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1 Mandibular molar root and pulp cavity morphology in *Homo naledi* and other Plio-Pleistocene
2 hominins

3
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17

18 Keywords: Tooth root morphology; Root canal morphology; *Homo* sp.; *Australopithecus africanus*;
19 *Paranthropus robustus*; *Paranthropus boisei*

20

21 **Abstract**

22 The craniomandibular morphology of *Homo naledi* shows variable resemblances with species
23 across *Homo*, which confounds an easy assessment of its phylogenetic position. In terms of skull
24 shape, *H. naledi* has its closest affinities with *Homo erectus*, while mandibular shape places it closer
25 to early *Homo*. From a tooth crown perspective, the smaller molars of *H. naledi* make it distinct
26 from early *Homo* and *H. erectus*. Here, we compare the mandibular molar root morphology of six
27 *H. naledi* individuals from the Dinaledi Chamber to those of African and Eurasian Plio-Pleistocene
28 fossil hominins (totalling 183 mandibular first, second and third molars). The analysis of five root
29 metric variables (cervical plane area, root length, root cervix volume, root branch volume, and root
30 surface area) derived from microCT reconstructions reveals that the molar roots of *H. naledi* are
31 smaller than those of *Homo habilis*, *Homo rudolfensis*, and *H. erectus*, but that they resemble those
32 of three *Homo* sp. specimens from Swartkrans and Koobi Fora in size and overall appearance.
33 Moreover, though *H. naledi* molar roots are similar in absolute size to Pleistocene *Homo sapiens*,
34 they differ from *H. sapiens* in having a larger root volume for a given cervical plane area and less
35 taurodont roots; the root cervix-to-branch proportions of *H. naledi* are comparable to those of
36 *Australopithecus africanus* and species of *Paranthropus*. *Homo naledi* also shares a metameric root
37 volume pattern ($M_2 > M_3 > M_1$) with *Australopithecus* and *Paranthropus* but not with any of the
38 other *Homo* species ($M_2 > M_1 > M_3$). Our findings therefore concur with previous studies that found
39 that *H. naledi* shares plesiomorphic features with early *Homo*, *Australopithecus*, and *Paranthropus*.
40 While absolute molar root size aligns *H. naledi* with *Homo* from North and South Africa, it is
41 distinguishable from these in terms of root volumetric proportions.

42 **Introduction**

43 *Homo naledi*, from the late Middle Pleistocene of South Africa, is characterized by a mosaic of
44 ancestral and derived craniodental and postcranial anatomical features (Berger et al., 2015; Hawks
45 et al., 2017 and references therein). Despite its relatively recent date of 236–335 ka (Dirks et al.,
46 2017; Hawks et al., 2017), *H. naledi* retains a number of presumably ancestral features shared with
47 eastern and southern African early *Homo*, *Australopithecus*, and *Paranthropus* (e.g., small body
48 size, small brains both absolutely and relative to body size, curved manual phalanges, absence of
49 styloid process on the third metacarpal, distally increasing mandibular molar size gradient,
50 posteriorly directed humeral head, and flared ilium; Berger et al., 2015; Kivell et al., 2015;
51 Feuerriegel et al., 2017; Garvin et al., 2017; VanSickle et al., 2017). In other anatomical
52 characteristics (e.g., limb proportions, minimal body size dimorphism, proximal carpal anatomy,
53 foot morphology) it shares derived features with *Homo sapiens*, *Homo heidelbergensis*, and *Homo*
54 *neanderthalensis* (Harcourt-Smith et al., 2015; Kivell et al., 2015; Garvin et al., 2017). Analyses of
55 skull morphology have yielded conflicting signals; a study of cranial shape suggests that *H. naledi*
56 is phenetically similar to *H. erectus* (Laird et al., 2017), while an analysis of mandibular shape
57 places *H. naledi* more closely with basal *Homo* (i.e., *Homo habilis*; (Schroeder et al., 2017). Thus,
58 the phylogenetic place of *H. naledi* remains ambiguous (Dembo et al., 2016), but the emerging
59 picture is one of a taxon that overlaps in time and possibly space with early *H. sapiens* but remains
60 anatomically distinct. Such anatomical differences hint at possible marked ecological and
61 behavioral differences between *H. sapiens* and *H. naledi*.

62 From a dental perspective, *H. naledi* has fairly small postcanine teeth with simple, crenulation-
63 free crowns, lacking mass additive traits (Berger et al., 2015; Irish et al., 2018). The mandibular
64 molar crown area gradient is $M_1 < M_2 < M_3$ (Berger et al., 2015; Hawks et al., 2017), which is the
65 generally observed pattern in early hominins, including *H. habilis* (Evans et al., 2016). Yet, its

66 mandibular first molar crowns are buccolingually narrower than those of *Australopithecus sediba*,
67 *H. habilis*, *Homo rudolfensis*, and early *H. erectus* (from Africa and Georgia; (Berger et al., 2015;
68 Hawks et al., 2017). The mandibular premolars are somewhat molarized, with an expanded talonid,
69 uniformly two-rooted P₃, and variably two-rooted P₄, which distinguishes *H. naledi* from *H. habilis*
70 (see Berger et al., 2015). Likewise, the mandibular premolars of *H. erectus* from Georgia (P₃) and
71 *Homo antecessor* from Spain (P₃ and P₄) are also said to be two-rooted (Bermúdez de Castro et al.,
72 1999, 2014). The anterior teeth (incisors and canines) of *H. naledi* have crown and root dimensions
73 most similar to those of modern *H. sapiens* and are smaller than those of early Homo (Le Cabec et
74 al., 2017).

75

76 Tooth root morphology in fossil hominins

77 The external and internal morphology of both anterior (incisors and canines) and postcanine
78 tooth (premolars and molars) roots has been used to unravel the taxonomic status of, and the
79 phylogenetic relationships among, fossil hominins (Abbott, 1984; Wood et al., 1988; Kupczik and
80 Hublin, 2010; Emonet et al., 2012; Le Cabec et al., 2013; Emonet et al., 2014; Moore et al., 2016).
81 In particular, the assessment of the number and configuration of mandibular premolar roots has
82 revealed two distinct P₃ morphoclines in hominins deriving from the ancestral form with a circular
83 mesiobuccal root and a buccolingually extended distal root (Wood et al., 1988). Generally, while *H.*
84 *erectus* and modern humans, as well as *P. robustus*, have simplified and reduced P₃ roots,
85 *Paranthropus boisei* has molar-like P₃ roots (Wood, 1988). However, more recent studies have
86 demonstrated that there is considerable variation in premolar root morphology within a single
87 species and even within an individual (Kupczik et al., 2005; Shields, 2005; Moore et al., 2015;
88 Moore et al., 2016), which would argue against the unrestricted validity of this trait in phylogenetic
89 studies.

90 In this regard, molar root morphology appears to be more useful as at least the number of roots is
91 less variable than that of premolars. Generally, the mandibular molars of hominins have two
92 separated blade-like roots. In some modern human populations, high occurrences of three-rooted
93 mandibular first molars (the mesial and distal roots plus a distinct distolingual accessory root) have
94 been reported (e.g. Turner, 1971; Scott et al., 2018). Sperber (1974) also noted three-rooted M₃ in
95 two South African hominin specimens (*P. robustus* SK841b with an accessory mesiobuccal root
96 and *A. africanus* TM1518 with an accessory mesiolingual root. In the majority of two-rooted
97 mandibular molars, both mesial and distal root portions are flattened mesiodistally, but the mesial
98 root is buccolingually broader than the distal. In *P. robustus* from Swartkrans, the mesial root of the
99 M₁ has been described to be larger than the distal one, while the opposite is the case for the M₂
100 (Robinson, 1956; Sperber, 1974). There are no reported root length data for the *P. robustus* M₃, but
101 the mesial root was described to be directed vertically downward, while the distal root points
102 distally and tapers (Robinson, 1956). Robinson (1956) was also the first to notice that the mesial
103 roots of the M₁ in *P. robustus* exhibited a longitudinal depression (or gutter) on the mesial face of
104 the root ending in a bifid or double apex of the root. In cross-section this is called a dumbbell-
105 shaped root (see Fig. 1), and it has also been observed in the mesial roots of M₁ and M₂ of other
106 early hominins, such as *Australopithecus afarensis*, *P. boisei*, *H. habilis*, and *H. rudolfensis* (Ward
107 et al., 1982; Kullmer et al., 2011). Although there is some overlap in the extent of this mesiodistal
108 root constriction in earlier hominins, the roots of later Homo (i.e., *H. erectus* and *H. sapiens*) appear
109 to be more circular, without a constriction (Robinson, 1956; Kullmer et al., 2011).

110 Bifurcation height in the molars (i.e., the point where the root cervix splits into the mesial and
111 distal root branches; see Fig. 1) can vary considerably within and between species. Following
112 observations by Gorjanovic-Kramberger (1907, 1908) and Adloff (1907) on the molar roots of *H.*
113 *neanderthalensis* from Krapina, Keith (1913) introduced the term ‘taurodontism’ to describe the

114 enlargement of the cervix and underlying pulp chamber at the expense of length of the root
115 branches. Based on the varying degree of the apical displacement of the floor of the pulp chamber,
116 molars have been classified into cyno-, hypo-, meso- and hypertaurodont forms using the so called
117 taurodont index (Keene, 1966; Constant and Grine, 2001). While the anthropological and clinical
118 dental assessment of taurodontism has traditionally been done using 2D lateral radiographs,
119 Kupczik and Hublin (2010) used 3D surface models of mandibular molars and quantified the
120 relative proportion of the volume of the root cervix and root branches, expressed as the volumetric
121 bifurcation index. These authors found that hypertaurodont M₂ and M₃ with completely fused roots
122 containing a single enlarged pulp cavity were common in *H. neanderthalensis*; in contrast, Kupczik
123 and Hublin (2010) found no hypertaurodont molar roots in their sample of Late Pleistocene and
124 recent *H. sapiens*. The pulp chamber and root canals house the dental pulp, blood vessels and
125 nerves. The pulp tissue contains, among other things, odontoblasts, which deposit dentine at the
126 periphery of the chamber during tooth development and in response to applied stimuli such as
127 caries, trauma and wear (Berkovitz et al., 2002). It has been suggested that large pulp cavities of *H.*
128 *neanderthalensis* may be an adaptation to a high-attrition dietary regimen because it allows for the
129 deposition of secondary and tertiary dentine on the pulp walls following the loss of enamel and
130 coronal dentine and thus prolongs tooth longevity (Blumberg et al., 1971; Constant and Grine,
131 2001; Kupczik and Hublin, 2010; Benazzi et al., 2015).

