



## LJMU Research Online

**Scott, GR, Dern, LL, Pastore, AJ, Sullivan, MR, Nesbitt, H, O'Rourke, DH, Irish, JD and Hoffeecker, JF**

**World variation in three-rooted lower second molars and implications for the hominin fossil record**

<http://researchonline.ljmu.ac.uk/id/eprint/18971/>

### Article

**Citation** (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

**Scott, GR, Dern, LL, Pastore, AJ, Sullivan, MR, Nesbitt, H, O'Rourke, DH, Irish, JD and Hoffeecker, JF (2023) World variation in three-rooted lower second molars and implications for the hominin fossil record. Journal of Human Evolution. 177. ISSN 0047-2484**

LJMU has developed [LJMU Research Online](#) for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact [researchonline@ljmu.ac.uk](mailto:researchonline@ljmu.ac.uk)

<http://researchonline.ljmu.ac.uk/>

World variation in three-rooted lower second molars and implications for the hominin fossil record

G. Richard Scott<sup>a,\*</sup>, Laresa L. Dern<sup>a</sup>, Arielle J. Pastore<sup>a</sup>, Mackenzie R. Sullivan<sup>a</sup>, Heather Nesbitt<sup>b</sup>, Dennis H. O'Rourke<sup>c</sup>, Joel D. Irish<sup>d,e</sup>, John F. Hoffecker<sup>f</sup>

<sup>a</sup> *Department of Anthropology, University of Nevada Reno, Reno NV 89557, USA*

<sup>b</sup> *Department of Anthropology, Texas State University, San Marcos TX 78666, USA*

<sup>c</sup> *Department of Anthropology, University of Kansas, Lawrence KS 66045, USA*

<sup>d</sup> *Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, Liverpool, UK*

<sup>e</sup> *The Centre for the Exploration of the Deep Human Journey, University of the Witwatersrand, Johannesburg, South Africa*

<sup>f</sup> *Institute of Arctic and Alpine Research, University of Colorado at Boulder, Boulder CO 80309, USA*

**\*Corresponding author.**

Email address: [grscott@unr.edu](mailto:grscott@unr.edu) (G. Richard Scott)

## **Acknowledgment**

Christy G. Turner II was working on anthropological problems until the day of his passing in 2013. Although no longer with us, his prodigious efforts over three decades of data collection live on in the C.G. Turner II Legacy Project. Although he addressed a wide range of problems during his life, he could not get to everything. This is our small way of 'kicking the can down the road' in his honor. JDI thanks all individuals at the various institutions and field sites from which the African data were collected. Funding provided by the Polish Research Center, National Science Center of Poland, National Science Foundation (BCS-0840674, BNS-0104731, BNS-9013942), National Geographic Committee for Research & Exploration (#8116-06),

Wenner-Gren Foundation (#7557), Hierakonpolis Expedition, Combined Prehistoric Expedition, and an American Museum of Natural History Collections Study Grant. The authors kindly thank the anonymous reviewers whose salient comments made for a much stronger paper.

1 Short Communication

2

3 World variation in three-rooted lower second molars and implications for the hominin fossil  
4 record

5

6 **Keywords:** Dental morphology; Phenotype variants; Global variation; Homoplasia

7

8

## 9 1. Introduction

10

11 Little research has been conducted on three-rooted lower second molars ( $3RM_2$ ), but the  
12 presence of an accessory third root in first molars ( $3RM_1$ ) shows a distinct pattern of global  
13 variation. The latter trait attains its highest frequencies in East Asians and American Arctic  
14 populations (ca. 25%), with intermediate frequencies in Southeast Asians, Polynesians and  
15 Northwest North Americans (ca. 12%), low frequencies in non-Arctic Americans and Australo-  
16 Melanesians (ca. 5%), and very low frequencies (ca. 0–1%) in Western Eurasians and sub-  
17 Saharan Africans (Scott et al., 2018). Because of these differences, the trait is a powerful tool in  
18 assessing population origins and relationships. Turner (1971), for example, used  $3RM_1$  to  
19 develop a three-wave model for the peopling of the Americas based on this single trait. The  
20 addition of many more crown and root traits in biodistance studies did not alter the original  
21 model (Turner, 1984, 1985, 1986; Greenberg et al., 1986).

22 Because of the striking contrast between European and African populations viz. Asian  
23 and Asian-derived populations,  $3RM_1$  is useful as an indicator of gene flow in boundary

24 populations (Heim et al., 2016). Whether the 3RM<sub>1</sub> has any adaptive significance is currently  
25 unknown (Scott et al., 2018). The trait may prove to be a genetic hitchhiker linked to other traits  
26 of selective consequence. For example, incisor shoveling in North and East Asian populations  
27 may be a by-product of selection for the effects of EDAR V370A on mammary ductal branching  
28 (Hlusko et al., 2018).

