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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 (G. Richard Scott)

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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; Homoplasy
7	
8	
9	1. Introduction
10	
11	Little research has been conducted on three-rooted lower second molars (3RM <sub>2</sub> ), but the
12	presence of an accessory third root in first molars (3RM1) 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

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

Two Middle Pleistocene fossils from the sites of Penghu on Taiwan (Chang et al., 2015) 29 and Xiahe on the Tibetan Plateau (Chen et al., 2019) exhibit an accessory root on the lower 30 second molar, positioned lingually between the mesial and distal roots. Bailey et al. (2019a) 31 suggested that the high frequencies of 3RM<sub>1</sub> in modern Asians represent gene flow from archaic 32 forms such as Xiahe and Penghu. Scott et al. (2019), however, noted that in Penghu and Xiahe, 33 34 the extra root differs in location from the archetypical  $3RM_1$ , 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.

Here, to aid researchers interested in assessing molar root variation among modern and 38 fossil hominins, we provide global frequencies for the little studied  $3RM_2$  to complement those 39 for  $3RM_1$ . We also assess the extent to which frequencies of  $3RM_2$  and  $3RM_1$  covary, as high 40 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  $3RM_1$  and  $3RM_2$  are homologous traits. Specifically, we ask, is it likely that the 3RM<sub>2</sub> lingual accessory roots in the Asian fossils represent the same trait 44 45 as the distolingual accessory roots that characterize 3RM<sub>1</sub>?

#### 2. Materials and methods

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 3RM1 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).					

**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 $3RM_1$ and $3RM_2$ . 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 $3RM_2$
81	was associated with a 3RM1 that expressed a distolingual accessory root or with a 2RM1 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 $3RM_2$ 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

figure presents a contrast to the global frequency of 9.5% for  $3RM_1$ .

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 $3RM_2$ (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 $3RM_1$ and $3RM_2$ . In East Asians, where $3RM_1$ 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 $3RM_2 > 1.5\%$ . For the same combined grouping mentioned in the introduction with							
97	the highest 3RM1 occurrence, i.e., East Asian and American Arctic at ca. 25%, the corresponding							
98	$3RM_2$ value is 0.92%. For the abovementioned grouping with intermediate $3RM_1$ 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 $3RM_2$ frequencies of $<1.0\%$ . Only four cases of $3RM_2$ were recorded in Africa							
103	$(0.16\%; none associated with 3RM_1)$ and two in Europe (0.24; none with 3RM_1), 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 (TGFß, 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 of the tooth, including the formation of individual cusps (Jernvall and Thesleff, 2000). For root 115 development, the role of enamel knots is largely assumed by Hertwig's epithelial root sheath 116 (HERS) operating in conjunction with the cranial neural crest mesenchyme. Hertwig's epithelial 117 root sheath is a bilayer of the outer and inner dental epithelium that is initiated at the crown-root 118 119 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, tongue-like projections extend horizontally until they merge at a furcation where the primary 121 122 (and accessory) roots are outlined; after they merge, HERS extends apically as in a single-rooted tooth (Huang et al., 2010; Huang and Chai, 2012). 123

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

As part of the Eda pathway, the SNP EDAR V370A is associated with several dental morphological crown traits, including shoveling, double-shoveling, and lower molar cusp number (Kimura et al., 2009; Park et al., 2012). Given its impact on crown traits, Kataoka et al. (2021) explored the relationship between this SNP and root number. In a contingency analysis comparing root number to the three EDAR V370A genotypes (V/V, V/A, A/A), they found a significant difference between one-rooted and two-rooted P<sup>1</sup> and C-shaped one-rooted and tworooted M<sub>2</sub>. However, they found no significant relationship between the three genotypes and P<sup>2</sup>, M<sup>2</sup>, and M<sub>1</sub> root number. They reported a weak but significant Spearman's rho (0.135) between the EDAR V370A genotype and 3RM<sub>1</sub>, but this correlation is much lower than that between this SNP and shoveling (0.457).

