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

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Short Communication

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Keywords: Dental morphology; Phenotype variants; Global variation; Homoplasy

1. Introduction

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

Because of the striking contrast between European and African populations viz. Asian and Asian-derived populations, $3RM_1$ is useful as an indicator of gene flow in boundary populations (Heim et al., 2016). Whether the $3RM_1$ 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) and Xiahe on the Tibetan Plateau (Chen et al., 2019) exhibit an accessory root on the lower second molar, positioned lingually between the mesial and distal roots. Bailey et al. (2019a) suggested that the high frequencies of $3RM_1$ in modern Asians represent gene flow from archaic forms such as Xiahe and Penghu. Scott et al. (2019), however, noted that in Penghu and Xiahe, the extra root differs in location from the archetypical $3RM_1$, where the accessory root is distolingual. For this reason, and because the expression of a third root on molars of different positions may not be homologous, Scott et al. (2019) questioned the basis of Bailey et al.'s (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 fossil hominins, we provide global frequencies for the little studied $3RM_2$ to complement those for $3RM_1$. We also assess the extent to which frequencies of $3RM_2$ and $3RM_1$ covary, as high covariation might suggest that these traits have similar genetic and/or developmental underpinnings while low covariation would suggest the opposite. Relative to these data and analysis, we assess the likelihood that $3RM_1$ and $3RM_2$ are homologous traits. Specifically, we ask, is it likely that the $3RM_2$ lingual accessory roots in the Asian fossils represent the same trait as the distolingual accessory roots that characterize $3RM_1$?

2. Materials and methods

Lower molars normally have two roots, one mesial and one distal. The mesial root exhibits a groove halfway between the buccal and lingual root cones (or radicals) and each cone has its own canal (Fig. 1A). The distal root is more conical in shape and has one root canal but generally no root groove (Calberson et al., 2007). There are several ways that lower molars manifest three roots, but the standard $3RM_1$ has as a distinguishing characteristic—a distolingual accessory root (Fig. 1B, C). This is explicit in the definition of Turner et al. (1991:25): "3. Three roots. A third (supernumerary) root is present on the distolingual aspect. It may be very small but is usually about one-third the size of the normal distal root."

INSERT FIG. 1

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

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

INSERT FIG. 2

While $3RM_1$ is one of Turner's 29 key traits, with frequencies available on computer printouts (cf. appendix in Scott and Irish, 2017), this is not the case for the second molar. As such, we evaluated 11,382 score sheets from the C.G. Turner II database of archaeological remains (a few hundred to ~10,000 years of age) to calculate $3RM_2$ frequencies, with special emphasis on the Americas, Asia, the Pacific, and Europe. To characterize global variation in $3RM_2$, these observations were augmented by unpublished data from 2,373 North and South Africans (see Irish, 2000, 2005, 2006, 2016; Irish et al. 2014, for details).

From Turner's data sheets, we could calculate $3RM_2$ frequencies and evaluate the relationship between $3RM_1$ and $3RM_2$. While a relationship might be presumed, the sheets only specify total number, not the presence or absence of a distolingual accessory root. This is noteworthy given that there are different forms of expression. We tallied instances where $3RM_2$ was associated with a $3RM_1$ that expressed a distolingual accessory root or with a $2RM_1$ lacking this extra root.

3. Results

To generalize on root number variation, we combined information for subregions within the major regions of the world (Africa, Pacific, Asia, Europe, Americas). After compiling data on all individuals, we found that instances of $3RM_2$ are extremely rare. There are four cases from Africa, 13 from the Pacific, 18 from Asia, two from Europe, and 14 from the Americas (Table 1). 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 $3RM_1$.

For the 51 individuals exhibiting 3RM_2, four did not retain a LM_1 for comparison. Of the 47 cases with observations on both first and second lower molars, 13 of 43 3RM_2 (30.2%) were associated with a 3RM_1. In the Arctic, where 3RM_1 attains its highest frequency, five of eight individuals have 3RM_1 and 3RM_2. In East Asians, where 3RM_1 is second most common, there are 16 cases of 3RM_2, but only four were associated with 3RM_1. No regional group has a frequency of 3RM_2 > 1.5%. For the same combined grouping mentioned in the introduction with the highest 3RM_1 occurrence, i.e., East Asian and American Arctic at ca. 25%, the corresponding 3RM_2 value is 0.92%. For the abovementioned grouping with intermediate 3RM_1 frequencies globally, namely Southeast Asians, Polynesians and Northwest North Americans at ca. 12%, their 3RM_2 incidence is 0.49%. On an individual sample basis, East Asians exhibit a 1.0% frequency of 3RM_2, with Polynesians at 1.5%. Even Circumpolar samples with the highest 3RM_1 frequencies have 3RM_2 frequencies of <1.0%. Only four cases of 3RM_2 were recorded in Africa (0.16%; none associated with 3RM_1) and two in Europe (0.24; none with 3RM_1), suggesting a weak relationship between frequencies and expression of 3RM_1 and 3RM_2.

