 2012; Ungar et al., 2012)¹. It has been argued that more
83 complex microwear textures could also be a product of increased quartz consumption, due to living in a
84 more arid environment (Lucas et al., 2013; Schulz et al., 2013; Merceron et al., 2016)—meaning that the
85 observed differences between *A. africanus* and *P. robustus* could be due to greater dust or grit
86 consumption, as a result of increased aridity (Vrba, 1975, 1985; Reed, 1997; Lee-Thorp et al., 2007).
87 However, a broad analysis of extinct hominins and bovids and experimental work on dust suggests that
88 increasing dust and/or grit in the diet is unlikely to explain the interspecific and regional differences
89 observed in hominin microwear (Merceron et al., 2016; Ungar et al., 2016). As *P. robustus* and *Homo* sp.
90 fossils have been recovered from the same stratigraphic units at Swartkrans and Drimolen (e.g., Grine et al.,
91 2009; Moggi-Cecchi et al., 2010), differences in dental microwear between them are likely due to diet.

92 Assessing tooth size and structure, *P. robustus* has relatively larger molars with thicker enamel than
93 many other hominins, possibly indicating an adaptation towards bulk feeding (i.e., the consumption of large
94 amounts of poor quality foods), high bite force production, and/or consumption of more dietary abrasives
95 (McHenry, 1984; Madden, 2015; Skinner et al., 2015; Ruiz and Arsuaga, 2017). The C₄ and dental microwear
96 signatures make a shift towards bulk feeding less likely, as bulk feeding tends to manifest in higher C₄
97 values and more scratches/less pits. Compared to *P. robustus*, *Homo* sp. has smaller teeth with absolutely
98 and relatively thinner enamel (Skinner et al., 2015), which, given that the two taxa lived in the same
99 environment, points towards dietary differentiation, possibly due to different food processing methods

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 (Berthoume, 2016b).

100 (e.g., extraoral food processing with tools and/or cooking foods in *Homo*; Wrangham, 2009; Zink et al.,
101 2014). Functional studies have produced contradictory results, suggesting that *A. africanus* was both better
102 and worse adapted for consuming hard, brittle food items than *P. robustus* (Spears and Crompton, 1994;
103 Berthaume et al., 2010). Although disparities can arise depending on the method used and how the results
104 are interpreted, all studies point toward ecological differentiation among South African taxa.

105

106 *Dental topography*

107 A popular method for quantifying tooth shape, dental topographic analysis, is used here to
108 contextualize potential ecological differentiation in *H. naledi* (Zuccotti et al., 1998; Evans, 2013). Dental
109 topography is “a method of quantifying and representing 2.5 or 3D whole tooth shape with a single metric”
110 (Berthaume, 2016a: p. 680), and has successfully been used to correlate tooth shape to diet (Ungar, 2004;
111 King et al., 2005; Godfrey et al., 2012; Ledogar et al., 2013; Winchester et al., 2014; Berthaume and
112 Schroer, 2017). Originally developed using geographic information systems (GIS) technology (Zuccotti et al.,
113 1998; Ungar and Williamson, 2000), it has since come to encompass several non-GIS specific methods
114 (Evans, 2013). Besides inferring dietary ecology, dental topography has also been used to predict enamel
115 surface morphology from the shape of the enamel-dentine junction (Skinner et al., 2010; Guy et al., 2015),
116 to investigate evolutionary pressures, such as niche partitioning (Boyer et al., 2012; Godfrey et al., 2012;
117 Berthaume and Schroer, 2017), and to describe and assign a primate fossil to a new species (Boyer et al.,
118 2012). The relationship between tooth shape and food item breakdown have additionally been investigated
119 (Thiery et al., 2017a, 2017b), but how foods break down during mastication is not yet fully understood, and
120 the proposed categories (e.g., crushing, grinding) need to be better defined from a fracture mechanics
121 standpoint before this classification system can be used (Berthaume, 2016b; Thiery et al., 2017b).

