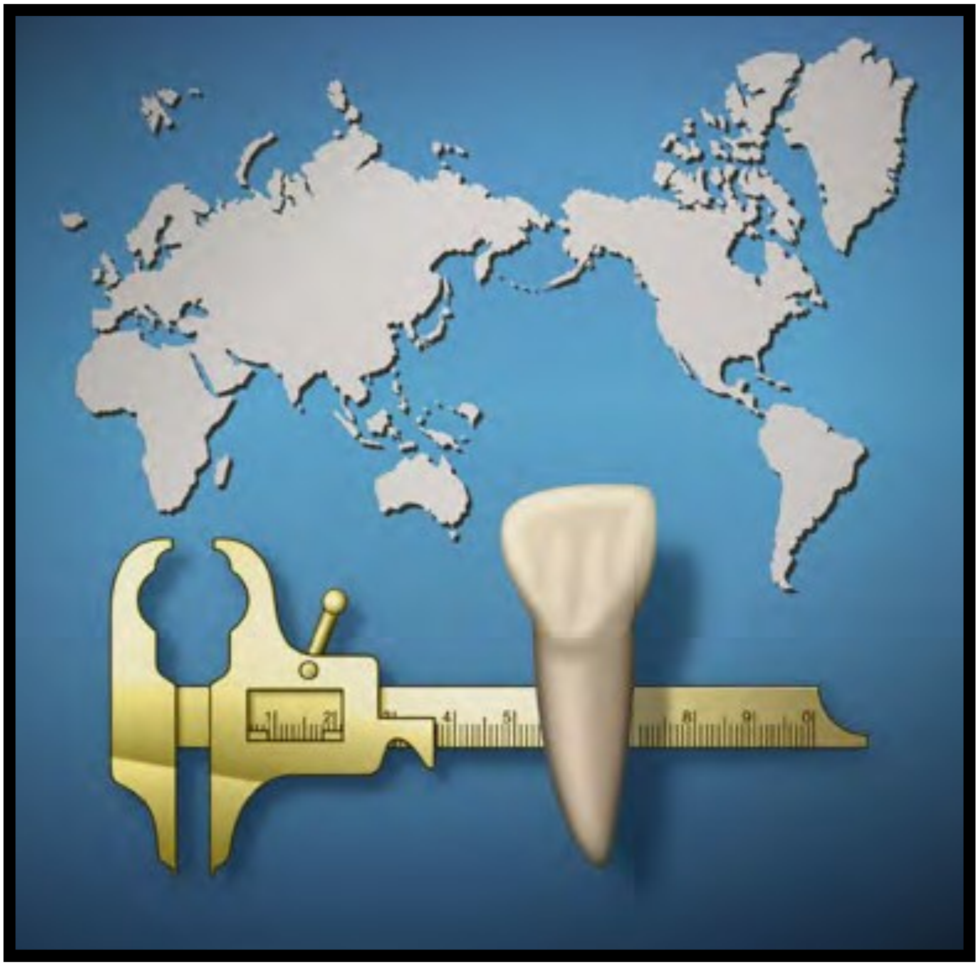
Volume 32, Issue 01, 2019 **ISSN 1096-9411**

Dental Anthropology

A Publication of the Dental Anthropology Association



Dental Anthropology

Volume 32, Issue 01, 2019

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Case Study: Expression of Two Near Absent Dental Traits, Lingual Cuspule and Paraconid, on One Archaic Period Modern Human from the Ohio Valley

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Keywords: Dental variation, dental evolution, rare trait

ABSTRACT Dental anomalies in modern humans are used to discuss biological variation and evolutionary changes. Presented here are the lingual cuspule and paraconid; two traits considered near absent (occurring <1%) in world populations. The only other example of a lingual cuspule comes from an African population. The paraconid was thought to have been lost in primate evolution starting in the Oligocene (34-23 MYA). Both traits were found on the lower third molars of a male individual from the late Archaic (2500-500 BC) site of Shick in Handcock County, Ohio. Here the lingual cuspule is present unilaterally on the right third molar, whereas the other reported case shows the trait being expressed bilaterally on the first molars. Therefore, the lingual cuspule can be found on molars across the row. Additionally, each example exhibits a fully developed cuspule with a free apex. These data indicate the lingual cuspule could be incorporated into studies of biodistance and morphological variation. Contextualizing the paraconid is more challenging given that the only reported examples of this trait in extant primates come from the tarsier. The expression of a paraconid in modern humans could suggest secondary evolution of this trait. Further reporting of both the lingual cuspule and paraconid are necessary to better understand these traits and discuss their importance in modern human variation.