132

133 Aim of the study

134 By using the morphology of the mandibular molar roots, this study aims to shed further light on
135 the taxonomic status of *H. naledi* compared to other Plio-Pleistocene fossil hominins from Africa
136 and western Eurasia. Given the generally plesiomorphic signal of the dentition (Berger et al., 2015;
137 Hawks et al., 2017) and similarities in mandibular shape (see Schroeder et al., 2017), we expect that

138 H. naledi will be more similar in root form to early Homo than to H. sapiens and H.
139 neanderthalensis, with which it overlaps in time.

140

141 **Materials and methods**

142 Sample

143 A total of 183 mandibular first, second and third molars of three fossil hominin genera
144 (Australopithecus, Paranthropus and Homo) were selected for this study (Table 1, Supplementary
145 Online Material [SOM] Table S1). The specimens derive from collections housed at the following
146 institutions: University of Witwatersrand, Johannesburg, South Africa; Ditsong National Museum
147 of Natural History, Pretoria, South Africa and Iziko South African Museum, Cape Town, South
148 Africa; National Museums of Kenya, Nairobi, Kenya; Sackler School of Medicine, Tel Aviv
149 University, Tel Aviv, Israel; Institut National des Sciences de l'Archéologie et du Patrimoine,
150 Rabat, Morocco; Geologisch-Paläontologisches Institut der Universität Heidelberg, Heidelberg,
151 Germany; and the National Museum, Belgrade, Serbia. The H. naledi sample consisted of 13
152 mandibular molars belonging to six individuals from the Dinaledi Chamber of the Rising Star Cave
153 in South Africa. The comparative Homo sample includes H. habilis and H. erectus (Kenya), H.
154 rudolfensis (Malawi), H. heidelbergensis (Mauer and Balanica), H. neanderthalensis (various
155 Eurasian sites), Pleistocene H. sapiens (also known as early anatomically modern humans) from
156 Morocco (Dar es-Soltan, El Harhoura, and Irhoud), South Africa (Die Kelders and Equus Cave) and
157 Israel (Qafzeh), as well as Homo sp. indet. from Kenya (Koobi Fora) and South Africa (Swartkrans
158 and Cave of Hearths), respectively. Although KNM-ER 1805 has been assigned to H. habilis
159 (Wood, 1991), SK 15 from Swartkrans Member 2 to H. erectus (Grine, 2005; Ungar et al., 2006),
160 and Cave of Hearths to H. sapiens rhodesiensis (Tobias, 1971), there does not seem to be a

161 consensus on the taxonomic status of these specimens and we therefore took a more conservative
162 approach by not assigning these fossils to any species. The same applies to SK 45 from Member 1
163 of Swartkrans, which resembles *H. habilis* more than it does *H. erectus* according to Grine (2005).
164 In addition, with the exception of Amud 1 and Tabun C2, we used previously published data for *H.*
165 *heidelbergensis* (see Skinner et al., 2016), *H. neanderthalensis*, and recent *H. sapiens* for
166 comparison (see Kupczik and Hublin, 2010).

167

168 Microcomputed tomography imaging and image processing

169 The *H. naledi* dental remains were scanned on Nikon Metrology XTH 225/320
170 microtomography (microCT) scanner housed at the University of the Witwatersrand. The remaining
171 fossil hominin mandibles, with the exception of the Equus Cave (EQ H-71/33) and Die Kelders
172 Cave (SAM AP 6242) specimens, were scanned using a BIR ACTIS 225/300 high-resolution
173 industrial microCT system or a SkyScan 1172 microtomographic scanner of the Max Planck
174 Institute for Evolutionary Anthropology, Leipzig, Germany. The isometric voxel size ranged
175 between 0.03 and 0.09 mm. EQ H-71/33 was scanned at ID 19 of the European Synchrotron
176 Radiation Facility (Grenoble, France) with a voxel size of 0.03 mm, while SAM AP 6242 was
177 scanned on a ScanCo 20 microCT system (Department of Biomedical Engineering, Stony Brook
178 University, NY, USA) with a voxel size of 0.016 mm. All resulting CT images were filtered using a
179 three-dimensional median filter (kernel size of 1) followed by a mean of least variance filter (kernel
180 size of 1) following Kupczik and Hublin (2010). The filtering results in more homogenous dental
181 tissue classes (enamel, dentine, pulp, bone) and allocates pixels with intermediate gray-scale values
182 at tissue interfaces (e.g., enamel-dentine, dentine-pulp) to the appropriate tissue (Wollny et al.,
183 2013). Each filtered dataset was imported into Avizo 9.1 (ThermoFisher Scientific™, Waltham,
184 MA, USA) and, where possible, the enamel, dentine, and pulp were segmented using a combination

185 of semiautomatic thresholding and manual editing of the images. Some fossil specimens did not
186 allow for a separation of the enamel from the coronal dentine, due to low contrast, and were thus
187 segmented as one tissue material (i.e., dentine). After segmentation, triangulated surface models
188 were generated using the constrained smoothing algorithm in Avizo. Subsequently, each molar
189 model was virtually bisected into its anatomical crown and root parts by using a best-fit plane
190 defined by up to 20 equally spaced points along the cemento-enamel junction in Avizo. An
191 additional plane parallel to this cervical plane was placed through the center of the interradicular
192 surface (the bifurcational plane) to divide the roots into the root cervix and root branch (Fig. 1).

193

194 Tooth root morphometric analysis and statistical analysis

195 Observed variations in tooth root and pulp cavity morphology were described and visually
196 shown through screenshots of the 3D molar models. The following terminology was used for
197 describing variation in pulp morphology (Fig. 1): 1) pulp chamber = situated inside the crown and
198 root cervix and houses nerves and blood vessels; 2) mesial root canal = thin, circular structure in the
199 mesial roots extending from the base of the pulp chamber into the root branch; the inferior alveolar
200 nerve and blood vessels enter through a single or double opening in the apex ; 3) distal root canal =
201 elliptical or buccolingually flat conduit in the distal roots usually with a single foramen at the apex.

202 Furthermore, the following variables were quantified from the sectioned molar models (Fig. 1):
203 root length (RL, in mm), cervical plane area (CPA, in mm²), root surface area (RSA, in mm²), total
204 root volume (RV), root cervix volume (V_{cervix}) and root branch volume (V_{branch}), all in mm³. To
205 quantify the level of bifurcation, we computed a volumetric bifurcation index (VBI, in %) following
206 Kupczik and Hublin (2010): $V_{\text{cervix}} / (V_{\text{cervix}} + V_{\text{branch}}) \times 100$. Corresponding with the classification
207 scheme of Keene (1966) a value of 0–24.9% denotes a cynotaurodont molar, a value of 25–49.9% a
208 hypotaurodont molar, a value 50–74.9% a mesotaurodont molar, and a value of 75–100% a

209 hypertaurodont molar. Bivariate associations between CPA and both RSA and RV were
210 investigated using Pearson's correlation coefficient and ordinary least squares regression. A
211 principal component analysis (PCA) using RL, CPA, V_{cervix} , and V_{branch} was conducted to compare
212 tooth root morphology of *H. naledi* to the other fossil hominins in bivariate space. Moreover, a non-
213 parametric multivariate analysis of variance (PERMANOVA) with pairwise PERMANOVAs
214 between all pairs of taxonomic groups as a post hoc test was used to test for significant differences.
215 All statistical analyses were performed in PAST v. 3.20 (Hammer et al., 2001).

216

217 **Results**

218 Comparative molar root and pulpal morphology

219 Lateral and apical views of the mandibular molar roots of the fossil hominins are presented in
220 Figures 2 and 3, respectively. Detailed descriptions of the root and pulp morphology of each of the
221 fossil specimens investigated here are presented in SOM S1 and illustrated in SOM Figs. 1–5. With
222 the notable exception of the M_2 of U.W. 101-001 (*H. naledi*), Mauer, Irhoud 11, Qafzeh 9, and
223 Qafzeh 25 (also the M_3), all fossil hominins have mandibular molars with well-separated, blade-like
224 mesial and distal roots when viewed laterally (Fig. 2, SOM Figs. S1–S5). It is noteworthy that in *H.*
225 *naledi* the distal roots of the M_3 are buccally offset relative to the mesial roots when viewed apically
226 (Fig. 3). The deflection of the distalmost root is also observed in *Homo* sp. from Swartkrans (SK
227 15) and in *P. robustus* (Fig. 3; SOM Fig. S5). Moreover, in the *H. naledi* specimens U.W. 101-001,
228 361, 516 and 1261 the mesial and distal root apices of the M_3 show a depression on the buccal
229 (U.W. 101-361 and 1261) or lingual (U.W. 101-001 and 516) aspect, which appears to be related to
230 the inferior alveolar canal (Fig. 2; SOM Fig. S1). This feature is not observed in any of the other
231 hominins. In all hominins, the mesial roots generally have bifid root apices, which correspond with

232 two separated root canals inside the root, while most of the distal roots house a single
233 buccolingually expanded root canal (Fig. 4; SOM Figs. S1–S5). In cross section, the mesial roots
234 have a figure-of-eight shape, whereas the distal roots are comma-shaped (Figs. 1 and 3). Unlike in
235 the South African and Eurasian Pleistocene *H. sapiens*, where the root apices taper, in *H. naledi* the
236 mesial root tips are set apart mesiodistally (SOM Figs. S1 and S4). The pulp chambers of the *H.*
237 *naledi* molars are of low height in coronal-apical direction, similar to those of *H. rudolfensis*, *H.*
238 *sapiens* (Irhoud 11), *Homo* sp. from Swartkrans, *A. africanus*, *P. boisei* and *P. robustus* (Fig. 4;
239 SOM Figs. S1, S2, and S5). These are unlike the tall pulp chambers of *H. erectus*, *H.*
240 *heidelbergensis*, *H. neanderthalensis* and *H. sapiens* (except Irhoud 11; Fig. 4; SOM Figs. S2–S4).