29 Two Middle Pleistocene fossils from the sites of Penghu on Taiwan (Chang et al., 2015)  
30 and Xiahe on the Tibetan Plateau (Chen et al., 2019) exhibit an accessory root on the lower  
31 second molar, positioned lingually between the mesial and distal roots. Bailey et al. (2019a)  
32 suggested that the high frequencies of 3RM<sub>1</sub> in modern Asians represent gene flow from archaic  
33 forms such as Xiahe and Penghu. Scott et al. (2019), however, noted that in Penghu and Xiahe,  
34 the extra root differs in location from the archetypical 3RM<sub>1</sub>, where the accessory root is  
35 distolingual. For this reason, and because the expression of a third root on molars of different  
36 positions may not be homologous, Scott et al. (2019) questioned the basis of Bailey et al.'s  
37 (2019) inference regarding gene flow from these archaic forms into modern Asians.

38 Here, to aid researchers interested in assessing molar root variation among modern and  
39 fossil hominins, we provide global frequencies for the little studied 3RM<sub>2</sub> to complement those  
40 for 3RM<sub>1</sub>. We also assess the extent to which frequencies of 3RM<sub>2</sub> and 3RM<sub>1</sub> covary, as high  
41 covariation might suggest that these traits have similar genetic and/or developmental  
42 underpinnings while low covariation would suggest the opposite. Relative to these data and  
43 analysis, we assess the likelihood that 3RM<sub>1</sub> and 3RM<sub>2</sub> are homologous traits. Specifically, we  
44 ask, is it likely that the 3RM<sub>2</sub> lingual accessory roots in the Asian fossils represent the same trait  
45 as the distolingual accessory roots that characterize 3RM<sub>1</sub>?

46 **2. Materials and methods**

47

48 Lower molars normally have two roots, one mesial and one distal. The mesial root exhibits a  
49 groove halfway between the buccal and lingual root cones (or radicals) and each cone has its  
50 own canal (Fig. 1A). The distal root is more conical in shape and has one root canal but generally  
51 no root groove (Calberson et al., 2007). There are several ways that lower molars manifest three  
52 roots, but the standard 3RM<sub>1</sub> has as a distinguishing characteristic—a distolingual accessory root  
53 (Fig. 1B, C). This is explicit in the definition of Turner et al. (1991:25): “3. Three roots. A third  
54 (supernumerary) root is present on the distolingual aspect. It may be very small but is usually  
55 about one-third the size of the normal distal root.”

56

57 INSERT FIG. 1

58

59 Although the definition of Turner et al. (1991) specifies a distolingual accessory root,  
60 lower molar root number on the Turner data entry sheets does not accommodate variations in  
61 form. When three roots are present, it is noted as such without comment on the nature of the  
62 accessory root. For the lower first molar, a notation of three invariably refers to a distolingual  
63 accessory root. For the lower second molar, three may refer to a distolingual accessory root but  
64 alternative phenotypes would also be noted as three (cf., Fig. 1D–F).

65 In the dental literature, the term for a distolingual accessory root on a lower molar is  
66 ‘radix entomolaris’ (Carlsen, 1987), but in the anthropological literature it is designated by the  
67 shorthand 3RM. This accessory root is most common on the first but can also be present on the  
68 second and third lower molars (Fig. 2A, B).

69

INSERT FIG. 2

70           While 3RM<sub>1</sub> is one of Turner's 29 key traits, with frequencies available on computer  
71 printouts (cf. appendix in Scott and Irish, 2017), this is not the case for the second molar. As  
72 such, we evaluated 11,382 score sheets from the C.G. Turner II database of archaeological  
73 remains (a few hundred to ~10,000 years of age) to calculate 3RM<sub>2</sub> frequencies, with special  
74 emphasis on the Americas, Asia, the Pacific, and Europe. To characterize global variation in  
75 3RM<sub>2</sub>, these observations were augmented by unpublished data from 2,373 North and South  
76 Africans (see Irish, 2000, 2005, 2006, 2016; Irish et al. 2014, for details).

77           From Turner's data sheets, we could calculate 3RM<sub>2</sub> frequencies and evaluate the  
78 relationship between 3RM<sub>1</sub> and 3RM<sub>2</sub>. While a relationship might be presumed, the sheets only  
79 specify total number, not the presence or absence of a distolingual accessory root. This is  
80 noteworthy given that there are different forms of expression. We tallied instances where 3RM<sub>2</sub>  
81 was associated with a 3RM<sub>1</sub> that expressed a distolingual accessory root or with a 2RM<sub>1</sub> lacking  
82 this extra root.

83

### 84 **3. Results**

85           To generalize on root number variation, we combined information for subregions within the  
86 major regions of the world (Africa, Pacific, Asia, Europe, Americas). After compiling data on all  
87 individuals, we found that instances of 3RM<sub>2</sub> are extremely rare. There are four cases from  
88 Africa, 13 from the Pacific, 18 from Asia, two from Europe, and 14 from the Americas (Table 1).  
89 In total, 51 cases out of a sample of 13,755 individuals yield a global incidence of 0.37%. This  
90 figure presents a contrast to the global frequency of 9.5% for 3RM<sub>1</sub>.