Over the course of human evolution there is a simplification in the expression of tooth traits (i.e. a reduction in cusp number, and occlusal ridges; Bailey and Hublin, 2013); however, there still exists considerable variation in the expression of dental morphology in world populations (Turner et al., 1991; Scott and Turner, 1997; Hanihara, 2008; Scott et al., 2016; Irish, 2016). Placement of tooth cusps, both principal and accessory, can be used to discuss morphological variation. Generally, accessory cusps are initiated after the principal cusps have formed (Kraus and Jordan, 1965; Hillson 1996) making their expression more variable and less frequent than principal cusps. While many mandibular paramolar structures, such as the Mandibular Molar Pit-Tubercle (MMTP; Weets, 2009) and protostylid (Dahlberg, 1950), have been identified and described in several populations, there are several traits that are less common. For example, odontomes on premolars, the mesial canine ridge (Scott and Turner, 1997), and the labial talon cusp on incisors (Stojanowski and Johnson, 2011) are much less common traits within a given population. Traits that are found in 4-7% of a population are considered "rare"; "very rare" traits are found in 1 - 3% of a population, and "near absent" when they are found in less than 1% of a population (Scott and Turner 1997: 191, 193). Assessing patterns of dental trait expressions are useful to understand biological variation, migration of modern human populations around the world (Scott and Turner, 1997; Hanihara, 2013; Scott et al., 2018), and evolutionary changes within and between hominin taxa (Bailey and Hublin, 2013; Martinon-Torres et al., 2013; Guatelli-Steinberg 2016).

The goals of this paper are to 1) describe two rare lower molar traits, the lingual cuspule (Irish, 1991) and the paraconid, and 2) contextualize them in modern human variation. Only one other study has identified the lingual cuspule, which was observed on a single individual (Irish, 1991). The paraconid is a principle cusp which has been identified in early primate ancestors, but appears to have been lost, with the exception of tarsiers, before the emergence of hominins (Gregory, 1922; Ankel-Simons, 2007; Fleagle, 2013). To date, no studies have reported this cusp in modern humans. Both the lingual cuspule and the paraconid were observed on mandibular third molars of a single individual from the Archaic period (2500-500 BC) in the Ohio Valley. Neither of these dental anomalies has been extensively documented in modern humans, and both may be considered near absent in world populations. It is possible that these molar cusps are simply over-

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looked, in which case studies should highlight them, or that they are misinterpreted, which would indicate new methods should be used to amend recording procedures.

Materials and Methods

This study was conducted on human skeletal remains from the Archaic Period in the Ohio Valley. The individual presented in this paper was found at the Shick site located in Mount Cory, Handcock County, Ohio occupied between 2500-500 BC. The skeletal collections are housed at the Ohio History Connection in Columbus, Ohio. The Shick site settlements during the Archaic period were considered "sizable" compared to earlier periods, and were occupied on a seasonal basis (Sciulli and Oberly 2002). Late Archaic communities practiced a hunting and gathering subsistence (Sciulli and Oberly 2002).

Fourty-eight individuals from the Late Archaic period were examined. Tooth traits for all individuals were recorded using the Arizona State University Dental Anthropology System (ASUDAS; Turner et al. 1991). Reference manuals, recent publications (Scott and Turner, 1997; Weets, 2009; Marado and Silva, 2016; Scott et al., 2016; Scott and Irish, 2017), and consultation with Joel Irish were used to identify these traits as neither the lingual cuspule nor paraconid are included in the ASUDAS. Based on information from available sources, the descriptions presented below were used to identify the two cusps.

The lingual cuspule is described as a "triangular-shaped structure" located on the disto-lingual enamel surface, not associated with the metaconulid (cusp 7), and similar in form, though not in location, to the protostylid (found on the buccal surface; Irish, 1991:2). Originating at the cemento-enamel junction just distal on the metaconid, the lingual cuspule is not an occlusal trait (Irish, 1991), but a rather is a peripheral accessory cusp.

Taking up the mesial portion of the trigonid of lower molars, the paraconid is described as a principal cusp located most anterior and mesiolingually to the other lower molar cusps (Gregory, 1922; Ankel-Simons, 2007; Fleagle, 2013). The paraconid is noted as being an archaic primate feature that reduces in size and disappears altogether by the Oligocene (Gregory, 1922; Simons, 1989; Ankel-Simons, 2007; Fleagle, 2013). The tarsier is the only reported example of a modern primate to have retained the paraconid (Swindler, 2002; Ankel-Simons, 2007).

Results

Of the 48 individuals observed from the Late Archaic sample, only one was found to have either a lingual cuspule or a paraconid (A4489-6). The lingual cuspule was observed on this individual's mandibular right third molar and the anterior cusp (paraconid) was expressed bilaterally. While the lingual cuspule and the paraconid are the two cusps of interest in this paper, individuals in the Late Archaic sample exhibited a variety of other lower molar traits including low-grade expressions of the protostylid (n=20), fully developed cusp 6 (n=11), large cusp 7 (n=1), deep anterior fovea (n=8), and defined deflecting wrinkle (n=4). In addition to the lingual cuspule and the paraconid, the individual presented here also exhibited a low-grade expression of the protostylid (pit in the buccal groove; Turner et al., 1991) on all lower molars as well as a bifurcated hypoconulid on the lower right third molar. The upper molars of this individual exhibit a reduction in size of the hypocone from the first to third molars on both sides.