241

242 Molar root metrics and root volumetric proportions

243 Summary statistics are presented in Table 2 (individual specimen values are given in SOM Table
244 S1). Overall, *H. naledi* root volumes fall within the same range as *A. africanus*, *H.*
245 *neanderthalensis*, Pleistocene *H. sapiens*, and *Homo* sp. (Koobi Fora and Swartkrans), but are
246 markedly smaller than those of *P. boisei*, *P. robustus*, *H. rudolfensis*, *H. habilis*, *H. erectus*, and *H.*
247 *heidelbergensis*. In *H. naledi*, the M_2 has the largest root volume followed by the M_3 and M_1 (Fig.
248 5). Similar metamerism variation is found in *A. africanus*, *P. robustus*, and *Homo* sp. from
249 Swartkrans, while late *Homo* (*H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*)
250 tend to have larger M_1 than M_3 roots. *Paranthropus boisei* is the only hominin where the root
251 metamerism variation is $M_3 > M_2 > M_1$ (Fig. 5).

252 *Homo naledi* molar roots have volumetric bifurcation values of $\leq 43\%$ throughout all molar
253 positions (with the exception of the M_3 of U.W. 101-1142, which has a value of 53%; SOM Table
254 S1) and are thus classified as hypotaurodont (Table 2; Fig. 6). While the M_2 roots of the *P. boisei*
255 specimen KNM-ER 3230 are cynotaurodont (17%), hypotaurodont molars are also found in the two

256 Paranthropus species (in particular at M₁) and in the Homo sp. specimens from Koobi Fora (KNM-
257 ER 1805: M₂ = 37%, M₃ = 30%) and Swartkrans (SK 45: M₁ = 30%, M₂ = 34%), but not SK 15 (M₁
258 = 46%, M₂ = 46%, M₃ = 56%) and Cave of Hearths (M₁ = 48%; SOM Table S1). The molar roots of
259 H. habilis and H. erectus are also hypotaurodont, while H. rudolfensis is mesotaurodont (Fig. 6;
260 SOM Table S1). The hypotaurodont molars of H. naledi are contrasted by the meso- and
261 hypertaurodont molar roots of late Homo species (specifically Pleistocene H. sapiens from Equus
262 Cave and Qafzeh) with values $\geq 50\%$, in particular at M₂ and M₃ (Table 2; SOM Table S1; Fig. 6).

263

264 Bivariate associations

265 Cervical plane area (CPA) is highly correlated with both RV and RSA in all three molar
266 positions (Table 3; Fig. 7; SOM Figs. S6 and S7). Relative to CPA, H. erectus, H. heidelbergensis,
267 H. neanderthalensis, Homo sp. KNM-ER1805 (M₃ only) and P. boisei (M₂ and M₃ only) have
268 relatively large root volumes, as indicated by the positive regression residuals (Fig. 7; SOM Fig.
269 S6). Likewise, H. naledi M₁ and M₂ have relatively large RV for a given CPA, while the M₃ has a
270 RV as expected for its CPA (Fig. 7; SOM Fig. S6). In contrast, A. africanus, H. habilis, H.
271 rudolfensis, Homo sp. from Swartkrans, and H. sapiens (both Pleistocene and recent) have
272 relatively small molar RV for a given CPA (Fig. 7; SOM Fig. S6, negative residuals). The same
273 relationship is largely observed when RSA is considered (SOM Fig. S7).

274

275 Principal components analysis and PERMANOVA

276 Principal component loadings reveal that, for all three molar positions, RL, CPA and V_{branch}
277 contribute most to the first component (PC1), whereas V_{cervix} contributes most to the second (PC2;
278 Table 4). Homo naledi forms a separated cluster from the remainder of the sample in all three molar

279 positions (Fig. 8). Along PC1, *H. naledi* is most comparable to *H. sapiens* (Pleistocene and modern)
280 and *H. neanderthalensis*, which reflects its small root size. Along PC2, *H. naledi* overlaps with *P.*
281 *boisei* and *P. robustus*, which reflects the hypotaurodont root morphology captured in the univariate
282 analysis above. *Australopithecus africanus* overlaps with some Pleistocene *H. sapiens*, *H.*
283 *neanderthalensis*, and *P. robustus*. Perhaps with the exception of the M_1 of SK 15, which is similar
284 to that of the Pleistocene *H. sapiens* from Temara, the molar roots of the *Homo* sp. fossils from
285 Swartkrans and Koobi Fora are closer to *H. naledi* than to any other African *Homo* (Fig. 8; SOM
286 Fig. S8). *Homo erectus* (in particular the M_1) also forms a separate cluster from the rest of the fossil
287 hominins and does not bear much resemblance with the *H. naledi* hypodigm.

288 The PERMANOVAs revealed significant differences across the taxonomic groups at all three
289 molar positions (M_1 : $F = 16.89$; M_2 : $F = 12.86$; M_3 : $F = 10.65$; all $p < 0.0001$). The pairwise
290 PERMANOVAs as a post hoc test between all pairs of groups showed some significant differences
291 (at $p < 0.05$) for M_1 (SOM Table S2): between *H. naledi* and recent *H. sapiens*; between recent *H.*
292 *sapiens* and *H. neanderthalensis*, Pleistocene *H. sapiens* and *P. robustus*; and between *H.*
293 *neanderthalensis* and *P. boisei*. For the M_2 , pairwise significant differences were found between *P.*
294 *robustus* and *H. neanderthalensis*, and between *P. robustus* and both Pleistocene and recent *H.*
295 *sapiens* (SOM Table S3). No significant pairwise difference was found in M_3 (SOM Table S4).

296

297 **Discussion**

298 When root size and proportion as well as metameric variation collectively are taken into account,
299 *H. naledi* shows a mix of ancestral (early *Homo*, *A. africanus*, *P. boisei*, and *P. robustus*) and
300 derived (late *Homo*) features (Figs. 4–8). *Homo naledi* has markedly smaller roots than those of
301 eastern African *H. rudolfensis*, *H. habilis*, and *H. erectus* but shares similar root and pulp (*H.*

302 rudolfensis only) proportions with these taxa (Table 2; Figs. 4–8). In contrast, *H. naledi* has molar
303 root sizes comparable to Pleistocene *H. sapiens* but, unlike these, has different root proportions (i.e.,
304 they are less taurodont with a narrow pulp chamber in *H. naledi*; see Table 2; Figs. 4–6).
305 Interestingly, the three *Homo* fossils from Swartkrans (SK 45 from Member 1 and SK 15 from
306 Member 2) and Koobi Fora (KNM-ER 1805), which have been assigned by some to *H. erectus*,
307 *Homo* sp. indet., and *H. habilis*, respectively (Broom and Robinson, 1949, 1950; Robinson, 1961;
308 Wood, 1991; Grine, 2005; Ungar et al., 2006; Grine et al., 2009; Moggi-Cecchi et al., 2010), bear
309 the largest resemblance in overall appearance (i.e., root size, proportion and metamerism variation)
310 with the *H. naledi* hypodigm (see Figs. 3–6 and 8). Both *H. naledi* and *Homo* sp. SK 15 exhibit
311 distal M_3 roots which are buccally offset relative to the mesial roots; a feature they share with *P.*
312 *robustus* (Fig. 3). In *H. naledi* this root deflection in conjunction with the observed depression on
313 the buccal aspect of both the mesial and distal M_3 roots appears to be related to the passage of the
314 inferior alveolar canal running parallel to the M_3 root rather than beneath it as can be seen in *A.*
315 *africanus* Stw 498c (Fig. 3; SOM Figs. S1 and S5).

316 *Homo naledi* and *Homo* sp. SK 15 are also similar in terms of the corono-apical constriction of
317 the pulp chamber, which is also found in African early hominins but not in late *Homo* with the
318 exception of *H. sapiens* from Irhoud (Fig. 3). Meso- and hypertaurodont molars are the result of
319 enlarged pulp cavities and these are particularly common in *H. heidelbergensis* and *H.*
320 *neanderthalensis* (Kupczik and Hublin, 2010; Skinner et al., 2016). This trait is suggested to be an
321 adaptation to counter marked occlusal wear because a large pulp chamber may allow for the
322 deposition of secondary dentine on the walls of the pulp (Blumberg et al., 1971; Constant and
323 Grine, 2001), although the physiological mechanism may be different across species. For example,
324 it was found that in worn molars of Middle Pleistocene *H. neanderthalensis* the pulp horns and
325 walls were obliterated with secondary deposition, while in hypotaurodont molars of late Pleistocene

326 *H. sapiens* from North Africa dentine was predominantly deposited on the roof and floor in the
327 center of the pulp chamber (Kupczik and Hublin, 2010). Although some of the M_1 and M_2 of *H.*
328 *naledi* are heavily worn with dentine exposure (e.g., U.W. 101-001 and U.W. 101-361; see SOM
329 Fig. S1), there is no indication of an obliterated pulp chamber or root canal.

330 Moreover, while SK 15 has relatively smaller roots when scaled to cervical plane area compared
331 to both *H. naledi* and SK 45 (root surface area only; see Fig. 7; SOM Fig. S7), it shares with *H.*
332 *naledi* the same root size gradient ($M_2 > M_3 > M_1$; see Fig. 5). This gradient is also found in *A.*
333 *africanus*, *P. robustus*, and *P. boisei* specimen KNM-ER 15930 (KNM-ER 729 has $M_2 = M_3 > M_1$)
334 but not in any of the other *Homo* fossils, including *H. erectus* and Pleistocene *H. sapiens* from
335 North Africa and the Near East ($M_2 > M_1 > M_3$; Fig. 5)¹. Since the *H. erectus*/late *Homo* root
336 volume sequence is also found in two African great apes, *Pan troglodytes* and *Gorilla gorilla*
337 (Kupczik, 2003), this may in fact constitute the plesiomorphic state; thus, it is derived in *A.*
338 *africanus*, *P. robustus*, *P. boisei* and *H. naledi*. In contrast, cervical plane area follows the
339 previously reported crown area gradient of $M_3 > M_2 > M_1$ (Table 2), which is also present in *H.*
340 *habilis* but not in *H. erectus* or late *Homo* (see Berger et al., 2015; Evans et al., 2016; Hawks et al.,
341 2017).