INSERT TABLE 1

4. Discussion

To put accessory roots in context, it is helpful to provide a general characterization of the factors underlying root development. Experimental research demonstrates that signaling molecules from four conserved families (TGFß, FGF, SHH, Wnt) play a central role in tooth crown development (Tummers and Thesleff, 2009). Li et al. (2017) note that factors governing root development involve the same four signaling families along with BMP. For crown 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 development, the role of enamel knots is largely assumed by Hertwig's epithelial root sheath (HERS) operating in conjunction with the cranial neural crest mesenchyme. Hertwig's epithelial root sheath is a bilayer of the outer and inner dental epithelium that is initiated at the crown-root junction, or cervical loop, and extends vertically or horizontally to produce single-rooted or 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 (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).

Li et al. (2017) provide a table that shows root defects associated with mutations in the 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 or precludes HERS from moving in a horizontal direction, preventing a furcation in a multi-rooted tooth. The result is an elongated tooth trunk and pulp chamber, to produce a taurodont tooth like that often found in Neanderthals. Fons Romero et al. (2017:1296) note that "the *Eda* 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 development of multiple roots, resulting in taurodont teeth.

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^1 and C-shaped one-rooted and two-rooted M_2. However, they found no significant relationship between the three genotypes and P^2, M^2, and M_1 root number. They reported a weak but significant Spearman's rho (0.135) between the EDAR V370A genotype and $3RM_1$, 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 TGFß 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 $3RM_1$ (Aung and Myint, 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 Western Eurasians and sub-Saharan Africans. By contrast, as shown here, cases of $3RM_2$ are rare in all groups with a global frequency of <1%. Although some individuals have $3RM_1$ paired with $3RM_2$, the association is weak. An added complication is that $3RM_2$ can be expressed in several forms, only one of which is the classic accessory distolingual root.

Variation in the form of $3RM_2$ is relevant to late Middle Pleistocene hominin remains from the Tibetan Plateau (Chen et al., 2019; Bailey et al., 2019a) and Taiwan (Chang et al., 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 $3RM_2$ frequencies, this conclusion was based on geographic variation in $3RM_1$ and the presumption that the 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 exhibit the classic distolingual form. Initially, these authors thought that the third root was the product of a bifurcated mesial member (cf. Fig 1D) based on the published image in Bailey et al. (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 comparable extra roots that are likely homologous. This phenotype has been observed in recent humans (Fig. 2D, E), but it is exceptionally rare. For it to occur in two Middle Pleistocene Asian hominins may be noteworthy in assessing phylogenetic relationships.

Homoplasy is the issue when $3RM_1$ in recent human populations is compared to $3RM_2$ in 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 lingual root between the mesial and distal roots of lower molars is an interesting, rare, and 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 sufficient to provide a definitive answer to this question, the lack of covariation between the $3RM_1$ and $3RM_2$ in recent human populations suggests that these two traits are not homologous.

Additional research is warranted, but in the extensive literature on $3RM_1$ there is no confusion about what constitutes this specific phenotype—the presence of a distolingual accessory root. This is evident in countless photographs and X-rays. Bailey et al. (2019a) used a photo from a modern human to illustrate a $3RM_1$ and it shows a distolingual accessory root. 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_1, while the key tooth for the lingually positioned accessory root is M_2.

Although we argue that, based on position, the lingual accessory root on the lower second molars of two Asian hominins differs from the distolingual accessory root of the classic $3RM_1$, it is true that both $3RM_1$ and $3RM_2$ are more common in Asian and Asian-derived populations than Africans and Europeans. For the latter populations there was no instance of $3RM_2$ associated with $3RM_1$ and only four total cases of $3RM_2$ out of 3242 individuals (0.0012). For Asian and Asian-derived groups, 13 of 10,513 individuals (0.0012) had both $3RM_1$ and $3RM_2$ while 28 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 accessory roots are more common in Asia. Again, the large East Asian and American Arctic combined sample has a $3RM_1$ incidence of 25% and $3RM_2$ of 0.9%, both of which are ≥2.5x the respective global averages of 9.5% and 0.37%; of course, given the rarity of $3RM_2$, these percentages should be interpreted with caution. For Southeast Asians, Polynesians, and Northwest North Americans combined, with $3RM_1$ of 12% and $3RM_2$ of 0.49%, the figures are ≥1.2x the global average. Individual Asian-derived samples vary as indicated (e.g., Polynesia $3RM_2$, 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 $3RM_1$ and $3RM_2$ (including variation in accessory root locations), could help determine if the same genes are responsible for their expression.