Lingual Cuspule

The lower right third molar of this individual exhibits a large, fully developed cuspule located mesially on the lingual surface of both the paraconid and metaconid of a right third molar (Figure 1, arrow 1). The lingual cuspule is nearly equal in size to the protoconid, metaconid, and paraconid. The tooth appears to have been rotated buccally such that the paraconid is oriented toward the buccal aspect of the mandible, rather than to the distal portion of M2; the orientation brings the lingual cuspule into contact with the hypoconulid of M2.

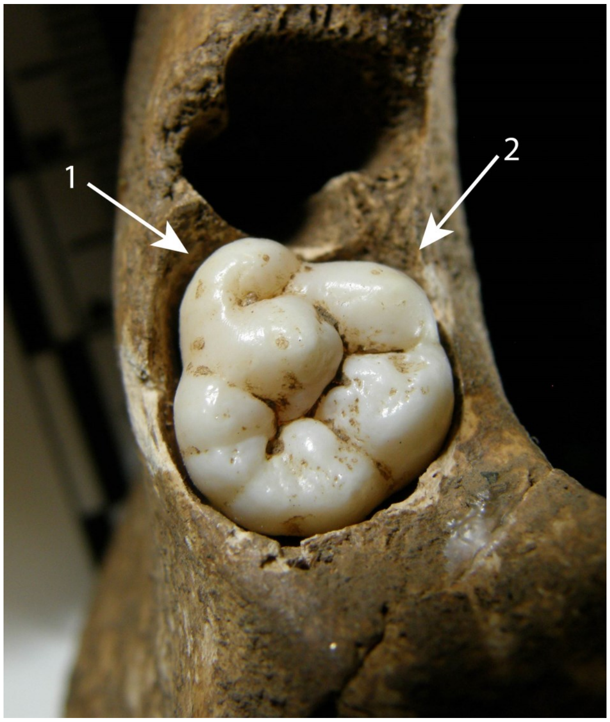

Figure 1. Lower right third molar from burial A4489-6 (Archaic period; Mt. Cory Ohio, Handcock County) with a fully developed lingual cuspule (arrow 1) and paraconid (arrow 2).

Figure 2. Lower left third molar from burial A4489-6 (Archaic period; Mt. Cory Ohio, Handcock County) with a fully developed paraconid (white arrow).

Paraconid

On the right and left third molar, this individual possesses a cusp in the location where, by definition (Gregory, 1922; Ankel-Simons, 2007; Fleagle, 2013) the paraconid develops. In both expressions, a fully developed mesial cusp with a free apex is present (Figure 1, arrow 2 and Figure 2). The cusp appears to originate at the cemento-enamel junction between the protoconid and metaconid. The root exhibits a seamless transition with the enamel suggesting the cusp was formed along with other principal cusps during the initial down-folding of the enamel epithelium (Jernvall and Thesleff, 2000) and is not a peripheral accessory cusp. The cusp is equal in size to the protoconid and metaconid.

Discussion

Based on the available literature, it appears that the lingual cuspule and the paraconid are near absent traits in modern human populations. While more information is needed about both traits to complete a more in depth discussion on how they might inform on studies of migration, or biodistance, it is possible to demonstrate their eventual usefulness in these applications.

Scott (2008) identifies a set of criteria, or principles, to use when including a new trait into studies of biodistance. These criteria begin with 1) the presence of a distinct trait, 2) a consistent expression of the trait within the same tooth type, and 3) examination of multiple diverse populations for presence of the trait. After these steps have been satisfied, there can be a more in-depth analysis of the trait wherein a scoring system is developed (Scott, 2008). Both the lingual cuspule and the paraconid satisfy the first criteria of being distinct traits. With the inclusion of other sources, a discussion of criterion two and three is possible for the lingual cuspule, and will be undertaken below. Given the lack of paraconid examples in modern humans, contextualizing this trait within Scott's (2008) criterion cannot be done here. The paraconid can, however, be discussed in an evolutionary context.

Lingual cuspule

Scott's (2008) second criteria requires that the trait in question be consistently expressed within the same tooth type. Regarding the lingual cuspule, the only other reported case was found bilaterally on both the left and right lower first molars of a male individual (Irish, 1991). The cuspule is noted to be a triangular shape with a free apex, and located on the distolingual surface just distal to a small metaconulid (Irish, 1991). The individual presented in the current study possesses a unilateral expression of the lingual cuspule found on the lower right third molar of a male individual. This expression of the trait is larger, more bulbus at the apex, and more mesially placed than the example described by Irish (1991). An example of what here is called the lingual cuspule may also be present on the lower left third molar of a female individual but is recorded there as an expression of the MMTP (Marado, 2014: 236). The MMTP is expressed as an ident, pit, or fully developed cusp high on the buccal surface of the protocone (Weets, 2009; Marado and Silva, 2016) whereas the lingual cuspule has been identified as a fully developed cusp found on the lingual surface of the crown. The examples presented here suggest this trait's expression is consistently found on first and third mandibular molars from both the left and right sides.