342 It has recently been suggested that the Middle Pleistocene Cave of Hearths mandible, which has
343 been assigned to *H. sapiens rhodesiensis* (Tobias, 1971), could belong to *H. naledi* (Berger et al.,
344 2017). However, this is unlikely given that the Cave of Hearths mandible differs from the latter in
345 several dental morphological features including occlusal topography of the M_2 (Berthaume et al.,
346 2018), overall premolar and molar crown morphology (L.K.D., pers. obs.) and, as shown here, M_1
347 root morphology (SOM Figs. S2, S3, and S7). In fact, both external root form (e.g., the tapering

¹ It appears that KNM-ER 1805 has the same root size sequence as *H. naledi* and SK 15 (Fig. 2); however, we did not report the M_1 root metrics here because the tooth is partially broken at the cervix.

348 mesial M_1 root) and the morphology of the root canals of the Cave of Hearths specimen resemble
349 those of Middle and Upper Pleistocene *H. sapiens* from North Africa (Irhoud 11), South Africa (Die
350 Kelders, Equus Cave) and Qafzeh (see Kupczik and Hublin, 2010: Fig. S1; SOM Figs. S2 and S4).
351 These results suggest that this specimen is most closely affiliated with samples of fossil *H. sapiens*
352 (or potentially *H. rhodesiensis* if the early part of the *H. sapiens* lineage is distinguished at the
353 species rank). Other notable African Middle Pleistocene *Homo* fossils, such as the ca. 700 ka
354 Tighenif 2 from Algeria (Geraads et al., 1986), differ in mandibular molar root volume and
355 metameric variation from *H. naledi* and rather fall within the upper range of the Aterian *H. sapiens*
356 (Kupczik and Hublin, 2010; Zanolli and Mazurier, 2013). Based on the data in Zanolli and Mazurier
357 (2013: Table 1), the sequence of root volumes of Tighenif 2 follows the $M_2 > M_1 > M_3$ pattern seen
358 in late *Homo* ($M_1 = 951.07 \text{ mm}^3$, $M_2 = 1051.29 \text{ mm}^3$, $M_3 = 773.39 \text{ mm}^3$). Although there are no root
359 metric data available for the mandibular teeth of *H. erectus* from Dmanisi, at least the mandible
360 D211 is distinct from the *H. naledi* lower molar roots inasmuch as the M_1 appears to be larger than
361 the M_2 (see also Hawks et al., 2017). Moreover, while the M_1 has clearly separated roots, the M_2
362 and M_3 roots of D211 appear to be fused or hypertaurodont (see Margvelashvili et al., 2013: their
363 Fig. 2). In contrast, the molars of the mandibles D2735 and D2600 have separated mesial and distal
364 roots. It is also interesting to note that, on visual inspection of the reconstructions of the Dmanisi
365 teeth (see Margvelashvili et al., 2013), the large mandible D2600 has long and distally curved molar
366 roots with a high bifurcation, while the smaller D2735 (comparable in size with D211) has
367 concomitantly shorter and straight molar roots. Unlike in the Dmanisi sample, the differences in
368 molar root morphology within the *H. naledi* sample investigated here do not appear to be as
369 marked.
370

371 **Conclusions**

372 The present findings on mandibular molar root morphology concur with those of previous
373 studies that *H. naledi* is characterized by a mosaic of ancestral and derived cranial and postcranial
374 features. Thus, while absolute molar root size aligns *H. naledi* with late *Homo*, including Middle
375 and Late Pleistocene *H. sapiens* from South Africa (Cave of Hearths, Die Kelders, Equus Cave) and
376 North Africa (Irhoud, Temara, Dar-Es-Soltan), this species shares hypotaurodont roots and a root
377 size gradient with early *Homo* and *Paranthropus*. The latter root traits likely constitute the ancestral
378 condition and are thus symplesiomorphies between *H. naledi* and these earlier hominins. Although
379 this study did not necessarily aim to resolve the phylogenetic relationships of *H. naledi* per se, the
380 present findings shed some light of the possible evolutionary trends of hominins in eastern and
381 southern Africa. If specimens like Cave of Hearth are indeed much older than our sample of *H.*
382 *naledi*, it points to an ancient origin for the modern human molar root pattern and suggests that it is
383 unlikely that modern humans derive substantial ancestry from *H. naledi*. Since molar root form has
384 the advantage of being conservative in its phenotypic expression and roots are often better
385 preserved than crowns in the fossil record, molar root morphological characters may prove useful in
386 future studies on the evolutionary relationships in hominins in general.

387

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598 **Figure legends**

599 **Figure 1.** Microtomography-based 3D-reconstructions of a modern human left M₂ (center) and pulp
600 cavity morphology (left) in mesiolingual view. The tooth was virtually trisected into the crown, root
601 cervix and root branch at the cervical plane and bifurcational plane, respectively (right). The area
602 between the crown and the root cervix is the cervical plane area (CPA). Root length (RL) was
603 measured at the mesial root as the projected distance between the cervical plane and the root tip.
604 The cross-sections illustrate the shape of the mesial and distal root in the apical third of the root
605 (bottom).

606

607 **Figure 2.** Microtomographic-based 3D reconstructions of mandibular molars in fossil hominins in
608 buccal view: a) U.W. 101-1261 (right); the arrows indicate a depression in the apices of the mesial
609 and distal roots of the M₃; b) SK 15 (right); c) Irhoud 11 (left); d) Amud 1 (left); e) HCRP-UR501
610 (right M₁ and M₂); f) KNM-ER 1802 (left M₁ and M₂); g) KNM-ER 1805 (left); h) KNM-ER 730
611 (left); i) STW 404 (left); j) SK 23 (left); k) KNM-ER 729 (right). M₁ is to the left of the molar row.
612 Note that the right molar rows are horizontally flipped. m=mesial, l=lingual.

613

614 **Figure 3.** Microtomographic-based 3D reconstructions of mandibular molars in fossil hominins in
615 apical view: a) U.W. 101-001 (right M₁–M₃); b) U.W.101-1261 (right M₁–M₃); c) U.W.101-1142
616 (right M₂–M₃); d) U.W.101-361 (left M₂–M₃); e) U.W.101-516 (left M₃); f) SK 15 (right M₁–M₃);
617 g) KNM-ER 730 (left M₁–M₃); h) KNM-ER 1805 (left M₁–M₃); i) Irhoud 11 (left M₁–M₃); j)
618 Qafzeh 2 (left M₁–M₃); k) EQ-H71-33 (left M₂–M₃); l) Mauer (right M₁–M₃); m) Amud 1 (left M₁–
619 M₃); n) Stw 498c (left M₁–M₃); o) SK 23 (left M₁–M₃); p) KNM-ER 15930 (left M₁–M₃). Mesial is
620 to the top and buccal to the right. The arrows indicate a buccally deflected distal M₃ root relative to

621 the mesial root. Note that the left molar rows are horizontally flipped. m=mesial, b=buccal.

622

623 **Figure 4.** Pulp chamber morphology of mandibular second molars in *H. naledi* compared to other
624 hominin species in lateral view: a) *A. africanus* (Stw 498c), *P. robustus* (SK 1586), and *P. boisei*
625 (KNM-ER 729) with low pulp chambers; b) species of *Homo* with low pulp chambers (left to right:
626 HCRP-UR 501, SK 15, Irhoud 11, and UW101-1142); c) species of *Homo* with tall pulp chambers
627 (left to right: KNM-ER 992, BH1, and Tabun II C2). All molars are aligned using the lower
628 horizontal line marking the lower border of the pulp cavity. The upper line marks the upper border
629 of the pulp cavity of *H. naledi*.

630

631 **Figure 5.** Box-and-whisker plot of mandibular molar root volume (in mm³). The horizontal lines
632 depict medians, the boxes indicate the lower and upper quartile, respectively, and the lower and
633 upper whiskers show the lowest and highest value, respectively.

634

635 **Figure 6.** Relative proportions of cervical and root branch volumes (scaled to 100%) in Plio-
636 Pleistocene fossil hominins

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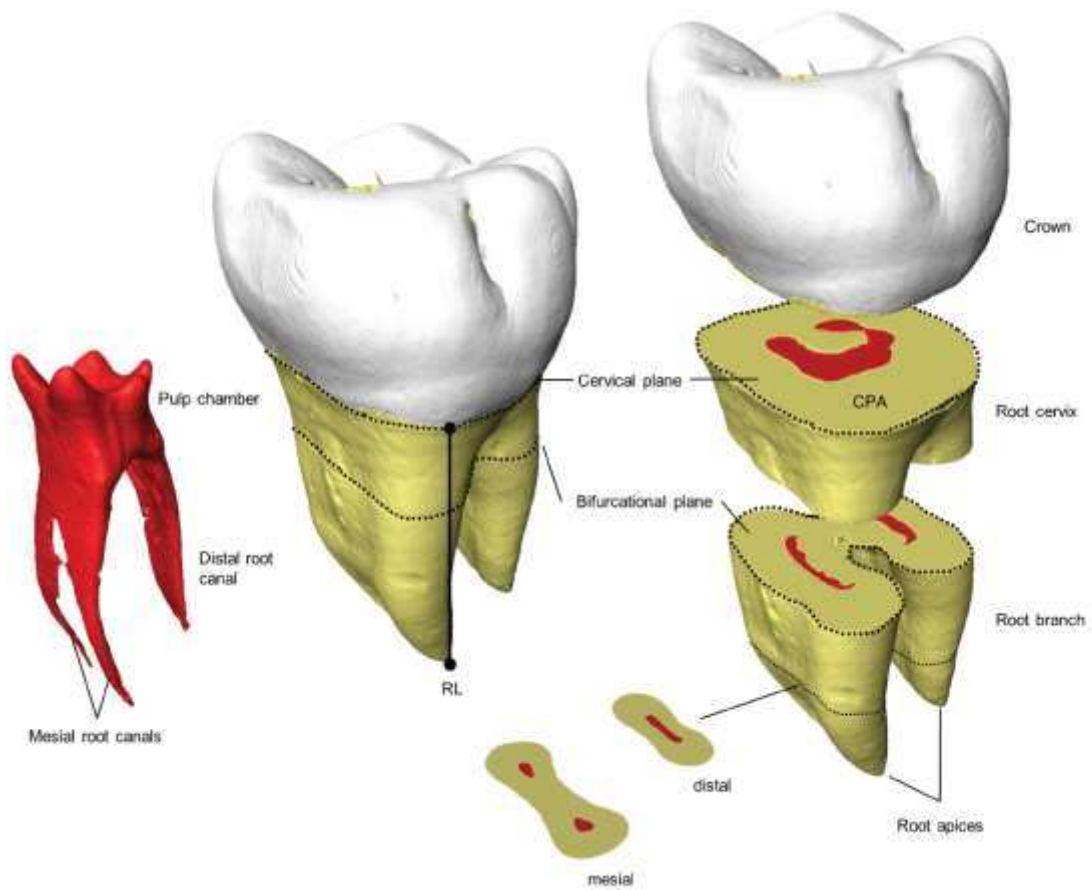
638 **Figure 7.** Bivariate plot of molar root area against cervical plane area in a) M₁, b) M₂, and c) M₃.
639 Ordinary least square regression line (solid) and 95% confidence intervals (dashed) are shown.