122 The first metrics to reliably quantify tooth shape and relate it to dietary ecology, shearing ratio and
123 shearing quotient, established that teeth with relatively longer shearing crests were more efficient at
124 masticating fibrous and chitinous foods in small mammals (Sheine and Kay, 1977, 1982). A major drawback
125 of this approach is that shearing crests can be measured only on unworn teeth with defined shearing
126 crests. Dental topography overcomes these limitations and can be used to quantify dental morphologies at

127 all wear stages (Ungar and M'Kirera, 2003; Winchester et al., 2014). We employ four dental topographic
128 metrics in the South African hominins: orientation patch count rotated (OPCR), Dirichlet normal energy
129 (DNE), relief index (RFI) and ambient occlusion (PCV, portion de ciel visible or 'portion of visible sky').
130 Orientation patch count rotated is used to quantify occlusal complexity (Evans et al., 2007). From a
131 functional perspective, it quantifies the number of 'tools' (e.g., cusps, crests, crenulations, and cutting
132 edges) on the tooth's surface: a tooth with more tools is more efficient at chewing foods with structural
133 fibers and has a higher OPCR value. Dirichlet normal energy is a measure of surface curvature, and is used
134 to quantify tooth sharpness, with sharper teeth having higher DNE values (Bunn et al., 2011). Unlike other
135 measures of curvature (e.g., curvature in Guy et al., 2013), DNE does not differentiate between convexities
136 and concavities (i.e., positive and negative curvatures). However, it is strongly positively correlated to
137 shearing quotient and shearing ratio in unworn teeth, indicating that it is a good measure of positive tooth
138 curvature (Bunn et al., 2011; Winchester et al., 2014). Unlike shearing quotient and shearing ratio, DNE can
139 be used for teeth with a variety of morphologies in a variety of wear stages (Pampush et al., 2016).
140 Depending on the surface cropping method used (i.e., the entire crown or just the portion of the crown
141 superior to the lowest point on the talonid basin), relief index (RFI) quantifies relative crown and/or cusp
142 height. High-crowned/cusped teeth have higher RFI values, while teeth with lower crowns/cusps have
143 lower RFI values (Ungar and M'Kirera, 2003; Boyer, 2008). Finally, ambient occlusion, a relatively new
144 dental topographic metric, quantifies the likelihood of tooth wear (Berthaume, 2016a). Ambient occlusion
145 is a method for making 3D images appear more realistic by approximating the amount of ambient lighting
146 that would be shining across the surface. Measured from above the occlusal surface, a point with higher
147 ambient occlusion, or PCV, will be more likely to contact a food item/opposing tooth during a masticatory
148 cycle than a point with lower PCV. Consequently, areas of the tooth with higher PCV values have an
149 increased probability of wearing during a masticatory cycle. Portions of the tooth responsible for food item
150 fracture (e.g., cusps and crests) tend to have higher PCV values, while areas responsible for
151 trapping/stabilizing the food item and increasing dental longevity (e.g., basins, and the sides of the crown,
152 respectively) tend to have lower values (Fig. 1; Berthaume, 2016a). When all PCV values are averaged over
153 the surface, teeth with lower mean PCV values are less likely to experience large levels of wear during

154 mastication and are, therefore, more wear resistant. In addition to the dental topographic metrics, tooth
155 size, measured via projected cross-sectional area (Boyer, 2008), was quantified, as this measure is
156 correlated to diet in primates.