The third criteria on Scott's (2008) list necessitates the observation of the trait in question across multiple distinct populations. The lingual cuspule has been reported in one individual from the Bantu-speaking Central Sotho from South Africa (Irish, 1991). The individual presented in the current study is from a Native American population in the Ohio Valley. The possible third example, discussed above, comes from a Portuguese population (Marado, 2014). Additionally, Joel Irish (1991: 2-3) recalls A. Dahlberg observing the lingual cuspule once before in a Native American population, though no additional information on this example is included. Therefore, at present the lingual cuspule has been identified in two populations, South African and Native American, with the possibly if its occurrence in a third, Portuguese. Lack of reporting on the lingual cuspule may be because the trait is being conflated with other paramolar structures, such as the MMTP. Although the MMTP is described as occurring on the buccal surface of mandibular molars (Weets, 2009; Marado and Silva, 2016), it is possible that similar expressions on the lingual surface are being lumped together during observation and recording since no formal scoring is in place for lingual expressions.

Paraconid

While the paraconid is a distinct trait, there are no other examples of its expression in modern human populations; therefore, determining a consistent expression within a tooth type, or addressing its prevalence within multiple world populations cannot be attempted here. However, a discussion of paraconid evolution and contextualizing this trait within human dental variation may be more informative.

First seen in the Mesozoic era, the paraconid is a mandibular principal cusp located on the mesial border between the protoconid and metaconid, as part of the trigonid (Gregory, 1922; Ungar 2017). The gradual reduction, and then complete loss of the paraconid in primate evolution is contemporaneous with the appearance of the upper molar hypocone (Gregory, 1922). By the middle Eocene, *Notharctus* (an extinct form of North American *Adapoidea*) exhibits a paraconid of reduced size (Gregory, 1922; Fleagle, 2013). Parapithecids in the Oligocene have lost the paraconid altogether, resulting in an absence of this trait in modern Cercopithecidae (Gregory, 1922; Ankel-Simons, 2007). Although this does not directly speak to hominins and modern humans, based on the lack of acknowledgement in the literature, including a recent review of evolutionary changes associated with hominin and modern human dentition (Guatelli-Steinberg, 2016), the paraconid appears to have been absent in hominin evolution as well (pers. com. Joel Irish). Because only one individual of the fourty-eight within the study population expresses the paraconid, occurrence within this group can be considered near absent.

Despite being lost prior to hominin emergence, a cusp that is likely a paraconid is present in a modern human dental arcade. This expression could suggest that humans have not completely lost the ability to express a paraconid. However, the retained ability to develop a paraconid does not seem likely since this cusp was lost with the Parapithecids (Gregory, 1922) and has only been documented in tarsiers since the Oligocene (Swindler, 2002; Ankel-Simons, 2007). Alternatively, it is possible that the presence of a paraconid in a modern human is an example of a secondarily derived trait. Although it is not common for traits to reappear once lost, there are examples in the dentition where this has occurred (Lipson and Pilbean, 1982; Luo et al., 2004). If other modern human populations also exhibit a remnant paraconid, the discussion could lead to valuable insights into the recent evolution of hominin dentition.

Conclusions

Both the lingual cuspule and the paraconid appear to be rare, if not near absent, traits in modern human populations. Based on the data presented here, the lingual cuspule has the potential to satisfy the criteria set by Scott (2008) and be included in studies of dental morphology and biodistance. If more examples of this trait can be identified, a scoring system could be determined, allowing the lingual cuspule to act as an additional source of information in understanding modern human dental variation. It is currently unclear whether or not the paraconid could be included in biodistance studies as the example presented here is the only one reported in modern humans. Looking at this trait from an evolutionary approach, the presence of a paraconid on a modern human tooth could represent an example of a secondarily derived trait. Additional examples from a variety of populations are necessary to further discuss what information these two traits could offer in studies of human teeth.

Acknowledgments

These findings are part of a research project funded by the Ohio State University Alumni Grant for Graduate Research and Scholarship, and the Larsen Research and Travel Award. I wish to thank Ohio History Connection for allowing me to conduct research on their collections, and permission to use photographs of dentition. Special thanks are given to Joel Irish for consulting on this "weird" tooth. Thank you to Tim Sefczek for reading drafts of this manuscript. Lastly, I thank editors and reviewers of the *Dental Anthropology Journal* for their comments on this manuscript.