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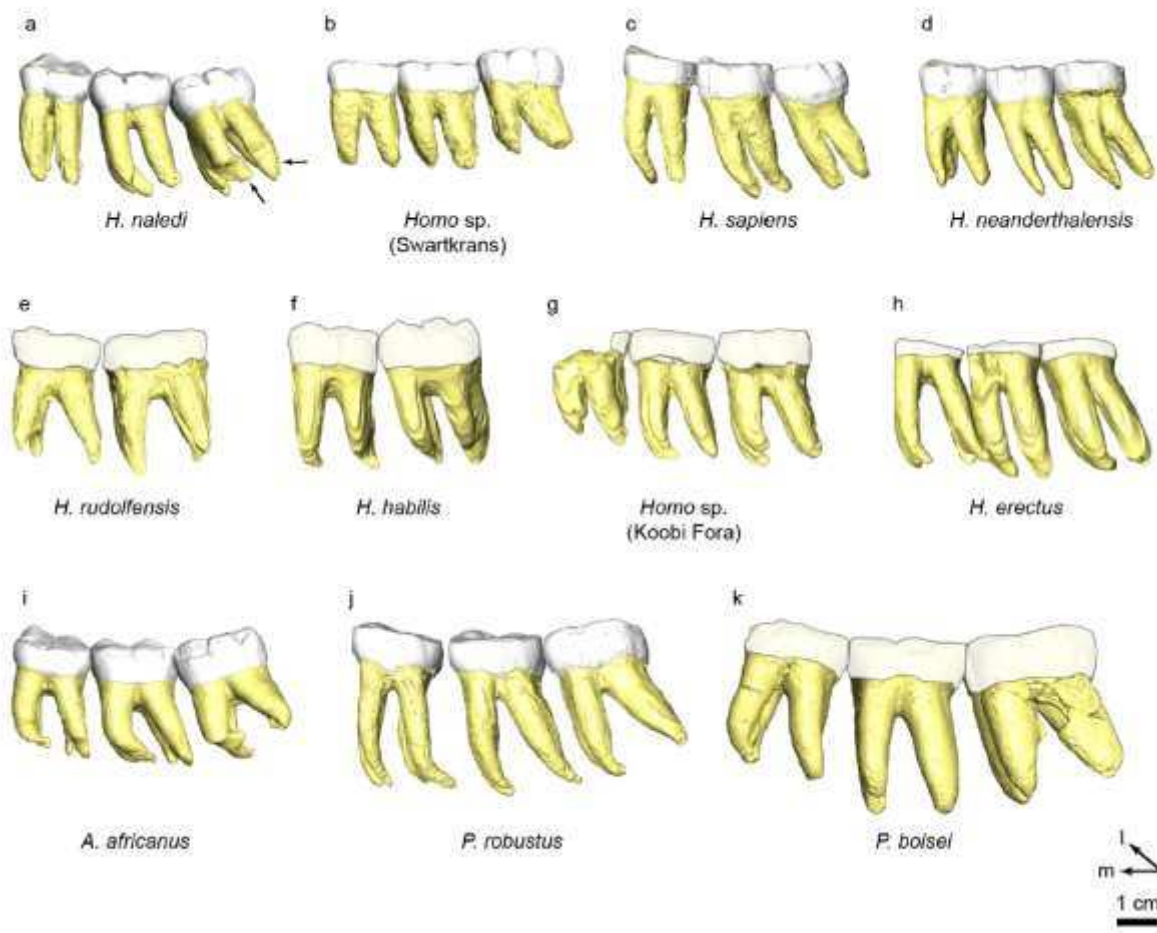
641 **Figure 8.** Bivariate plots of second vs. first principal components (PC2 vs. PC1) using four root
642 metrics: a) M₁; b) M₂; c) M₃. Abbreviations: Aa = *Australopithecus africanus*; Hb = *Homo*
643 *heidelbergensis*; He = *Homo erectus*; Hh = *Homo habilis*; Hn = *Homo neanderthalensis*; Hnl =

644 Homo naledi; Hr = Homo rudolfensis; Hs = recent Homo sapiens; HsP = Pleistocene Homo sapiens;
645 Pb = Paranthropus boisei; Pr = Paranthropus robustus.

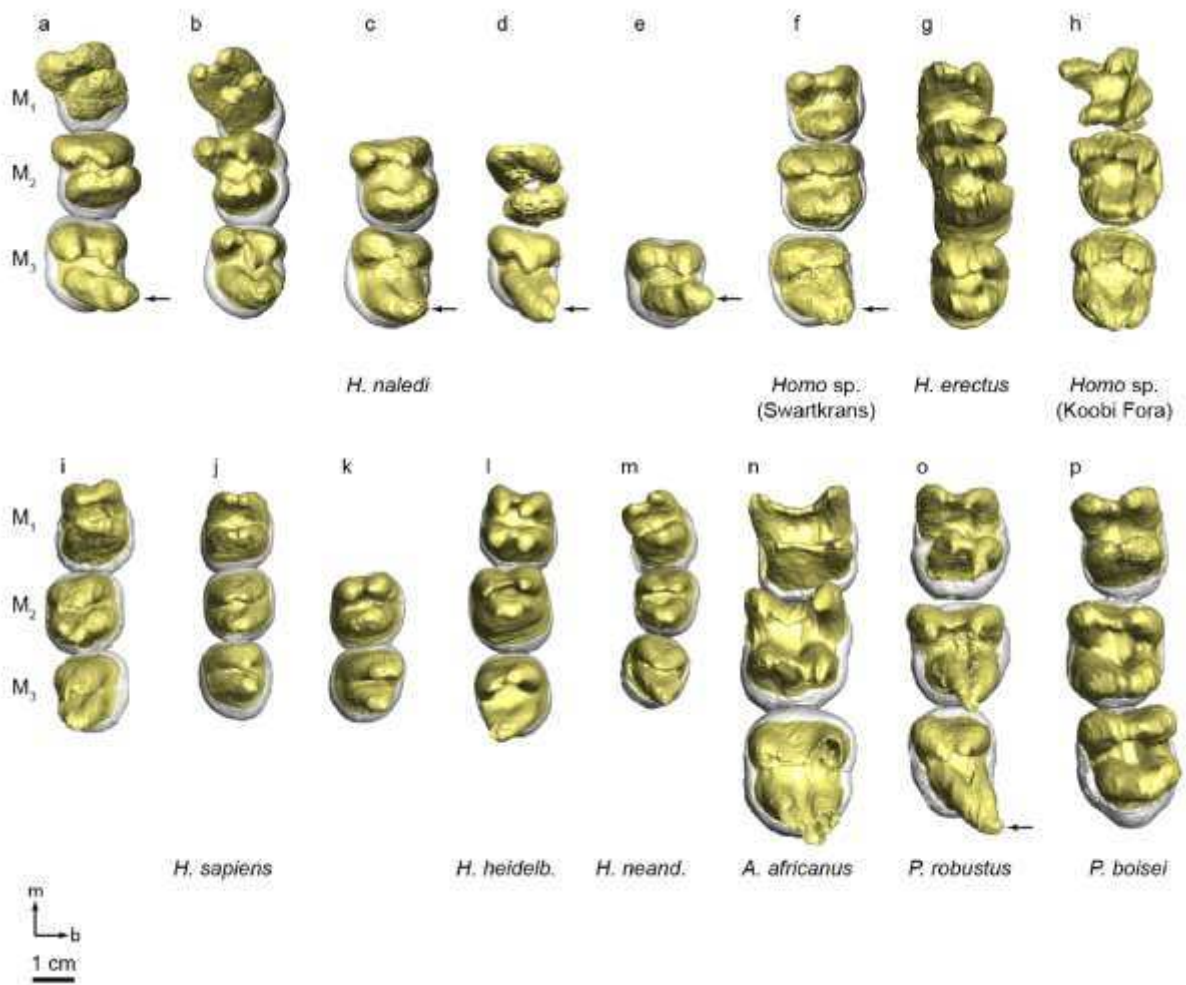
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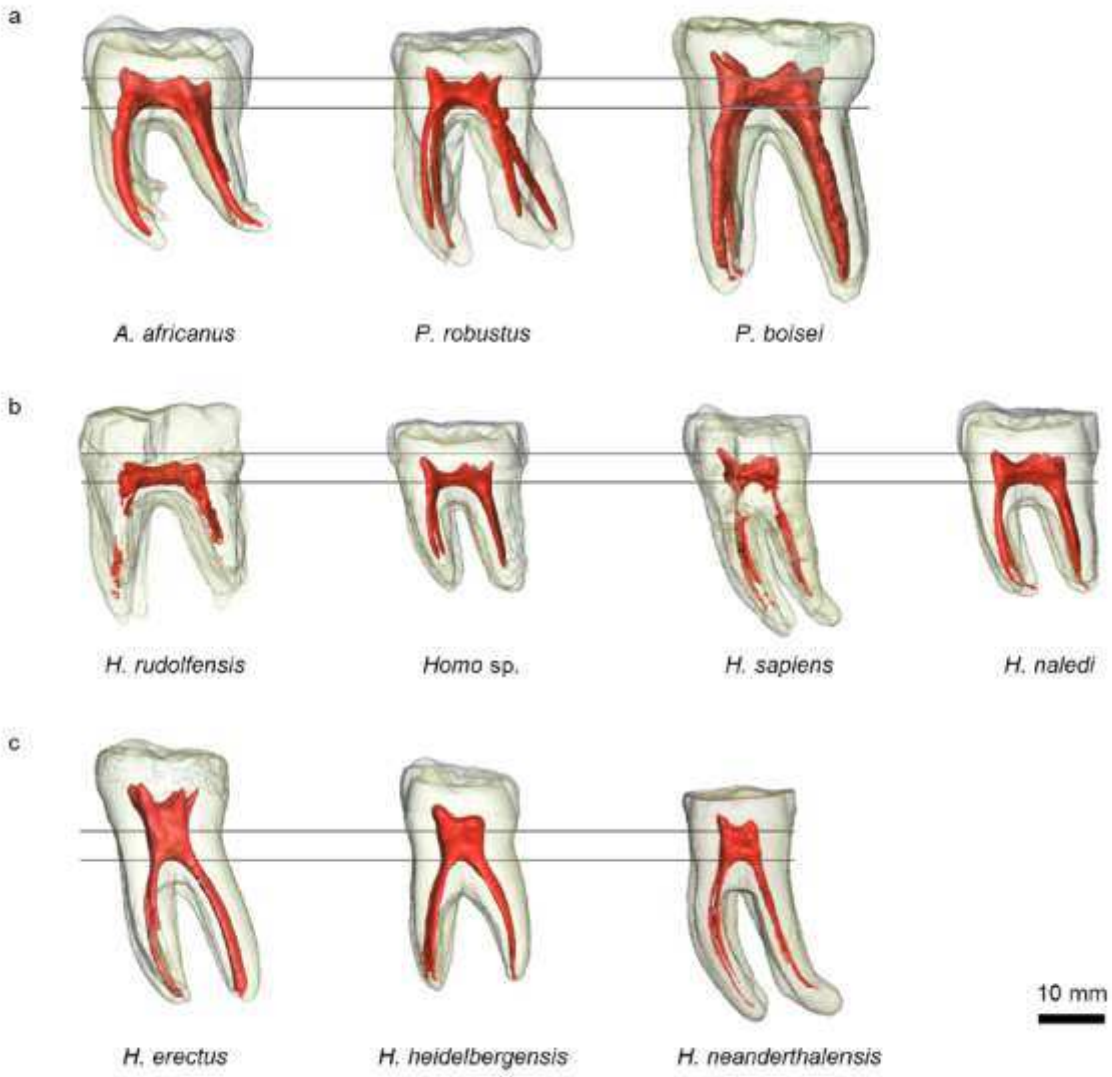