157

158 **Materials and methods**

159 *Sample*

160 Out of a total of 102 mandibular second molars available from eight South African fossil hominin-
161 bearing sites, 43 relatively unworn teeth with well-preserved enamel caps were selected for analysis (*A.*
162 *africanus* = 16, *P. robustus* = 16, *H. naledi* = 8, *Homo sp.* = 3; see Supplementary Online Material (SOM)
163 Tables S1 and S2 for accession numbers). Lower second molars were chosen because: 1) they are
164 morphologically highly (although not exclusively) representative of the postcanine dentition (Kay, 1975;
165 Sheine and Kay, 1977); 2) the relationship between M₂ shape and diet in primates is well established (e.g.,
166 Boyer, 2008; Godfrey et al., 2012; Ledogar et al., 2013; Winchester et al., 2014); and 3) dietary signatures
167 are stronger in mandibular than maxillary teeth in dental topographic analyses (Allen et al., 2015). This
168 does not imply other postcanine teeth hold no dietary signatures (e.g., Kay, 1975, 1981; Sheine and Kay,
169 1977, 1982; Berthaume, 2014; Winchester et al., 2014; Allen et al., 2015). The sample of *Homo sp.* includes
170 fossils from Swartkrans (i.e., SK 15), Sterkfontein Member 5 West (i.e., Stw 80), and the mandible from the
171 Cave of Hearths that have been referred to as *Homo ergaster/H. erectus*. The Cave of Hearths mandible is
172 poorly dated, but recovered from Acheulean levels (Herries, 2011). It was suggested that this mandible
173 could belong to *H. naledi* (Berger et al., 2017), but it differs from *H. naledi* in premolar and molar crown
174 morphology (L.K.D., pers. obs.), and plots out separately from *H. naledi* in most of our analyses. It is likely
175 younger than either the Swartkrans or Sterkfontein *Homo* material included in this study and may
176 represent *Homo rhodesiensis/H. heidelbergensis* (e.g., Tobias, 1971; Kuman and Clarke, 2000; Herries and
177 Shaw, 2011). Due to small sample size, two possible antimeres were included for *H. naledi*; in particular,
178 U.W. 101-507 and U.W. 101-145 are likely antimeres, and U.W. 101-377 and U.W. 101-789 have been
179 suggested to be antimeres (L.K.D., pers. obs.), although the former is 12.67% smaller than the latter

180 (128.334 mm² vs. 146.955 mm², quantified through outline area; Boyer, 2008). No antimeres were used for
181 *A. africanus* or *P. robustus*, and no antimeres were present for *Homo* sp.

182

183 *Surface digitization*

184 Digital representations of the teeth were created using a BIR Actis 300/255 FP, SkyScan 1172, or a
185 Nikon Metrology XTH 225/320 microtomography (microCT) scanner at resolutions of 14–91 µm (only four
186 teeth are at a resolution of 91 µm, all other teeth are at resolutions of 14-36 µm; see SOM Table S2 for
187 resolutions). CT scans were processed in Avizo 8.1 (FEI, Hillsborough, USA) by thresholding, removing any
188 matrix or bone touching the outer surface of the enamel cap, using the ‘smooth labels’ command (size = 3,
189 3D volume), and generating surfaces (smoothing type: existing weights). Surfaces files were imported into
190 Geomagic Studio 2013, where the outer surface of the enamel cap was isolated and edited (e.g., smoothed,
191 reconstructed, and/or erasing cracks; SOM Table S2). When necessary and possible, portions of missing
192 enamel along the cervical margin were repaired, and teeth were cropped.

193 Two surface cropping methods are commonly used for dental topography, using the entire enamel
194 cap (EEC) or the portion of the enamel cap superior to the lowest point on the occlusal basin (BCO). BCO is
195 popular because it is not always possible to mold or scan the entire tooth or because of enamel chipping
196 along the cervical margin (Zuccotti et al., 1998; Ungar and Williamson, 2000; M’Kirera and Ungar, 2003;
197 Ungar and M’Kirera, 2003; Dennis et al., 2004; King et al., 2005; Evans et al., 2007; Godfrey et al., 2012;
198 Berthaume and Schroer, 2017). Entire enamel cap was introduced in Boyer (2008) because there were taxa
199 for which the BCO could not be reliably employed. The EEC method is advantageous as it considers whole
200 tooth shape, providing information about tooth shape not responsible for food item breakdown that is
201 related to diet (e.g., relative crown height), but requires 3D scans. The BCO method is advantageous as it
202 attempts to isolate portions of the teeth responsible for food item breakdown and can be done with both
203 2.5 and 3D scans, as the cervix is not always imaged in 2.5D scans. Previous studies have reported no
204 significant differences in dental topographic values due to cropping method (Bunn et al., 2011; Godfrey et
205 al., 2012; Prufrock et al., 2016), but have suffered from small sample sizes. All teeth were subjected to both
206 the ECC and BCO to determine if the two cropping methods produced statistically different results.