91 For the 51 individuals exhibiting 3RM<sub>2</sub>, four did not retain a LM<sub>1</sub> for comparison. Of the  
92 47 cases with observations on both first and second lower molars, 13 of 43 3RM<sub>2</sub> (30.2%) were  
93 associated with a 3RM<sub>1</sub>. In the Arctic, where 3RM<sub>1</sub> attains its highest frequency, five of eight  
94 individuals have 3RM<sub>1</sub> and 3RM<sub>2</sub>. In East Asians, where 3RM<sub>1</sub> is second most common, there  
95 are 16 cases of 3RM<sub>2</sub>, but only four were associated with 3RM<sub>1</sub>. No regional group has a  
96 frequency of 3RM<sub>2</sub> > 1.5%. For the same combined grouping mentioned in the introduction with  
97 the highest 3RM<sub>1</sub> occurrence, i.e., East Asian and American Arctic at ca. 25%, the corresponding  
98 3RM<sub>2</sub> value is 0.92%. For the abovementioned grouping with intermediate 3RM<sub>1</sub> frequencies  
99 globally, namely Southeast Asians, Polynesians and Northwest North Americans at ca. 12%,  
100 their 3RM<sub>2</sub> incidence is 0.49%. On an individual sample basis, East Asians exhibit a 1.0%  
101 frequency of 3RM<sub>2</sub>, with Polynesians at 1.5%. Even Circumpolar samples with the highest 3RM<sub>1</sub>  
102 frequencies have 3RM<sub>2</sub> frequencies of <1.0%. Only four cases of 3RM<sub>2</sub> were recorded in Africa  
103 (0.16%; none associated with 3RM<sub>1</sub>) and two in Europe (0.24; none with 3RM<sub>1</sub>), suggesting a  
104 weak relationship between frequencies and expression of 3RM<sub>1</sub> and 3RM<sub>2</sub>.

105

106

INSERT TABLE 1

107

#### 108 **4. Discussion**

109 To put accessory roots in context, it is helpful to provide a general characterization of the  
110 factors underlying root development. Experimental research demonstrates that signaling  
111 molecules from four conserved families (TGF $\beta$ , FGF, SHH, Wnt) play a central role in tooth  
112 crown development (Tummers and Thesleff, 2009). Li et al. (2017) note that factors governing  
113 root development involve the same four signaling families along with BMP. For crown



114 development, enamel knots are reservoirs for signaling genes and molecules that guide the shape  
115 of the tooth, including the formation of individual cusps (Jernvall and Thesleff, 2000). For root  
116 development, the role of enamel knots is largely assumed by Hertwig's epithelial root sheath  
117 (HERS) operating in conjunction with the cranial neural crest mesenchyme. Hertwig's epithelial  
118 root sheath is a bilayer of the outer and inner dental epithelium that is initiated at the crown-root  
119 junction, or cervical loop, and extends vertically or horizontally to produce single-rooted or  
120 multi-rooted teeth. For single-rooted teeth, HERS only extends apically. For multi-rooted teeth,  
121 tongue-like projections extend horizontally until they merge at a furcation where the primary  
122 (and accessory) roots are outlined; after they merge, HERS extends apically as in a single-rooted  
123 tooth (Huang et al., 2010; Huang and Chai, 2012).

124 Li et al. (2017) provide a table that shows root defects associated with mutations in the  
125 major odontogenetic signaling pathways. In most instances, the defect is no roots or short roots.  
126 There is no mutation associated with accessory roots. However, a null mutant in *Wnt10a* delays  
127 or precludes HERS from moving in a horizontal direction, preventing a furcation in a multi-  
128 rooted tooth. The result is an elongated tooth trunk and pulp chamber, to produce a taurodont  
129 tooth like that often found in Neanderthals. Fons Romero et al. (2017:1296) note that "the *Eda*  
130 pathway has a direct role in root development, influencing proliferation and the angle of HERS  
131 and, therefore, the ability to form furcations" so *Wnt10a* and *Eda* both play a role limiting the  
132 development of multiple roots, resulting in taurodont teeth.

133 As part of the *Eda* pathway, the SNP EDAR V370A is associated with several dental  
134 morphological crown traits, including shoveling, double-shoveling, and lower molar cusp  
135 number (Kimura et al., 2009; Park et al., 2012). Given its impact on crown traits, Kataoka et al.  
136 (2021) explored the relationship between this SNP and root number. In a contingency analysis

137 comparing root number to the three EDAR V370A genotypes (V/V, V/A, A/A), they found a  
138 significant difference between one-rooted and two-rooted P<sup>1</sup> and C-shaped one-rooted and two-  
139 rooted M<sub>2</sub>. However, they found no significant relationship between the three genotypes and P<sup>2</sup>,  
140 M<sup>2</sup>, and M<sub>1</sub> root number. They reported a weak but significant Spearman's rho (0.135) between  
141 the EDAR V370A genotype and 3RM<sub>1</sub>, but this correlation is much lower than that between this  
142 SNP and shoveling (0.457).