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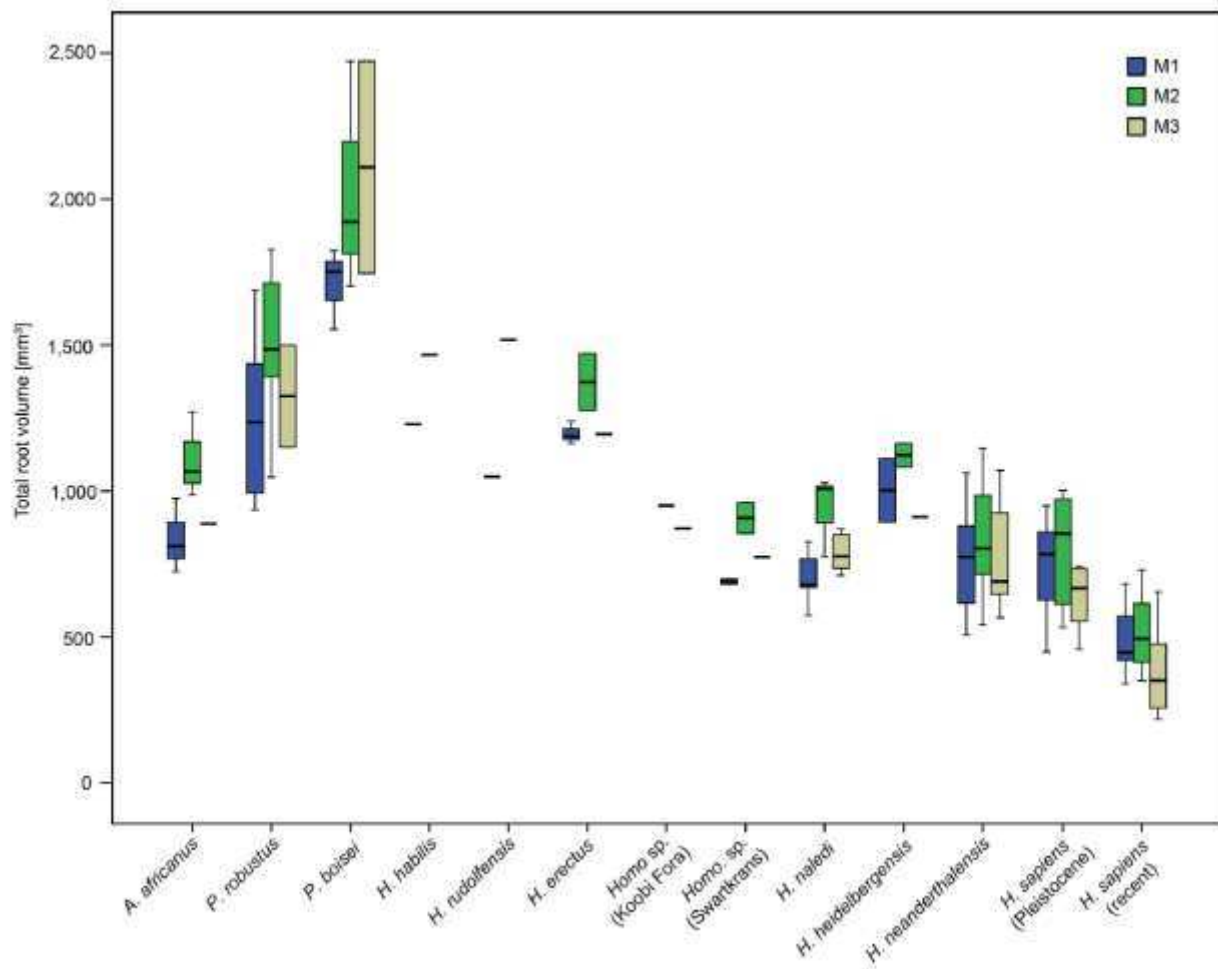


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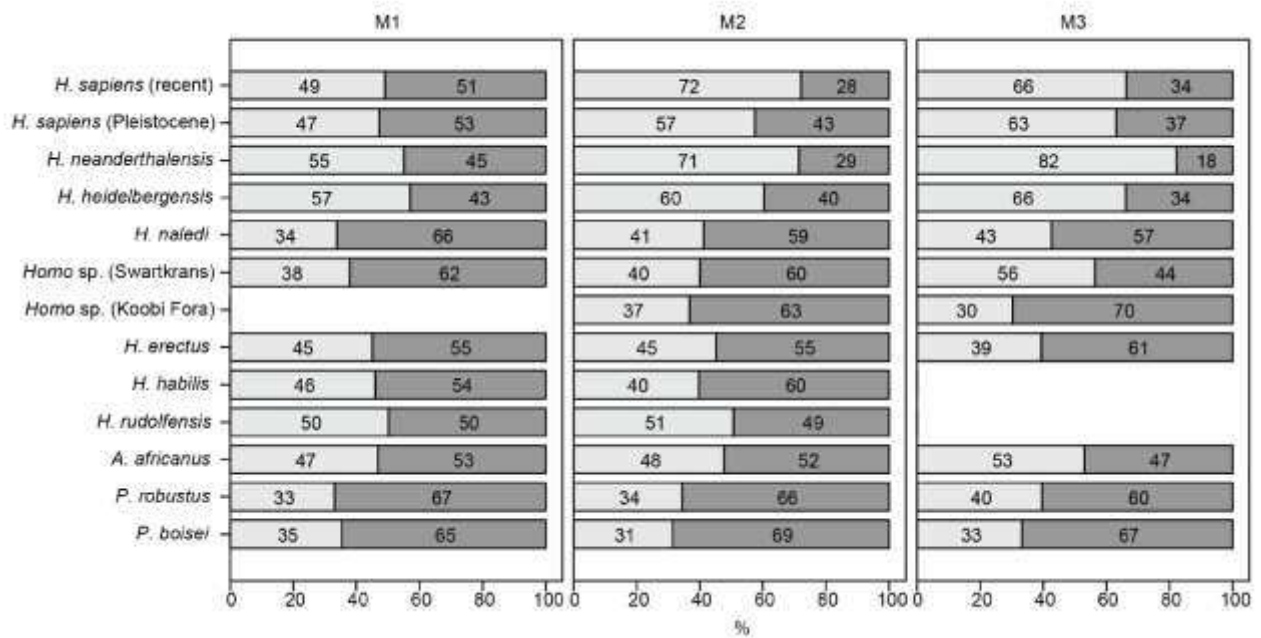