207 Edited tooth surfaces were reimported into Avizo, simplified down to 10,000 and 20,000 triangles, and
208 smoothed (100 iterations, $\lambda = 0.6$; Boyer, 2008; Bunn et al., 2011; Winchester et al., 2014). Triangle
209 counts of 10,000 are standard for DNE studies (Bunn et al., 2011; Winchester et al., 2014), but tend to
210 oversimplify large and complex teeth (Berthaume and Schroer, 2017). A triangle count of 20,000 was
211 suggested by Berthaume and Schroer (2017), but higher triangle counts have been recommended for other
212 dental topographic metrics (e.g., 22,000 and 55,000; Guy et al., 2013, 2015; Lazzari and Guy, 2014; Thiery et
213 al., 2017a). Simplified and full versions of the teeth were imported into CloudCompare (CloudCompare,
214 2017) and oriented into anatomically correct position, using fossils with portions of the mandible preserved
215 as guides. Specimen specific deviations from the procedure detailed in this section can be found in the SOM
216 Table S2.

217

218 *Calculating shape and size*

219 DNE, RFI, OPCR, and tooth size were calculated using Morphotester (Winchester, 2016). Two values
220 were reported for DNE, removing the top 1% (DNE 99%) and 5% (DNE 95%) energy*area values, as
221 taphonomic processes can cause an unusually high number of sharp edges at fissures on the occlusal
222 surface. This causes artificial inflations in DNE scores when 1% outlier removal was used; 5% outlier
223 removal discarded these artifacts. RFI is a function of surface and cross-sectional areas ($RFI = \ln$
224 $(\sqrt{SA/CA})$; Boyer, 2008). Cross-sectional area is also the measure of tooth size. OPCR here is not directly
225 comparable to OPCR calculated using 2.5D surfaces with regular grids (Evans et al., 2007; Wilson et al.,
226 2012; Evans, 2013; Winchester, 2016), but is correlated. PCV was calculated in CloudCompare using the
227 'PCV' function, with the 'fits a statistical model on the active scalar field' command, which reports on an
228 average PCV value (Berthaume, 2016a). Dental topography was performed on surfaces simplified to 10,000
229 triangles, as is typical in dental topographic studies (e.g., Godfrey et al., 2012; Winchester et al., 2014) and
230 20,000 triangles, as occlusal features were better preserved at 20,000 triangles. It is important to keep
231 triangle count constant, as some dental topographic metrics are sensitive to triangle count (e.g., DNE and
232 OPCR; Bunn, 2008; Bunn et al., 2011; Evans and Janis, 2014).

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

238

239 *Tooth wear*

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

247

248 *Statistical analyses*

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

258 As wear had a significant effect on some shape and size values, one-way ANOVAs were run on
259 moderate and lightly worn teeth separately to determine if there was any difference in shape and size

260 values between species in R and RStudio (R Development Core Team, 2015; Rstudio team, 2016). Tukey's
261 honestly significant difference (HSD) tests were run to determine where significant differences occurred
262 between species. Mann-Whitney U- and Student's t-tests were run to determine if there was any difference
263 in cropping methods. Although previous studies have shown there is a phylogenetic signal in tooth shape
264 and size (Winchester et al., 2014), it is not possible for us to run phylogenetically corrected analyses as
265 there is no secure, agreed, or well-quantified phylogeny for these taxa.

266

267 **Results**

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

277

278 *Wear*

279 Similar to previous studies (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003), a two-way
280 ANOVA showed many topographic metrics were significantly affected by occlusal wear and taxon, but not
281 the interaction variable between wear and taxon (Table 4). Additional two-way ANOVAs for different
282 triangle counts and cropping methods are found in SOM Tables S6 to S8. Taxon is important for DNE 99%,
283 but not DNE 95%—this difference is due to the top 5% of the 'curviest' parts of the surface being
284 disregarded in DNE 95% compared to the top 1% in DNE 99%. The drastic change in results is due to a large
285 number of highly curvy singularities on the surface of the tooth, usually located at the fissures that form at
286 the intersection of the cusps. Differences in DNE, OPCR, and PCV due to wear are easily visible for each