These are key directions for the future. New methods, together with the global root data presented here, can generate finer-grained data to complement the existing extensive dataset on crown traits. Among other key findings, such data may help address questions of homology vs. homoplasy in different forms of multi-rooted teeth (Turner et al., 1991; Scott and Irish, 2017) and, more specifically, the utility of the rare $3RM_2$ trait for assessing dental variation and relatedness among hominins of any age.

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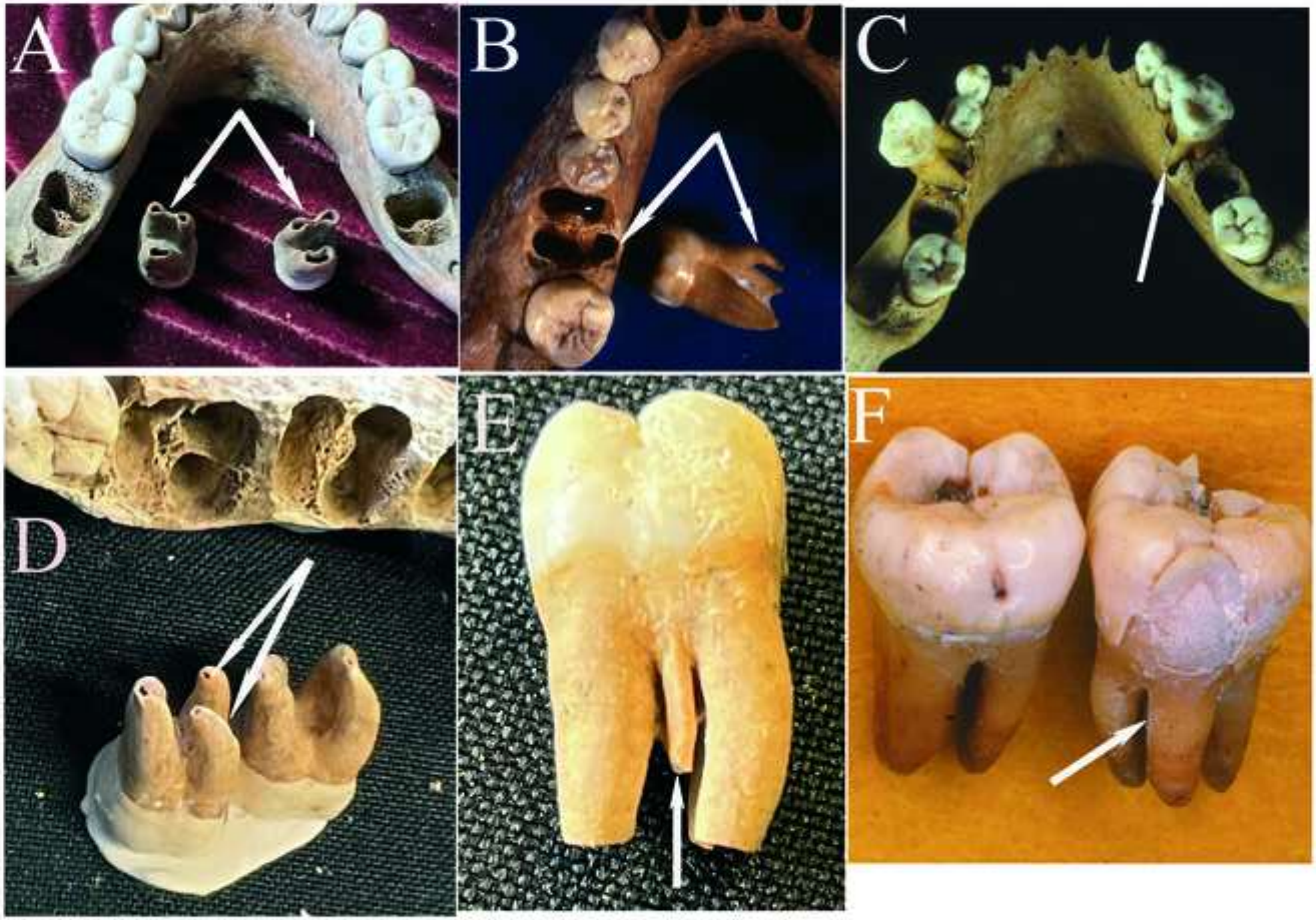
Figure captions

Figure 1. A) Lower second molars show a groove separating two cones of the mesial root, a feature not as evident on the distal root. B, C) Lower first molars showing distinct distolingual accessory roots which take the classic form of $3RM_1$. D) The first molar has two roots but the second molar has three roots produced by a distinct interradicular groove separating the two cones of the mesial root. E) Classic ‘radix paramolaris’ on the buccal side of the lower second molar between the mesial and distal roots. F) The lower second molar has three roots with an extra buccal root associated with a fused supernumerary tooth.