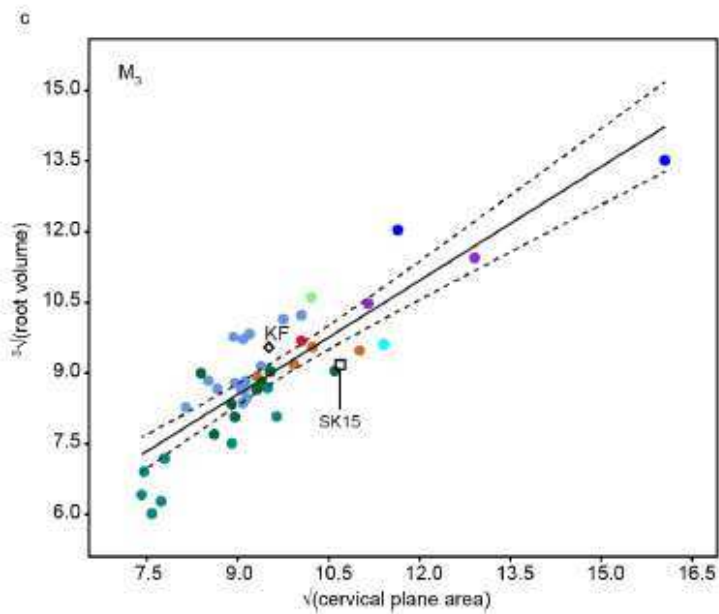
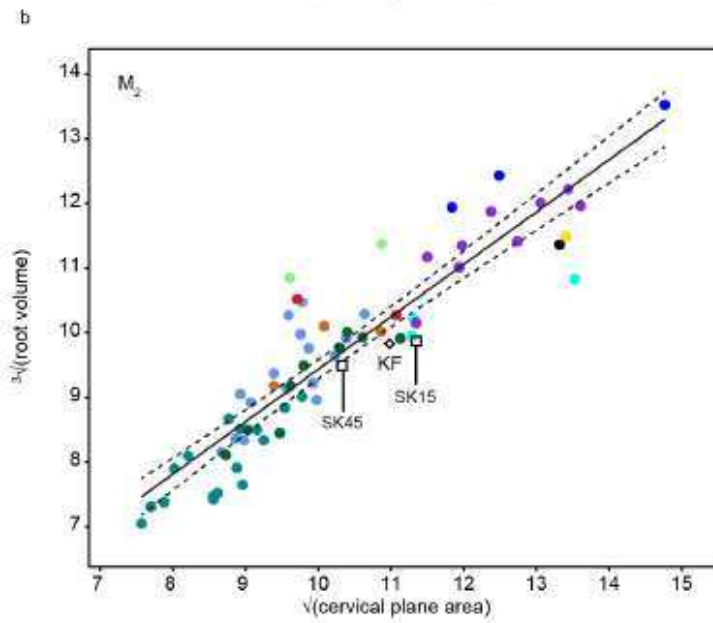
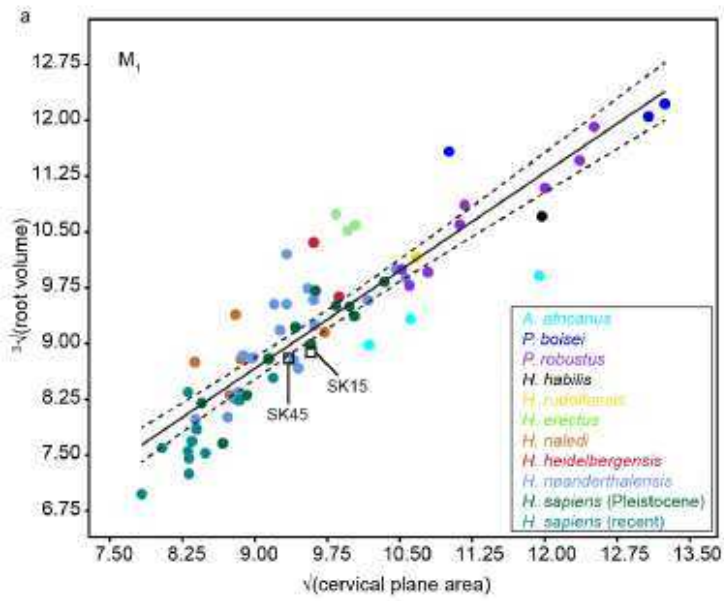
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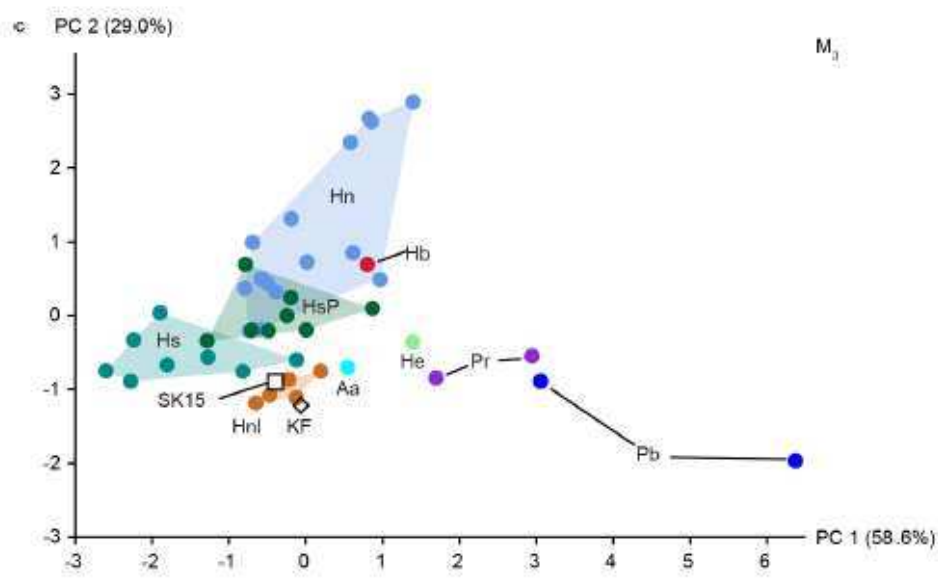
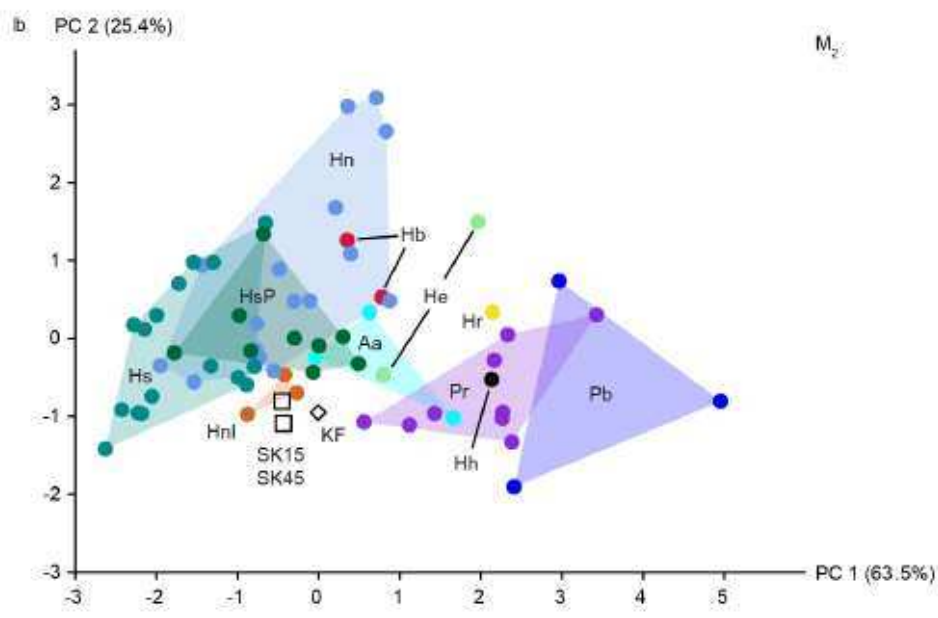
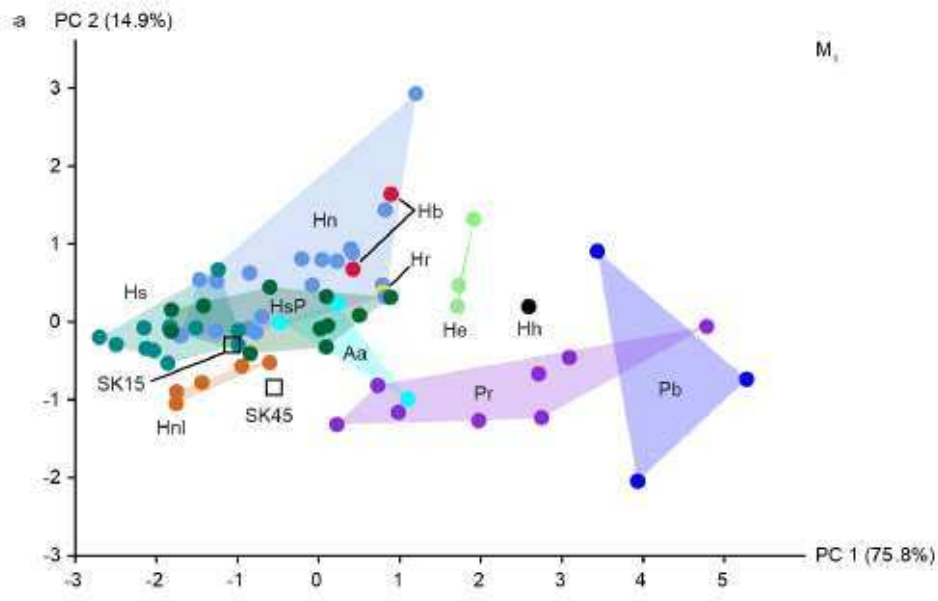


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655 **Table 1**

656 Sample list.

Taxon	Accession number (source)	M ₁	M ₂	M ₃	Total
<i>Australopithecus africanus</i>	Sts 52b, Stw 498c, Stw 404 (ESI)	3	3	1	7
<i>Paranthropus boisei</i>	KNM-ER 729, KNM-ER 3230, KNM-ER 15930 (NMK)	3	3	2	8
<i>Paranthropus robustus</i>	SK6, SK23, SK25, SK858, SK843.846a, SK1586, SK1587ab, SKW5, SKX4446, TM1600 (DNM)	8	9	2	19
<i>Homo sp. indet. (South Africa)</i>	SK15, SK45 (DNM), Cave of Hearths (ESI)	3	2	1	6
<i>Homo sp. indet. (Kenya)</i>	KNM-ER 1805 (NMK)	0	1	1	2
<i>Homo erectus</i>	KNM-ER 730, KNM-ER 992, KNM-WT 15000B (NMK)	3	2	1	6
<i>Homo habilis</i>	KNM-ER 1802 (NMK)	1	1	0	2
<i>Homo heidelbergensis</i>	BH1 (NMB), Mauer (GPIH)	2	2	1	5
<i>Homo naledi</i>	U.W. 101-001, U.W. 101-361, U.W. 101-377, U.W. 101-516, U.W. 101-582, U.W. 101-1142, U.W. 101-1261, U.W. 101-1287b (ESI)	5	3	5	13
<i>Homo neanderthalensis</i>	Amud 1, Tabun II C2 (TAU); and see	18	15	14	47