287 taxon (Fig. 2; note that RFI is a ratio and cannot be visualized). Kendall's correlations between wear and
288 shape and size metrics within each taxon revealed significant correlations between tooth wear and a) DNE
289 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.*
290 *robustus* ($p < 0.001$); and d) OPCR in *A. africanus* ($p = 0.044$; Table 5). Wear was never significantly
291 correlated to tooth size ($p = 0.111$ – 0.618), despite the presence of interproximal wear, which can
292 significantly affect tooth size (Wood and Abbott, 1983). This could be because we did not include heavily
293 worn teeth in our analysis. Kendall's correlations for other triangle counts and cropping methods are found
294 in SOM Tables S9 to S11. Pearson's correlations revealed nearly identical results (SOM Tables S12 to S15),
295 and, as such, are not reported here. We therefore analyzed lightly worn (Scott score < 3) and moderately
296 worn (Scott score 3+) teeth separately.

297

298 *Cropping method*

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

305

306 *Taxonomic differences*

307 One-way ANOVAs revealed taxonomic differences in RFI, PCV, and tooth size in lightly worn teeth
308 ($p < 0.001$). The small sample size of moderately worn *H. naledi* teeth ($n = 3$, Table 1) prevented their
309 inclusion in these statistical analyses. No differences existed between *A. africanus* and *P. robustus* in
310 moderately worn teeth (SOM Tables S19 to S22). In lightly worn teeth, a Tukey HSD test revealed
311 taxonomic differences in RFI and PCV, with *H. naledi* having the highest RFI, followed by *P. robustus*, then *A.*
312 *africanus* (Table 7). The opposite trend is found with PCV, indicating *H. naledi* had the most wear resistant
313 teeth, followed by *P. robustus*, then *A. africanus*. Significant differences exist between *H. naledi* and *P.*

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

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

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

334

335 Discussion

336 It has been observed that there is very low variation in tooth shape in *H. naledi* when compared to
337 other hominins (Skinner et al., 2016; Delezene et al., 2017). For lightly worn teeth in this study, *H. naledi*
338 has the lowest level of coefficient of variation for five of the six shape and size variables (*Homo* sp. was
339 excluded because of sample size; Table 9). Overall, it appears that there is less variation in tooth shape in *H.*
340 *naledi* than in *A. africanus* or *P. robustus*, which could be due to a) low variation within the species, b) the

341 *H. naledi* sample in this study being from a single chamber (i.e., the Dinaledi chamber), whereas both *A.*
342 *africanus* and *P. robustus* are represented from several sites spanning a larger temporal and geographical
343 range, or c) chance sampling and low sample sizes.

344 As in previous studies (e.g., M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; King et al., 2005;
345 Glowacka et al., 2016; Pampush et al., 2016), tooth wear played a significant role in some of the dental
346 topographic metrics. As expected, wear caused DNE 99%, DNE 95% and RFI to decrease, indicating the
347 teeth were becoming duller and lower crowned (Figs. 2 and 3). Wear caused PCV to increase, indicating
348 teeth became less wear resistant as they became more worn. OPCR was uncorrelated to tooth wear, which
349 initially seemed counterintuitive as teeth lose ‘tools’ (e.g., crenulations) as they wear. However, in the
350 initial stages of wear, the cusps and crests are all still essentially salient, which may be why OPCR was not
351 related to wear. It may only be in later stages of wear, when crests and cusps are obliterated and large
352 dentin pools begin to form, that OPCR is significantly correlated to wear in hominins. Although changes in
353 tooth size occur due to interproximal wear (Wood and Abbott, 1983), intraspecific variation plays a larger
354 role in variation in M₂ size in this study.

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

367 support the conclusion that *H. naledi* was not consuming foods that require bulk processing, such as
368 grasses or sedges.