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Global Distribution of Marginal Accessory Cusps of the Maxillary Premolars

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Keywords: marginal accessory cusps, maxillary premolars, ASUDAS, dental morphology

ABSTRACT The present study assesses the global distribution of marginal accessory cusps of the maxillary premolars. This trait, despite constituting one of the variables standardized by Turner and colleagues (1991), has received little attention in morphological studies. Frequencies were calculated from data sheets collected by Christy G. Turner II for mesial, distal, and mesial + distal grades. Different geographic patterns were identified for both types of expression on the upper premolars. The patterned geographic distribution of these traits indicates their utility in biodistance investigations. In addition, the distinction between mesial and distal accessory cusps specified by Scott and Irish (2017) is recommended, as these two traits exhibit different geographic patterns.

Despite marginal accessory cusps of the maxillary premolars comprising part of the Arizona State University Dental Anthropology System (ASUDAS; Turner et al., 1991), few data are available on their geographic distribution (Hanihara, 2008; Reyes-Centeno et al., 2017; Scott and Irish, 2017). This trait is characterized by additional cusps on either the mesial, distal, or both margins of the maxillary premolar apart from the primary buccal and lingual cusps. These are distinguished from the primary cusps by discrete parallel grooves (Figures 1 and 2). To be scored as a premolar accessory cusp, there has to be separating grooves (Turner et al., 1991). According to the ASUDAS, this trait is scored as present or absent (Turner et al., 1991). However, recent revisions to the ASUDAS published by Scott and Irish (2017) have amended scoring to specify where these cusps are located:

Grade 0: Marginal accessory cusp is absent.
Grade 1: Marginal accessory cusp is mesial.
Grade 2: Marginal accessory cusp is distal.
Grade 3: Marginal accessory cusps are present on the mesial and distal margin.

Marginal accessory cusps have been identified in ancient hominins. This trait has frequently been noted in individuals of likely Neanderthal identifi-

Figure 1. Mesial marginal accessory cusp on the left fourth premolar. Note the grooves separating the accessory cusp from the primary cusps.

Figure 2. Mesial marginal accessory cusp present on right fourth premolar. Note the grooves separating the accessory cusp from the primary cusps.

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cation (Bailey, 2002; Bailey and Hublin, 2006; Glatz et al., 2008; Benazzi et al., 2011; Hershkovitz et al., 2016). Some argue that more complex occlusal morphology of the maxillary premolars, including accessory ridges and cusps, is characteristic of Neanderthals compared to anatomically modern humans (Benazzi et al., 2011). Bailey (2002) notes these cusps occur in a high frequency in Neanderthals, particularly on the third premolar, with the distal cusps occurring almost twice as often as mesial accessory cusps. In addition to Neanderthals, grade 3 expression of this trait was identified in hominin remains from Dmanisi, Georgia (Martinón-Torres et al., 2008).

Few studies have explicitly addressed the frequency of this trait in modern humans. A sample of Afro-Colombians from Guapi, who are of primarily African ancestry (with some contribution from Europeans and Native Americans), had high frequencies of marginal accessory cusps on both maxillary premolars (Delgado-Burbano, 2007). Marginal accessory cusps contributed to differentiating Asian from African and European populations in a study by Adams and George (2018) for forensic ancestry estimation. To compare Neanderthals to modern humans, small samples representing seven regions were examined by Bailey (2002). Frequencies of both distal and mesial accessory cusps were moderate to high for both premolars, with mesial cusps exhibiting higher rates of occurrence. No geographic pattern was evident regarding the highest frequencies for tooth or locus in this study; however, the largest sample size for any of these populations was 40 (Bailey, 2002). Global analyses of dental morphological variation conducted by Hanihara (2008) and Reyes-Centeno et al. (2017) suggest distinct differences between Asian populations and African and European populations, though this pattern differs for the third and fourth premolars. However, both studies used the ASUDAS grades, collapsing mesial and distal accessory cusps into a single presence grade, precluding a more nuanced observation.

This study provides a comprehensive analysis of the global distribution of the marginal accessory cusps of the maxillary premolars. A secondary objective is to evaluate the utility of distinguishing between locus of expression in population analyses.

Materials and Methods

Frequencies for marginal accessory cusps of the maxillary third (UP3) and fourth (UP4) premolars were calculated from the original data sheets of Christy G. Turner II on populations around the world (Table 1; see Scott et al., [2018] for more information on these subdivisions). While the original trait descriptions outlined by ASUDAS do not designate the placement of these cusps, the updated descriptions by Scott and Irish (2017) distinguish mesial, distal, and mesial + distal expressions. These categories are used to evaluate differences in geographic frequency distributions for each configuration. For those individuals with mesial + distal expressions (Grade 3), these were separated into mesial accessory cusp (MAC) expression (Grade 1) and distal accessory cusp (DAC) expression (Grade 2) for calculation.

Chi-square tests were used to identify differences between males and females for each tooth and locus. Sex was unknown for many individuals, so only individuals designated as male or female were used to test for sexual dimorphism. All statistical analyses were performed in R Studio 1.1.442.