143 At this point, one cannot specify the signaling pathways and transcription factors  
144 associated with accessory roots of the lower molars. Research on EDAR V370A is a start but  
145 there are multiple genes and often dozens of SNPs associated with the BMP, FGF, SHH, EDA,  
146 and TGFβ pathways. It is likely that pleiotropy is involved as extra roots may be linked to other  
147 biological traits, similar to the Eda pathway that impacts variables of skin, hair, and teeth  
148 (Cheverud, 1996; Kimura et al., 2009).

149 In the global population, one of 10 individuals possesses a 3RM<sub>1</sub> (Aung and Myint,  
150 2022). However, as noted earlier, there are distinct differences among major geographic groups  
151 (Scott et al., 2018). The trait is most common in Asian and Asian-derived populations and rare in  
152 Western Eurasians and sub-Saharan Africans. By contrast, as shown here, cases of 3RM<sub>2</sub> are rare  
153 in all groups with a global frequency of <1%. Although some individuals have 3RM<sub>1</sub> paired with  
154 3RM<sub>2</sub>, the association is weak. An added complication is that 3RM<sub>2</sub> can be expressed in several  
155 forms, only one of which is the classic accessory distolingual root.

156 Variation in the form of 3RM<sub>2</sub> is relevant to late Middle Pleistocene hominin remains  
157 from the Tibetan Plateau (Chen et al., 2019; Bailey et al., 2019a) and Taiwan (Chang et al.,  
158 2015). Bailey et al. (2019a) proposed that the 3RM<sub>2</sub> in the Xiahe mandible could be used to infer  
159 deep ties between Denisovans and recent Asian populations. Lacking data on 3RM<sub>2</sub> frequencies,

160 this conclusion was based on geographic variation in 3RM<sub>1</sub> and the presumption that the  
161 lingually positioned third root was homologous with a distolingual accessory root. Scott et al.  
162 (2019) questioned this interpretation, noting that while the second molar had three roots it did not  
163 exhibit the classic distolingual form. Initially, these authors thought that the third root was the  
164 product of a bifurcated mesial member (cf. Fig 1D) based on the published image in Bailey et al.  
165 (2019a), but a reexamination shows the extra root is in a lingual position between the mesial and  
166 distal roots (Bailey et al., 2019b). In this regard, the Penghu and Xiahe mandibles exhibit  
167 comparable extra roots that are likely homologous. This phenotype has been observed in recent  
168 humans (Fig. 2D, E), but it is exceptionally rare. For it to occur in two Middle Pleistocene Asian  
169 hominins may be noteworthy in assessing phylogenetic relationships.

170 Homoplasmy is the issue when 3RM<sub>1</sub> in recent human populations is compared to 3RM<sub>2</sub> in  
171 hominins of any age. Is a root positioned between the mesial and distal members reflective of the  
172 same underlying genetic background as a distolingual accessory root? While an accessory  
173 lingual root between the mesial and distal roots of lower molars is an interesting, rare, and  
174 distinct trait, is it homologous with a distolingual accessory root? Although our current  
175 understanding of the genes and developmental processes underlying root development is not  
176 sufficient to provide a definitive answer to this question, the lack of covariation between the  
177 3RM<sub>1</sub> and 3RM<sub>2</sub> in recent human populations suggests that these two traits are not homologous.

178 Additional research is warranted, but in the extensive literature on 3RM<sub>1</sub> there is no  
179 confusion about what constitutes this specific phenotype—the presence of a distolingual  
180 accessory root. This is evident in countless photographs and X-rays. Bailey et al. (2019a) used a  
181 photo from a modern human to illustrate a 3RM<sub>1</sub> and it shows a distolingual accessory root.  
182 Moreover, the Penghu and Xiahe mandibles have first and second lower molars, and it is only the

183 second that exhibits the extra lingual root. This same condition has been observed in recent  
184 humans (Fig. 2E, F). Perhaps these distinctions are important in differentiating homoplasia from  
185 homology, where the key tooth for the classic three-rooted lower molar is  $M_1$ , while the key  
186 tooth for the lingually positioned accessory root is  $M_2$ .

187         Although we argue that, based on position, the lingual accessory root on the lower second  
188 molars of two Asian hominins differs from the distolingual accessory root of the classic  $3RM_1$ , it  
189 is true that both  $3RM_1$  and  $3RM_2$  are more common in Asian and Asian-derived populations than  
190 Africans and Europeans. For the latter populations there was no instance of  $3RM_2$  associated  
191 with  $3RM_1$  and only four total cases of  $3RM_2$  out of 3242 individuals (0.0012). For Asian and  
192 Asian-derived groups, 13 of 10,513 individuals (0.0012) had both  $3RM_1$  and  $3RM_2$  while 28  
193 exhibited a  $3RM_2$  with a  $2RM_1$  (0.0027). Regardless of whether the  $3RM_2$  in the Penghu and  
194 Xiahe fossils is homologous to the  $3RM_1$  of modern Asians, both lingual and distolingual  
195 accessory roots are more common in Asia. Again, the large East Asian and American Arctic  
196 combined sample has a  $3RM_1$  incidence of 25% and  $3RM_2$  of 0.9%, both of which are  $\geq 2.5x$  the  
197 respective global averages of 9.5% and 0.37%; of course, given the rarity of  $3RM_2$ , these  
198 percentages should be interpreted with caution. For Southeast Asians, Polynesians, and  
199 Northwest North Americans combined, with  $3RM_1$  of 12% and  $3RM_2$  of 0.49%, the figures are  
200  $\geq 1.2x$  the global average. Individual Asian-derived samples vary as indicated (e.g., Polynesia  
201  $3RM_2$ , 1.5%).