369 There are two probable adaptive scenarios for an increase in dental longevity in *H. naledi*. The first
370 is a dietary shift towards foods with a higher abrasive load, such as phytoliths, dust, or grit. A probable
371 candidate for such foods would be underground storage organs, which, if unwashed, would transfer large
372 amounts of grit to the oral cavity. The second is an environmental (climatic) shift towards increased aridity
373 led to an incidental increase in dust and/or grit consumption, affecting all food sources. Among *A.*
374 *africanus*, *P. robustus*, and *H. naledi*, temporal increases in relative crown height (RFI) and wear resistance
375 (PCV) are coincident with an increasingly dry and arid environment (Vrba, 1975, 1985; Lee-Thorp et al.,
376 2007). Therefore, it is possible that the foods being consumed by *H. naledi* had more inorganic abrasives on
377 them, which required more wear-resistant molars. A recent study reported an extremely high level of
378 dental chipping in *H. naledi* (Towle et al., 2017), suggesting the increase in dental longevity could be an
379 adaptation to offset high levels of wear due to accidental grit consumption. It is not possible from our data
380 to discern whether this is because of a dietary (e.g., underground storage organs, USOs) or an
381 environmental shift. Data from stable carbon isotope and dental microwear analyses for *H. naledi* (e.g.,
382 Henry et al., 2012) will shed light on this issue.

383 The great apes were found to have duller, less curvy teeth than hominins in some analyses (Fig. 4).
384 This may seem odd that, given their generally taller cusps generate relatively longer shearing crests that
385 would, presumably, increase tooth sharpness. However, it appears that the extremely crenulated surfaces
386 of some hominin teeth (i.e., *A. africanus* and *P. robustus*) may be making their occlusal surfaces, overall,
387 sharper: but this cannot be the case for *H. naledi*, which lacks crenulations (L.K.D., pers. obs.). The relatively
388 higher DNE values in *H. naledi*, *A. africanus*, and *P. robustus* imply their diets required higher shear forces,
389 for eating substances such as plant fiber and/or muscle fiber, compared to the great apes. Sharper teeth
390 are more efficient at producing high shear forces during mastication, which is advantageous for processing
391 foods high in structural fibers; this is the reason primates that consume more plant fiber have higher DNE
392 values (Godfrey et al., 2012; Winchester et al., 2014; Berthaume and Schroer, 2017). Foods high in
393 structural fiber can be low (e.g., grasses, sedges, bark, and leaves) or high (e.g., USOs, animal muscle

394 fascicles and fibers) quality². Therefore, from a fracture mechanics perspective, the higher DNE in *A.*
395 *africanus*, *P. robustus*, and *H. naledi* could be an adaptation towards consuming a large range of resources
396 requiring shear forces to process. Relative to the great apes and the other hominins, the apparent reversion
397 in DNE with *Homo* sp. could have occurred due to a dietary shift towards foods requiring lower shear
398 forces, because the introduction of cooking and/or food processing relaxed the selective forces acting on
399 tooth sharpness (Wrangham, 2009; Zink et al., 2014), or because their diet did not require high shear forces
400 to process. It is unlikely that differences in DNE are environmentally driven, as differences in DNE have not
401 been shown to be correlated with grit/dust consumption and/or tooth longevity.

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

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

²Foods 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.

418 differences in fallback foods, Ungar (2004, 2007) concluded that differences in tooth shape reflected
419 differences in fallback foods, and that the hominins, *Homo* sp. and *A. africanus*, fell back on 'tougher' foods
420 than *A. afarensis* and *P. robustus*, respectively. Since these pioneering studies, research has shown that
421 dental topography frequently reflects primary diet in primates (e.g., Winchester et al., 2014; Berthaume
422 and Schroer, 2017), so differences in tooth shape may reflect differences in preferred, not fallback, foods. It
423 appears that, from a topographic perspective, the relationship between tooth form and preferred vs.
424 fallback food is not straightforward. A recent study on great apes additionally showed that comparing
425 allopatric hominoids must be done carefully, as character displacement has occurred in great ape tooth
426 shape due to indirect competition over dietary resources (Berthaume and Schroer, 2017), although,
427 fortunately, the signature for relative fiber content appears to be unaffected by this evolutionary
428 phenomenon. The fact that *H. naledi* was temporally separated, and therefore allochronic from the other
429 hominins in our sample (Dirks et al., 2015), hinders an easy interpretation of the results of this study.
430 Without more associated faunal material, or other information on the paleoenvironment of *H. naledi* (see
431 Dirks et al., 2015), it is currently impossible to determine if the competitive environment in South Africa
432 was similar from the early to the late Middle Pleistocene, the time interval in which *A. africanus*, *P.*
433 *robustus*, *Homo* sp., and *H. naledi* existed. However, from a perspective of the functional morphology of the
434 molars, *H. naledi* seems unlikely to have had an *Australopithecus*-like pattern of resource exploitation,
435 despite sharing similarities in brain size, body size, and hand and shoulder morphology (Berger et al., 2017).