Results

Marginal accessory cusps follow the general pattern of most dental morphological traits – little to no sex dimorphism. Total frequencies calculated for each population are presented in Tables 2a and 2b. Only the DAT of the fourth premolar in Polynesians exhibits statistically significant sexual dimorphism. Some populations produced a chi-square value of NA when the trait was absent for either males or females. A brief overview is provided for each tooth and locus.

UP3: MAC (Table 2a)

This trait occurs in low to moderate frequencies around the globe. Frequencies range between 0.0% and 35.4% for the pooled sex frequencies, with North Africa exhibiting

Table 1. Geographic regions analyzed in the present study.

Supra-Geographic Region	Geographic Subdivisions
Western Eurasia	Eastern Europe, North Africa, Western Europe
Sub-Saharan Africa	West and South Africa
Sahul-Pacific	Australia, New Guinea, Melanesia
Sunda-Pacific	Southeast Asia (early), Southeast Asia (recent), Polynesia, Micronesia
Sino-Americas	East Asia, Northeast Siberia, American Arctic, Northwest Coast/Ne Dene, North America, Mesoamerica, South America, Jomon/Ainu

*Table 2a. Frequencies for MAC and DAC for each population for the third premolar. χ 2 values are present for degree of statistically significant differences between males and females. (fr = frequency, n = number of individuals, * = statistically significant).*

		MAC					DAC				
Population		Male	Female	Total	χ^2	p-value	Male	Female	Total	χ^2	p-value
West and South Africa	fr	0.000	0.111	0.023	0.523	0.470	0.176	0.000	0.140	0.669	0.414
	n	34	9	43			34	9	43		
Nubia	fr	0.125	0.000	0.077	<0.001	1.000	0.125	0.200	0.154	<0.001	1.000
	n	8	5	13			8	5	13		
North Africa	fr	0.000	0.000	0.000	NA	NA	0.000	0.000	0.000	NA	NA
	n	12	3	15			12	3	15		
South Asia	fr	0.025	0.000	0.019	<0.001	1.000	0.000	0.071	0.019	0.307	0.579
	n	40	14	54			40	14	54		
Western Europe	fr	0.034	0.016	0.027	0.034	0.853	0.023	0.032	0.027	<0.001	1.000
	n	87	63	150			87	63	150		
Eastern Europe	fr	0.023	0.066	0.040	1.601	0.206	0.015	0.022	0.018	<0.001	1.000
	n	132	91	223			132	91	223		
Central Asia	fr	0.086	0.075	0.081	0.024	0.876	0.031	0.045	0.037	0.103	0.748
	n	162	134	296			162	134	296		
East Asia	fr	0.359	0.338	0.354	0.231	0.631	0.038	0.033	0.037	0.015	0.902
	n	679	210	889			679	210	889		
Northeast Siberia	fr	0.152	0.154	0.153	<0.001	1.000	0.030	0.038	0.034	<0.001	1.000
	n	33	26	59			33	26	59		
American Arctic	fr	0.174	0.144	0.159	0.341	0.560	0.007	0.006	0.006	<0.001	1.000
	n	149	160	309			149	160	309		
Northwest Coast/Na Dene	fr	0.059	0.091	0.077	<0.001	1.000	0.000	0.000	0.000	NA	NA
	n	17	22	39			17	22	39		
North America	fr	0.079	0.071	0.075	<0.001	0.987	0.021	0.014	0.018	<0.001	0.994
	n	140	141	281			140	141	281		
Mesoamerica	fr	0.041	0.025	0.034	<0.001	1.000	0.000	0.025	0.011	0.010	0.919
	n	49	40	89			49	40	89		
South America	fr	0.075	0.067	0.071	<0.001	0.987	0.037	0.044	0.041	<0.001	1.000
	n	134	135	269			134	135	269		
Jomon/Ainu	fr	0.234	0.103	0.179	3.766	0.052	0.043	0.000	0.025	1.463	0.227
	n	94	68	162			94	68	162		
Southeast Asia (early)	fr	0.195	0.043	0.141	1.689	0.194	0.000	0.000	0.000	NA	NA
	n	41	23	64			41	23	64		
Southeast Asia (recent)	fr	0.146	0.145	0.145	<0.001	1.000	0.046	0.048	0.047	<0.001	1.000
	n	323	124	447			323	124	447		
Polynesia	fr	0.101	0.120	0.107	0.070	0.791	0.021	0.022	0.021	<0.001	1.000
	n	188	92	280			188	92	280		
Micronesia	fr	0.200	0.167	0.191	0.003	0.959	0.092	0.125	0.101	0.003	0.954
	n	65	24	89			65	24	89		
Melanesia	fr	0.075	0.075	0.075	<0.001	1.000	0.014	0.015	0.014	<0.001	1.000
	n	147	67	214			147	67	214		
Australia	fr	0.04	0.085	0.054	0.561	0.454	0.030	0.021	0.027	0.000	1.000
	n	101	47	148			101	47	148		
New Guinea	fr	0.067	0.050	0.062	<0.001	1.000	0.089	0.100	0.092	<0.001	1.000
	n	45	20	65			45	20	65		