202         Gellis and Foley (2021) recently developed new methods for classifying root variation  
203 using computed tomographic scans. More importantly, expanded genetic research, most notably  
204 comparing genotypes of individuals with both  $3RM_1$  and  $3RM_2$  (including variation in accessory  
205 root locations), could help determine if the same genes are responsible for their expression.

206 These are key directions for the future. New methods, together with the global root data  
207 presented here, can generate finer-grained data to complement the existing extensive dataset on  
208 crown traits. Among other key findings, such data may help address questions of homology vs.  
209 homoplasy in different forms of multi-rooted teeth (Turner et al., 1991; Scott and Irish, 2017)  
210 and, more specifically, the utility of the rare 3RM<sub>2</sub> trait for assessing dental variation and  
211 relatedness among hominins of any age.

212

## 213 **References**

- 214 Aung, M.N., Myint, K.K., 2022. Three-rooted mandibular first molars: a meta-analysis of  
215 prevalence. *Int. J. Dentistry*, 2022, Article ID 9411076, 30 pages.
- 216 Bailey, S.E., Hublin, J.J., Antón, S.C., 2019a. Rare dental trait provides morphological evidence  
217 of archaic introgression in Asian fossil record. *Proc. Nat. Acad. Sci. USA* 116, 14806-  
218 14807.
- 219 Bailey, S.E., Kupczik, K., Hublin, J.-J., Antón, S.C., 2019b. Reply to Scott et al: A closer look at  
220 the 3-rooted second molar of an archaic human from Xiahe. *Proc. Nat. Acad. Sci. USA*  
221 117, 39-40.
- 222 Calberson, F.I., de Moor, R.J., Deroose, C.A., 2007. The radix paramolaris and entomolaris:  
223 Clinical approach in endodontics. *J. Endodont.* 33, 58-62.
- 224 Carlsen, O., 1987. *Dental Morphology*. Munksgaard, Copenhagen.
- 225 Chang, C.-H., Kaifu, Y., Takai, M., Kono, R.T., Grun, R., Matsu'ura, S., Kinsley, L., Lin, L.-KI.,  
226 2015. The first archaic *Homo* from Taiwan. *Nat. Commun.* 6 (1), 1-10.

227 Chen, F., Welker, F., Shen, C.C., Bailey, S.E., Bergmann, I., Davis, S., Xia, H., Wang, H.,  
228 Fischer, R., Freidline, S.E., Yu, T.L., 2019. A late middle Pleistocene Denisovan  
229 mandible from the Tibetan Plateau. *Nature* 569, 409-412.

230 Cheverud, J.M., 1996. Developmental integration and the evolution of pleiotropy. *Am. Zool.* 36,  
231 44-50.

232 Fons Romero, J. M., Star, H., Lav, R., Watkins, S., Harrison, M., Hovorakova, M., Headon, D.,  
233 Tucker, A.S., 2017. The impact of the Eda pathway on tooth root development. *J. Dent.*  
234 *Res.* 96, 1290-1297.

235 Gellis, J., Foley, R., 2021. A novel system for classifying tooth root phenotypes. *Plos One*,  
236 16(11), p.e0251953. Greenberg, J.H., Turner, C.G., II, Zegura, S., 1986. The settlement of the  
237 Americas: A comparison of the linguistic, dental, and genetic evidence. *Curr. Anthropol.*  
238 24, 477-497.

239 Heim, K., Maier, C., Pilloud, M.A., Scott, G.R. (2016). Crossroads of the Old World: Dental  
240 morphological data and the evidence for a Eurasian cline. In: Pilloud, M.A., Hefner, J.T.  
241 (Eds.), *Forensic and Bioarchaeological Perspectives on Biological Distance*. Academic  
242 Press, San Diego, pp. 391-410.

243 Hlusko, L.J., Carlson, J., Chaplin, G., Elias, S.A., Hoffecker, J.F., Huffman, M., Jablonski, N.J.,  
244 Monson, T.A., O'Rourke, D.H., Pilloud, M.A., Scott, G.R., 2018. Evidence of  
245 environmental selection on the mother-to-infant transmission of vitamin D and fatty acids  
246 during the last ice age in Beringia. *Proc. Nat. Acad. Sci. USA* 115, E4426-E4432.

247 Huang, X.-F., Chai, Y., 2012. Molecular regulatory mechanism of tooth root development. *Int. J.*  
248 *Oral Sci.* 4, 177-181.

249 Huang, X.-F., Xu, X., Bringas, P., Jr., Hung, Y.P., Chai, Y., 2010. Smad4-Shh-Nfic signaling  
250 cascade-mediated epithelial-mesenchymal interaction is crucial in regulating tooth root  
251 development. *J. Bone Min. Res.* 25, 1167-1178.