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

In the global population, one of 10 individuals possesses a 3RM<sub>1</sub> (Aung and Myint, 149 150 2022). However, as noted earlier, there are distinct differences among major geographic groups (Scott et al., 2018). The trait is most common in Asian and Asian-derived populations and rare in 151 Western Eurasians and sub-Saharan Africans. By contrast, as shown here, cases of 3RM<sub>2</sub> are rare 152 153 in all groups with a global frequency of <1%. Although some individuals have  $3RM_1$  paired with 3RM<sub>2</sub>, the association is weak. An added complication is that 3RM<sub>2</sub> can be expressed in several 154 forms, only one of which is the classic accessory distolingual root. 155 Variation in the form of 3RM<sub>2</sub> is relevant to late Middle Pleistocene hominin remains 156 from the Tibetan Plateau (Chen et al., 2019; Bailey et al., 2019a) and Taiwan (Chang et al., 157

158 2015). Bailey et al. (2019a) proposed that the  $3RM_2$  in the Xiahe mandible could be used to infer

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  $3RM_1$  and the presumption that the 161 lingually positioned third root was homologous with a distolingual accessory root. Scott et al. (2019) questioned this interpretation, noting that while the second molar had three roots it did not 162 exhibit the classic distolingual form. Initially, these authors thought that the third root was the 163 product of a bifurcated mesial member (cf. Fig 1D) based on the published image in Bailey et al. 164 165 (2019a), but a reexamination shows the extra root is in a lingual position between the mesial and distal roots (Bailey et al., 2019b). In this regard, the Penghu and Xiahe mandibles exhibit 166 comparable extra roots that are likely homologous. This phenotype has been observed in recent 167 168 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.

Homoplasy is the issue when 3RM<sub>1</sub> in recent human populations is compared to 3RM<sub>2</sub> in 170 171 hominins of any age. Is a root positioned between the mesial and distal members reflective of the same underlying genetic background as a distolingual accessory root? While an accessory 172 lingual root between the mesial and distal roots of lower molars is an interesting, rare, and 173 174 distinct trait, is it homologous with a distolingual accessory root? Although our current understanding of the genes and developmental processes underlying root development is not 175 176 sufficient to provide a definitive answer to this question, the lack of covariation between the 3RM<sub>1</sub> and 3RM<sub>2</sub> in recent human populations suggests that these two traits are not homologous. 177 Additional research is warranted, but in the extensive literature on 3RM<sub>1</sub> there is no 178 179 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 second that exhibits the extra lingual root. This same condition has been observed in recent
humans (Fig. 2E, F). Perhaps these distinctions are important in differentiating homoplasy from
homology, where the key tooth for the classic three-rooted lower molar is M<sub>1</sub>, while the key
tooth for the lingually positioned accessory root is M<sub>2</sub>.

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<sub>1</sub>, it is true that both 3RM<sub>1</sub> and 3RM<sub>2</sub> are more common in Asian and Asian-derived populations than 189 Africans and Europeans. For the latter populations there was no instance of 3RM<sub>2</sub> associated 190 191 with 3RM<sub>1</sub> and only four total cases of 3RM<sub>2</sub> out of 3242 individuals (0.0012). For Asian and 192 Asian-derived groups, 13 of 10,513 individuals (0.0012) had both 3RM<sub>1</sub> and 3RM<sub>2</sub> while 28 193 exhibited a  $3RM_2$  with a  $2RM_1$  (0.0027). Regardless of whether the  $3RM_2$  in the Penghu and Xiahe fossils is homologous to the  $3RM_1$  of modern Asians, both lingual and distolingual 194 accessory roots are more common in Asia. Again, the large East Asian and American Arctic 195 combined sample has a  $3RM_1$  incidence of 25% and  $3RM_2$  of 0.9%, both of which are  $\geq 2.5x$  the 196 197 respective global averages of 9.5% and 0.37%; of course, given the rarity of 3RM<sub>2</sub>, these percentages should be interpreted with caution. For Southeast Asians, Polynesians, and 198 199 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<sub>2</sub>, 1.5%).

Gellis and Foley (2021) recently developed new methods for classifying root variation using computed tomographic scans. More importantly, expanded genetic research, most notably comparing genotypes of individuals with both 3RM<sub>1</sub> and 3RM<sub>2</sub> (including variation in accessory 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.						
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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

- 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.

	Regional				With	With	
Region	group	n	Present	Frequency	3RM1	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
Total		13755	51	0.0037	13	34	4