*Table 2b. Frequencies for MAC and DAC for each population for the fourth premolar. $\chi 2$ values are present for degree of statistically significant differences between males and females. (fr = frequency, n = number of individuals, * = statistically significant).*

Population		MAC					DAC				
		Male	Female	Total	χ^2	p-value	Male	Female	Total	χ^2	p-value
West and South Africa	fr	0.000	0.250	0.053	0.523	0.470	0.300	0.000	0.237	3.697	0.055
	n	30	8	38			30	8	38		
Nubia	fr	0.000	0.000	0.000	NA	NA	0.000	0.400	0.182	0.861	0.354
	n	6	5	11			6	5	11		
North Africa	fr	0.000	0.000	0.000	NA	NA	0.000	0.000	0.000	NA	NA
	n	2	6	8			2	6	8		
South Asia	fr	0.000	0.071	0.018	0.323	0.5696	0.024	0.000	0.018	<0.001	1.000
	n	41	14	55			41	14	55		
Western Europe	fr	0.033	0.077	0.054	0.361	0.548	0.050	0.038	0.045	<0.001	1.000
	n	60	52	112			60	52	112		
Eastern Europe	fr	0.033	0.037	0.035	<0.001	1.000	0.056	0.085	0.070	0.218	0.641
	n	90	82	172			90	82	172		
Central Asia	fr	0.088	0.054	0.071	0.523	0.470	0.053	0.054	0.053	<0.001	1.000
	n	114	111	225			114	111	225		
East Asia	fr	0.102	0.059	0.091	2.996	0.083	0.034	0.039	0.035	0.017	0.897
	n	649	205	854			649	205	854		
Northeast Siberia	fr	0.036	0.053	0.043	<0.001	1.000	0.000	0.000	0.000	NA	NA
	n	28	19	47			28	19	47		
American Arctic	fr	0.022	0.026	0.024	<0.001	1.000	0.011	0.026	0.020	0.110	0.740
	n	92	156	248			92	156	248		
Northwest Coast/ Na Dene	fr	0.000	0.000	0.000	NA	NA	0.000	0.000	0.000	NA	NA
	n	12	19	31			12	19	31		
North America	fr	0.033	0.034	0.033	<0.001	1.000	0.044	0.034	0.038	<0.001	1.000
	n	91	118	209			91	118	209		
Mesoamerica	fr	0.030	0.000	0.015	<0.001	1.000	0.061	0.030	0.045	<0.001	1.000
	n	33	33	66			33	33	66		
South America	fr	0.053	0.027	0.037	0.296	0.586	0.027	0.045	0.037	0.058	0.809
	n	75	112	187			75	112	187		
Jomon/Ainu	fr	0.089	0.063	0.077	0.071	0.790	0.000	0.031	0.014	0.750	0.386
	n	79	64	143			79	64	143		
Southeast Asia (early)	fr	0.074	0.083	0.078	<0.001	1.000	0.074	0.000	0.039	0.407	0.524
	n	27	24	51			27	24	51		
Southeast Asia (recent)	fr	0.062	0.071	0.064	0.012	0.912	0.079	0.106	0.086	0.468	0.494
	n	292	113	405			292	113	405		
Polynesia	fr	0.056	0.082	0.066	0.345	0.557	0.043	0.134	0.077	5.805	0.016*
	n	162	97	259			162	97	259		
Micronesia	fr	0.190	0.167	0.184	<0.001	1.000	0.159	0.167	0.161	<0.001	1.000
	n	63	24	87			63	24	87		
Melanesia	fr	0.075	0.102	0.083	0.119	0.730	0.067	0.102	0.078	0.285	0.594
	n	134	59	193			134	59	193		
Australia	fr	0.167	0.120	0.151	0.254	0.614	0.083	0.06	0.075	0.031	0.860
	n	96	50	146			96	50	146		
New Guinea	fr	0.182	0.125	0.162	0.069	0.792	0.182	0.083	0.147	0.544	0.461
	n	44	24	68			44	24	68		

the lowest and East Asians the highest prevalence of the trait. A distinct pattern is evident regarding Asian and Asian-derived populations. East Asians have the highest frequency of this trait (35.4%). Northeastern Siberians (15.3%), American Arctic (15.9%), Jomon/ Ainu (17.9%), Southeast Asia (early: 14.1%; recent: 14.5%), and Micronesia (19.1%) have intermediate frequencies. Native American [Northwest Coast/Na Dene (7.7%), North America (7.5%), Mesoamerica (3.4%), South America (7.1%)] and Pacific (Polynesia [10.7%], Melanesia [7.5%]) groups exhibit the lowest frequencies for Asian-derived groups. In general, from the point of highest prevalence in East Asia, frequencies decrease into the Americas and the Pacific.