252 Irish, J.D., 2000. The Iberomaurusian enigma: North African progenitor or dead end? *J. Hum.*  
253 *Evol.* 39, 393-410.

254 Irish, J.D., 2005. Population continuity vs. discontinuity revisited: Dental affinities among late  
255 Paleolithic through Christian-era Nubians. *Am. J. Phys. Anthropol.* 128, 520-535.

256 Irish, J.D., 2006. Who were the ancient Egyptians? Dental affinities among Neolithic through  
257 Postdynastic peoples. *Am. J. Phys. Anthropol.* 129, 529-543.

258 Irish, J.D., 2016. Who were they really? Model-free and model-bound dental nonmetric analyses  
259 to affirm documented population affiliations of seven South African “Bantu” samples.  
260 *Am. J. Phys. Anthropol.* 159, 655-670.

261 Irish, J.D., Black, W., Sealy, W., Ackermann, R.R., 2014. Questions of Khoesan continuity:  
262 Dental affinities among the indigenous Holocene populations of South Africa. *Am. J.*  
263 *Phys. Anthropol.* 155, 33-44.

264 Jernvall, J., Thesleff, I., 2000. Reiterative signaling and patterning during mammalian tooth  
265 morphogenesis. *Mech. Develop.* 92, 19-29.

266 Kataoka, K., Fujita, H., Isa, M., Gotoh, S., Arasaki, A., Ishida, H., Kimura, R., 2021. The human  
267 EDAR 370V/A polymorphism affects tooth root morphology potentially through the  
268 modification of a reaction–diffusion system. *Sci. Rep.* 11 (5143), 1-10.

269 Kimura, R., Yamaguchi, T., Takeda, M., Kondo, O., Toma, T., Haneji, K., Hanihara, T.,  
270 Matsukusa, H., Kawamura, S., Maki, K., Osawa, M., 2009. A common variation in

271 EDAR is a genetic determinant of shovel-shaped incisors. *Am. J. Hum. Genet.* 85, 528-  
272 535.

273 Li, J., C. Parada, Y. Chai, 2017. Cellular and molecular mechanisms of tooth root development.  
274 *Development* 144, 374-384.

275 Park, J.H., Yamaguchi, T., Watanabe, C., Kawaguchi, A., Haneji, K., Takeda, M., Kim, Y.I.,  
276 Tomoyasu, Y., Watanabe, M., Oota, H., Hanihara, T., 2012. Effects of an Asian-specific  
277 nonsynonymous EDAR variant on multiple dental traits. *J. Hum. Genet.* 57, 508-514.

278 Scott, G.R., Irish, J.D., 2017. *Human Tooth Crown and Root Morphology: The Arizona State*  
279 *University Dental Anthropology System*. University of Cambridge Press, Cambridge.

280 Scott, G.R., Turner, C.G., II, Townsend, G.C., Martinon-Torres, M., 2018. *The Anthropology of*  
281 *Modern Human Teeth: Dental Morphology and Its Variation in Recent and Fossil Homo*  
282 *sapiens*. Second edition. University of Cambridge Press, Cambridge.

283 Scott, G.R., Irish, J.D., Martín-Torres, M., 2020. A more comprehensive view of the  
284 Denisovan 3-rooted second molar from Xiahe. *Proc. Nat. Acad. Sci. USA* 117, 37-38.

285 Tummers, M., I. Thesleff, 2009. The importance of signal pathway modulation in all aspects of  
286 tooth development. *J. Experiment. Zool. Part B: Molec. Development. Evol.* 312, 309-  
287 319.

288 Turner, C.G., II, 1971. Three-rooted mandibular first permanent molars and the question of  
289 American Indian origins. *Am. J. Phys. Anthropol.* 34, 229-241.

290 Turner, C.G., II, 1984. Advances in the dental search for Native American origins. *Acta*  
291 *Anthropogenet.* 8, 23-78.



292 Turner, C.G., II, 1985. Dental evidence for the peopling of the Americas. Nat. Geog. Soc. Res.  
293 Rep. 19, 573-596.

294 Turner, C.G., II, 1986. The first Americans: The dental evidence. Nat. Geog. Res. 2, 37-46.

295 Turner, C.G., II, Nichol, C.R., Scott, G.R., 1991. Scoring procedures for key morphological traits  
296 of the permanent dentition: The Arizona State University dental anthropology system.  
297 In: Kelley, M.A., Larson, C.S. (Eds.), Advances in Dental Anthropology. Wiley-Liss,  
298 New York, pp. 13-31.