Figure 2. The rare occurrence where all three lower molars exhibit a distolingual accessory root as evident in actual roots (A) or in sockets (B). C) Lower second molar with distolingual accessory root. Although first molar roots are not shown, it is likely this tooth would exhibit $3RM_1$. D, E) Two cases where there is a lingually positioned accessory root that is not 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 molars.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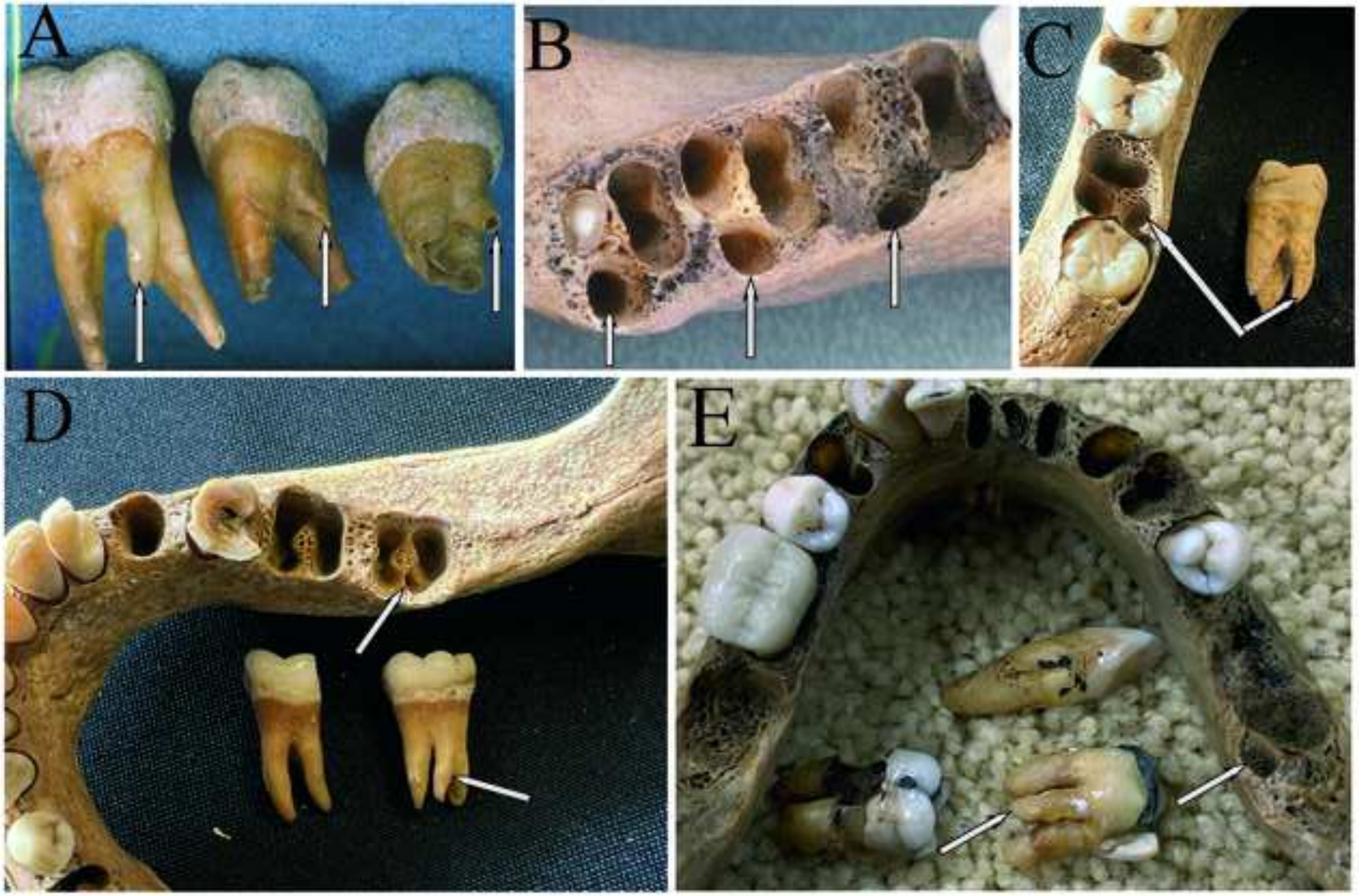
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Table 1

Global variation in three-rooted lower second molars.

Region	Regional group	*n*	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
Total		13755	51	0.0037	13	34	4