436 It could be argued that a drawback of this study comes from the potential decoupling between
437 morphology and diet. Dietary signatures drawn from morphology do not always match dietary signatures
438 from other methods, such as stable carbon isotope or dental microwear analyses. This was thought to be
439 the case with *Paranthropus boisei*, which has large teeth and a powerfully-built skull coupled with large
440 chewing muscles, leading many to expect that it consumed hard foods, such as nuts or seeds (Jolly, 1970;
441 Rak, 1983; Demes and Creel, 1988; Dzialo et al., 2013; Smith et al., 2015). However, more recent isotope
442 and microwear work has suggested it ate larger amounts of low quality, mechanically challenging foods,
443 such as grasses, sedges, or underground storage organs (Ungar et al., 2008; Cerling et al., 2011; Grine et al.,
444 2012). This and other discrepancies between morphology and isotopes/microwear have led some

445 researchers to question whether morphology can be used to predict diet (Strait et al., 2009, 2012, 2013;
446 Grine et al., 2010; Daegling et al., 2013). This debate was further fueled by observed discrepancies between
447 morphology and diet in extant taxa (e.g. King et al., 2005). But this need not be the case, as
448 isotope/microwear analyses can be used in conjunction with morphological analyses to produce new
449 hypotheses about the diets of extinct taxa (Dominy et al., 2008; Macho, 2014).

450

451 **Conclusions**

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

470

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486

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785

786 **Figure Captions**

787

788 **Figure 1.** 2D image of light shining from the superior direction onto the occlusal surface of the tooth.

789 Portions of the tooth that are more exposed to ambient light (i.e., high exposure) are more likely to come in
790 contact with food, grit, and/or an opposing tooth during mastication, making them more likely to
791 experience wear than areas less exposed to ambient light (i.e., low exposure). Teeth that are less exposed
792 to ambient light have a lower PCV score and are more wear resistant.

793

794 **Figure 2.** Lightly worn (gray background) and moderately worn M₂ for *Australopithecus africanus* (STW

795 560E and 109), *Paranthropus robustus* (DNH 60c, SK 858), *Homo naledi* (U.W. 101-307 and U.W. 101-1261),

796 and South African *Homo* sp. (Cave of Hearths and STW 80) with dental topographic scores approaching the
797 average for each species. Dark blue triangles along the cervical margin and at the intersections of the cusps
798 in the DNE 99% pictures represent triangles discarded using 1% outlier removal (energy*area). Note that
799 STW 80 is mirrored to make it comparable to the other teeth in the 3D views. Teeth are not to scale.

800
801 **Figure 3.** Dental topographic and tooth size results, per species, for lightly worn teeth (average Scott score
802 < 3). Triangle count = 20,000. Cropping method = EEC.

803
804 **Figure 4.** Ape vs. hominin DNE using published ape data (20,000 triangles, DNE 99%, BCO, lightly worn,
805 Laplacian smoothing = 2; Berthaume and Schroer, 2017). As in a previous study (Spradley et al., 2017),
806 Laplacian smoothing caused DNE to decrease from 3.62 to 23.67% for all teeth (except SKX 4446, which has
807 a 40% increase), but was necessary to make the hominin data comparable to the ape data. Hominin data
808 was recalculated with the BCO to make it comparable to the great ape data. All comparisons without the
809 apes were done using the entire enamel cap (EEC) without Laplacian smoothing. Abbreviations: *Ptt* = *Pan*
810 *troglodytes troglodytes*; *Ppa* = *Pan paniscus*; *Pts* = *Pan troglodytes schweinfurthii*; *Ppy* = *Pongo pygmaeus*;
811 *Ggg* = *Gorilla gorilla gorilla*; *Gbb* = *Gorilla beringei beringei*; *Gbg* = *Gorilla beringei graueri*; *Aa* =
812 *Australopithecus africanus*; *Pr* = *Paranthropus robustus*; *Hn* = *Homo naledi*; *Hsp* = *Homo* sp.

813