299

### 300 **Figure captions**

301

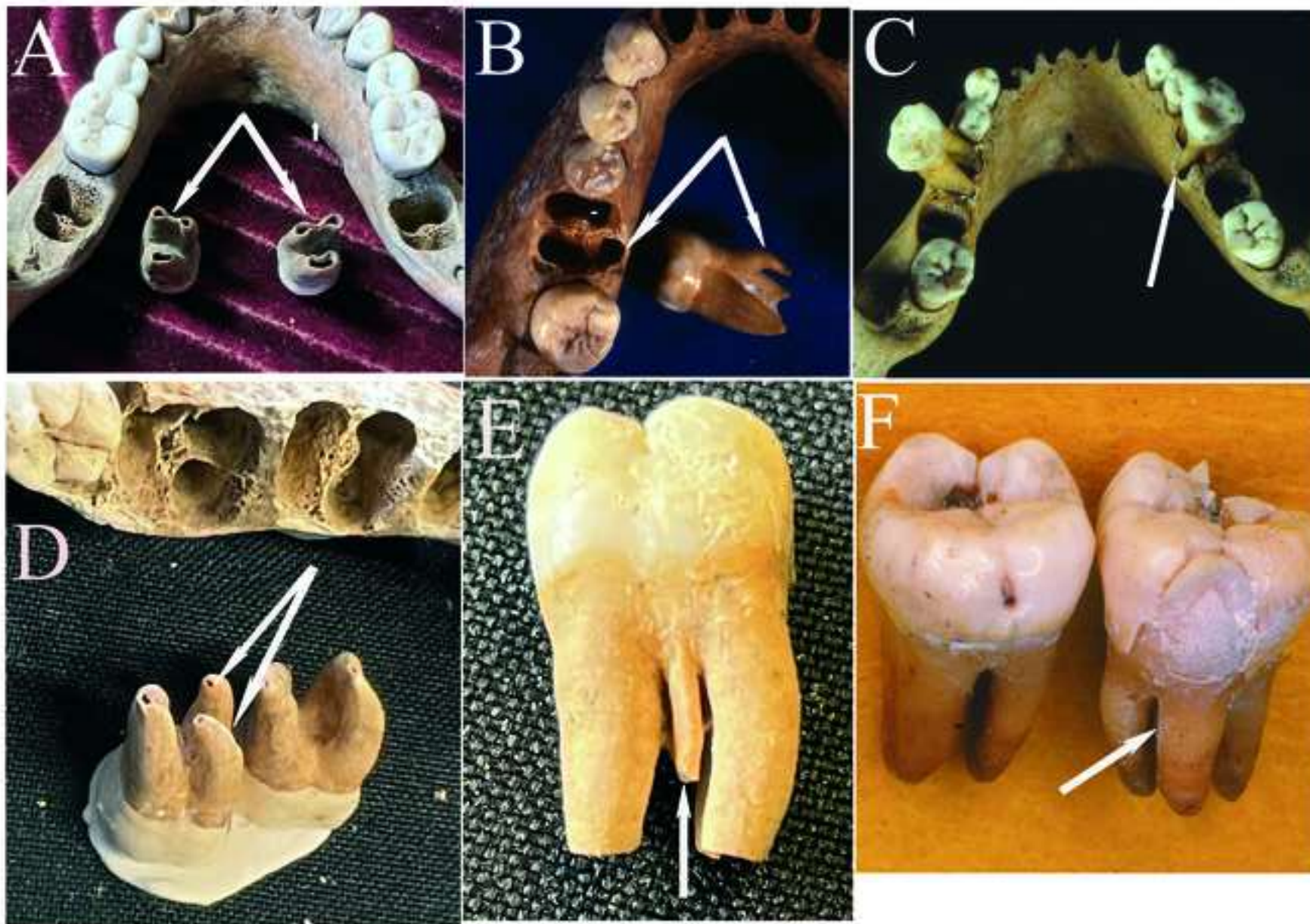
302 **Figure 1.** A) Lower second molars show a groove separating two cones of the mesial root, a  
303 feature not as evident on the distal root. B, C) Lower first molars showing distinct distolingual  
304 accessory roots which take the classic form of 3RM<sub>1</sub>. D) The first molar has two roots but the  
305 second molar has three roots produced by a distinct interradicular groove separating the two  
306 cones of the mesial root. E) Classic ‘radix paramolaris’ on the buccal side of the lower second  
307 molar between the mesial and distal roots. F) The lower second molar has three roots with an  
308 extra buccal root associated with a fused supernumerary tooth.