Kupczik and Hublin (2010)

Homo rudolfensis	HCRP-UR 501 (CMCK)	0	1	0	1
Homo sapiens (Pleistocene)	EQ-H71-33 (ISAM), Irhoud 11 (INSAP), Qafzeh 2, Qafzeh 9, Qafzeh 11, Qafzeh 25 (TAU), SAM AP 6242 (ISAM); and see Kupczik and Hublin (2010)	11	10	9	30
Homo sapiens (recent)	See Kupczik and Hublin (2010)	12	16	8	36

657 Abbreviations: BH = Mala Balanica Cave, Serbia; CMCK = Cultural and Museum Centre,
658 Karonga, Malawi; DNM = Ditsong National Museum of Natural History, Pretoria, South Africa;
659 ESI = Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa;
660 EQ = Equus Cave, South Africa; GPIH = Geologisch-Paläontologisches Institut der Universität
661 Heidelberg, Heidelberg, Germany; HCRP-UR = Hominid Corridor Research Project, Uraha,
662 Malawi; INSAP = Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat,
663 Morocco; ISAM = Iziko South African Museum, Cape Town, South Africa; KNM-ER = National
664 Museums of Kenya, east of Lake Turkana (formerly Lake Rudolf); KNM-WT = National Museums
665 of Kenya, West Turkana; NMB = National Museum, Belgrade, Serbia; NMK = National Museums
666 of Kenya, Nairobi; SK = Swartkrans, South Africa; SKW = Swartkrans, Witwatersrand, South
667 Africa; SKX = Swartkrans, Excavations, South Africa; Sts = Sterkfontein type site; Stw =
668 Sterkfontein, Witwatersrand, South Africa; TAU = Tel Aviv University, Israel; TM = Transvaal
669 Museum, South Africa; U.W. = University of Witwatersrand, South Africa.

670 **Table 2**

671 Summary statistics (sample, mean and standard deviation).

	Taxon	n ^a	Root length [mm]	Cervical plane area [mm ²]	Root surface area [mm ²]	Root volume [mm ³]	Cervical root volume [mm ³]	Root branch volume [mm ³]	Volumetric bifurcation index [%]
M ₁	A. africanus	3 (2)	14.67	119.56	707.31	836.81	391.73	445.07	47.59
			0.72	0.35	149.78	126.88	36.93	140.97	8.63
	P. boisei	3 (1)	20.15	155.81	1077.03	1709.86	604.63	1105.23	35.73
			2.41	30.04	—	139.25	113.15	220.28	8.83
	P. robustus	8 (7)	18.48	130.17	1011.16	1244.12	411.10	833.02	35.36
			2.88	18.33	217.81	269.04	137.80	143.40	11.17
	H. habilis	1	18.62	143.30	865.00	1229.35	564.97	664.38	45.96
			—	—	—	—	—	—	—

H. rudolfensis	1	14.87	113.93	826.36	1049.15	526.37	522.78	50.17
		—	—	—	—	—	—	—
H. erectus	3	19.68	98.92	893.63	1197.22	539.78	657.44	45.22
		0.50	2.08	57.01	38.80	62.89	98.63	6.60
H. naledi	5	13.20	79.37	627.61	703.12	237.81	465.31	33.52
		1.07	9.02	98.62	97.48	56.32	49.46	3.90
Homo sp. (SK)	2	14.55	89.63	696.23	690.39	262.24	428.15	37.88
		2.69	3.10	203.89	12.72	84.28	71.56	11.51
H. heidelbergensis	2	16.39	94.88	684.48	1002.91	572.15	430.76	56.71
		0.29	3.51	30.09	153.46	131.97	21.49	4.48
H. neanderthalensis ^b	19	15.63	87.43	566.52	760.15	419.22	340.93	54.62
		1.55	11.13	95.32	171.92	137.98	99.08	9.33
H. sapiens (Pleistocene) ^b	11	15.38	89.75	576.36	742.65	351.35	391.30	48.29

		(10)	1.79	11.25	108.48	162.20	55.86	117.84	6.51
	H. sapiens (recent) ^b	12	13.69	71.76	424.62	485.02	237.90	247.12	49.27
			0.94	7.02	65.58	104.04	58.52	70.09	7.25
M ₂	A. africanus	2	15.89	146.11	834.49	1108.00	528.78	579.22	48.51
			1.24	31.90	140.61	146.61	63.61	189.60	9.98
	P. boisei	3 (1)	20.16	171.41	1154.19	2033.11	637.52	1395.58	30.86
			0.65	41.25	—	395.62	305.33	324.09	13.89
	P. robustus	9 (8)	18.22	155.49	1107.32	1518.66	522.39	996.28	34.06
			1.56	20.50	196.49	244.97	144.06	148.94	5.45
	H. habilis	1	17.48	177.50	959.59	1466.41	582.31	884.10	39.71
			—	—	—	—	—	—	—
	H. rudolfensis	1	16.72	179.89	1056.66	1518.19	769.47	748.72	50.68
			—	—	—	—	—	—	—

H. erectus	2	19.79	105.19	957.35	1373.50	621.59	751.92	44.42
		0.99	18.28	24.52	138.49	288.86	150.37	16.55
H. naledi	3	14.63	102.62	704.33	936.85	386.37	550.47	40.78
		1.09	14.92	38.82	140.85	109.79	69.81	7.05
Homo sp. (SK)	2	14.15	117.70	740.51	907.66	363.45	544.21	39.69
		1.82	15.63	111.17	74.68	107.41	32.72	8.57
Homo sp. (KF)	1	15.64	120.56	956.46	950.19	348.67	601.52	36.69
		—	—	—	—	—	—	—
H. heidelbergensis	2	17.39	108.40	693.44	1123.01	678.91	444.10	60.33
		0.45	19.98	14.62	57.99	92.89	34.90	5.15
H. neanderthalensis ^b	16	16.47	92.50	551.20	835.19	596.53	238.66	70.65
		2.10	11.14	100.22	190.02	236.46	168.74	18.99
H. sapiens (Pleistocene) ^b	9	16.01	98.53	577.19	807.06	463.78	343.28	60.57

			1.37	15.40	120.02	183.45	64.45	197.60	18.37
	H. sapiens (recent) ^b	16	13.99	71.66	397.32	464.55	340.23	124.32	75.75
			1.74	11.10	88.11	118.18	146.69	142.36	25.21
M ₃	A. africanus	1	13.79	130.24	683.14	887.66	470.74	416.92	53.03
			—	—	—	—	—	—	—
	P. boisei	2 (1)	19.10	196.46	1111.63	2109.38	701.21	1408.17	33.19
			0.04	86.32	—	513.52	179.40	334.12	0.42
	P. robustus	2	17.93	145.51	935.72	1324.93	523.52	801.41	38.83
			0.33	29.92	100.06	247.50	194.16	53.34	7.40
	H. erectus	1	17.98	104.19	845.74	1194.73	470.77	723.96	39.40
			—	—	—	—	—	—	—
	H. naledi	7	14.55	101.04	585.93	864.51	393.85	470.66	45.31
			2.27	11.13	36.24	162.85	122.75	128.10	10.81

Homo sp. (SK)	1	11.37	114.18	599.31	773.90	436.65	337.25	56.42
		—	—	—	—	—	—	—
Homo sp. (KF)	1	14.55	90.52	1130.92	871.60	263.31	608.29	30.21
		—	—	—	—	—	—	—
H. heidelbergensis	1	17.40	101.09	586.30	910.96	602.38	308.58	66.13
		—	—	—	—	—	—	—
H. neanderthalensis ^b	15	16.39	82.58	488.53	763.08	627.84	135.24	80.66
		2.22	8.32	69.48	171.65	248.58	138.99	18.04
H. sapiens (Pleistocene) ^b	8	15.30	85.25	458.46	638.95	403.45	235.50	64.62
		1.62	13.02	73.29	107.08	61.65	115.67	15.11
H. sapiens (recent) ^b	8	12.49	68.82	322.33	380.02	251.96	128.06	72.84
		1.82	16.00	122.05	150.80	50.85	137.93	23.73

672 ^a Sample size in parenthesis for RSA only.

673 ^b Data partially from Kupczik and Hublin (2010).

674 **Table 3**

675 Ordinary least squares regression statistics for cervical plane area against root surface area (A) and
 676 root volume (V) in hominin mandibular molars.

Molar	A/V	n	Pearson's r correlation	Slope	Confidence intervals ^b
M ₁	Area	65	0.87 ^a	1.28	1.09, 1.47
	Vol	69	0.90 ^a	0.88	0.77, 0.98
M ₂	Area	65	0.90 ^a	1.24	1.09, 1.37
	Vol	68	0.91 ^a	0.81	0.72, 0.90
M ₃	Area	44	0.82 ^a	1.31	1.02, 1.62
	Vol	45	0.87 ^a	0.81	0.56, 0.93

677 ^a $p < 0.0001$, permutation test (n = 9999).

678 ^b 95% bootstrapped (n = 1999).

679

680

681 **Table 4**

682 Principal components analysis (PCA) component loadings.

Molar	Variable	PC1	PC2	PC3
M ₁	RL	0.511	0.180	-0.789
	CPA	0.528	-0.292	0.504
	V _{cervix}	0.449	0.762	0.351
	V _{branch}	0.510	-0.549	-0.040
	% variance	75.842	14.9	7.366
M ₂	RL	0.527	0.241	-0.772
	CPA	0.569	-0.231	0.518
	V _{cervix}	0.342	0.797	0.367
	V _{branch}	0.531	-0.504	-0.025
	% variance	63.511	25.376	9.76
M ₃	RL	0.498	0.384	-0.739
	CPA	0.582	-0.295	0.440
	V _{cervix}	0.383	0.684	0.489
	V _{branch}	0.516	-0.546	-0.145
	% variance	58.547	28.993	11.176

683 Abbreviations: CPA = cervical plane area; ; RL = root length; V_{branch} = root branch volume; V_{cervix} =
684 cervical root volume.

685