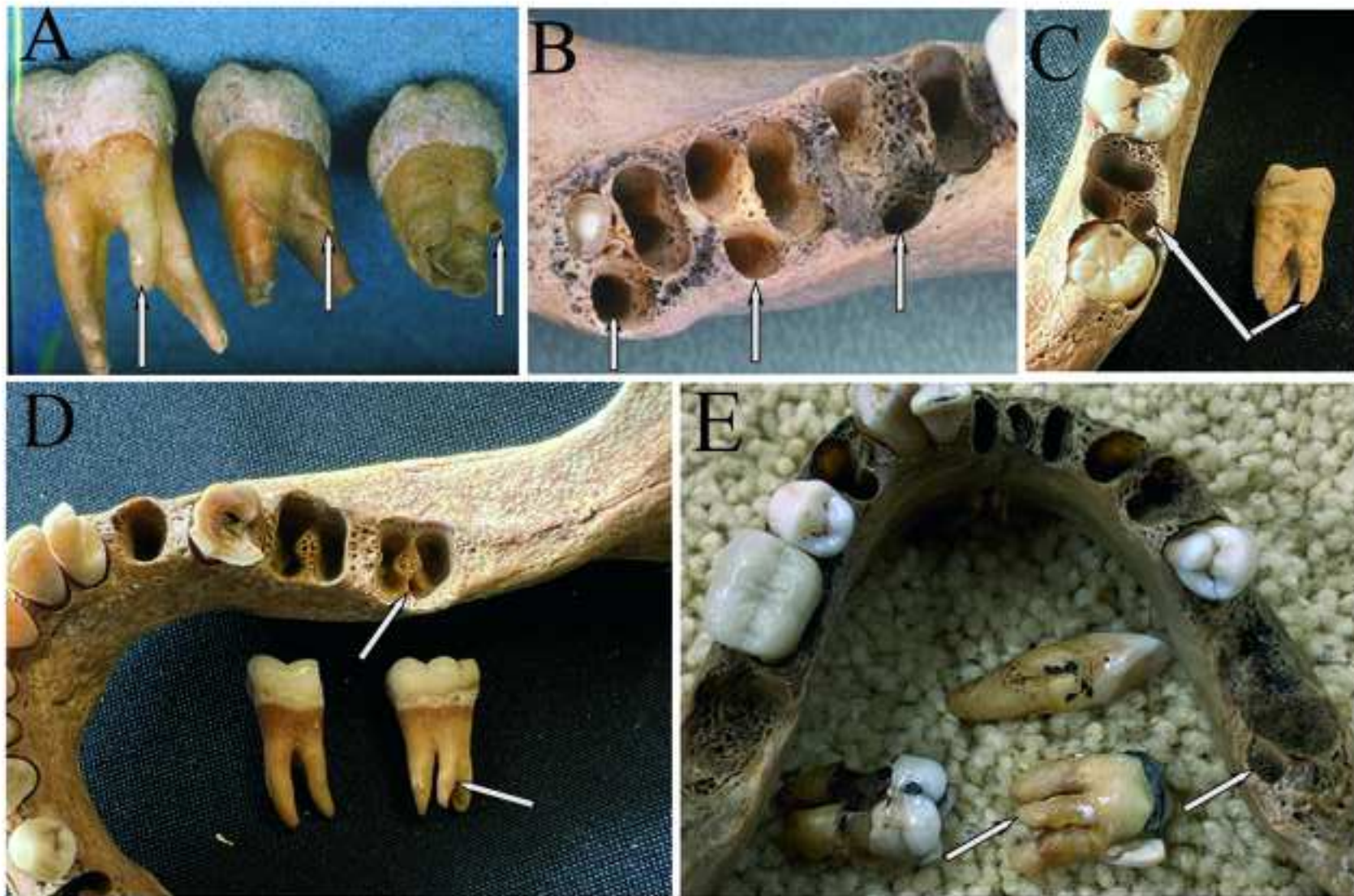
309

310 **Figure 2.** The rare occurrence where all three lower molars exhibit a distolingual accessory root  
311 as evident in actual roots (A) or in sockets (B). C) Lower second molar with distolingual  
312 accessory root. Although first molar roots are not shown, it is likely this tooth would exhibit  
313 3RM<sub>1</sub>. D, E) Two cases where there is a lingually positioned accessory root that is not  
314 homologous to the distolingual accessory root. Note that first molar in D has two roots while the

315 second molar has three roots—the same pattern exhibited by the Penghu and Xiahe lower  
316 molars.

317





**Table 1**

Global variation in three-rooted lower second molars.

Region	Regional group	<i>n</i>	Present	Frequency	With 3RM1	With 2RM1	LM1?
Africa	NW Africa	181	1	0.006	0	1	0
	NE Africa	1141	1	0.001	0	1	0
	West Africa	207	0	0.000	0	0	0
	Central Africa	139	0	0.000	0	0	0
	East Africa	238	1	0.004	0	1	0
	South Africa	194	0	0.000	0	0	0
	Saf Khoesan	273	1	0.004	0	1	0
Pacific	Australia	498	1	0.002	1	0	0
	New Guinea	110	1	0.009	0	1	0
	Melanesia	417	2	0.005	0	2	0
	Micronesia	185	1	0.005	0	1	0
	Polynesia	526	8	0.015	1	4	3
Asia	Southeast Asia	671	1	0.001	0	1	0
	East Asia	1524	16	0.010	4	12	0
	Central Asia	730	1	0.001	0	0	1
Europe	Europe	869	2	0.002	0	2	0

Americas	Alaska	720	6	0.007	4	2	0
	Canada	155	0	0.000	0	0	0
	Greenland	231	2	0.009	1	1	0
	Siberia	141	0	0.000	0	0	0
	Northwest Coast	653	0	0.000	0	0	0
	Western U.S.	488	0	0.000	0	0	0
	Southwest U.S.	1599	2	0.001	0	2	0
	Eastern U.S.	644	0	0.000	0	0	0
	Mesoamerica	318	1	0.003	1	0	0
	South America	903	3	0.003	1	2	0
<hr/>							
Total		13755	51	0.0037	13	34	4
<hr/>							