The lowest frequencies of MAC on UP3 are found in Western Eurasian (0.0% - 4.0%), African (2.3 – 7.7%), and Sahul-Pacific groups (5.4% - 6.2%).

UP3: DAC (Table 2a)

The distal accessory cusps exhibit a different pattern of geographic variation than the mesial variant on UP3. This trait typically occurs in low frequencies, ranging from 0.0% to 15.4%. Sub-Saharan Africans and some Pacific Island groups display the highest rates. West/ South Africa and Nubia have the highest frequencies with 14.0% and 15.4%, respectively. Although sample sizes are small for this region, this finding may indicate higher frequencies of UP3 DAC are characteristic of Sub-Saharan populations. New Guinea (9.2%) and Micronesia (10.1%) exhibit similar frequencies for the third premolar. Other global populations typically have a presence rate of less than 4.0%. North American groups range from 0.0% to 1.8%, while South American groups have a frequency of 4.1%, comparable to Central and East Asia. Melanesian (1.4%), Polynesian (2.1%), and Australian (2.7%) groups exhibit similar frequencies for DAC on the third premolar. Western Eurasian populations (ranging from 0.0 to 2.7%) are comparable to samples from the Americas.

UP4: MAC (Table 2b)

Cusp frequencies on this tooth are significantly lower than on the third premolar, with the highest incidence at 18.4% for Micronesians. Australians and New Guineans have slightly lower frequencies with rates of 15.1% and 16.2%, respectively. Melanesians, Polynesians, and Southeast Asians have comparable rates at 8.3%, 6.6%, and 6.4% (recent)/7.8% (early), respectively. These rates are intermediate to Sahul-Pacific and East Asian (9.1%) frequencies. The trait is uncommon in the Americas, with frequencies ranging from 0.0% (Northwest Coast/Ne Dene) to 3.7% (South America).

Western European MAC frequencies increase from 2.7% on UP3 to 5.4% on UP4. However, Eastern Europeans decrease from 4.0% to 3.5%. Less variation is present between populations due to uniformly low frequencies; however, there is some clustering of populations who most commonly exhibit this trait.

UP4: DAC (Table 2b)

While this trait typically occurs in low frequencies, African populations (West and South Africa: 23.7%, Nubia: 18.2%), along with Micronesia (16.1%), and New Guinea (14.7%), are exceptions to this trend. Melanesian (7.8%), Polynesian (7.7%), and Australian (7.5%) groups exhibit similar frequencies for the fourth premolar DAC. New Guinea (14.7%) and Micronesia (16.1%) exhibit slightly higher frequencies. North American (3.8%), Mesoamerican (4.5%), and South American (4.5%) groups have a higher presence of DAT than northern indigenous groups (American Arctic: 2.0%, Northwest Coast/Na Dene: 0.0%).

European DAC frequencies increase significantly on UP4 compared to UP3, increasing from to 2.7% to 4.5% in Western Europeans and 1.8% to 7.0% in Eastern Europeans. General regional differences are relatively similar between DAC of UP3 and DAC of UP4.

Discussion

Marginal accessory cusps of UP3 follow a pattern that corresponds to known population histories. Most notable is the distribution of this trait among Asian-derived populations. East Asian groups exhibit the highest frequencies (35.4%). This trait decreases in occurrence in more northern and southern Asian populations and in the Americas. Turner (1971) found a distinction between American Arctic and Native American groups in the rest of North America, with the former having three-rooted lower first molar frequencies of approximately 27-47% and the latter having a frequency of about 6%. The prevalence of the three-rooted LM1 was used to argue for a three-wave model of migration into the Americas: 1) the first being Amerinds [North and South American Indians], 2) the second being Northwest Coast groups and Na Dene speakers, 3) and the third being the ancestors of American Arctic groups (Turner 1971). Here there is a distinction between American Arctic populations (15.9%) and North and South American Indian groups ranging between 3.4 and 7.7%. The intermediacy of Northwest Coast/Na Dene populations found in previous dental morphological and genetic studies (Turner 1985; Powell 1993; Cavalli-Sforza et al. 1994; Scott and Turner 2008) is not present in this study. For marginal premolar cusps, this population has frequencies like Native North and South American groups.

The variation of MAC on UP3 also corresponds to the Sinodont-Sundadont dental complexes defined by

Turner (1981). The Sinodont complex is characterized by the addition of enamel and increased crown complexity, in contrast to the more simplified dental pattern that distinguishes the Sundadont complex (Turner 1981, 1985). This pattern does not extend to the fourth premolar or to the presence of UP3 DAC; however, the variation of this trait and its patterned distribution that follows known population history indicates MAC of UP3 is informative for studies of population affinity.

Additionally, the mesial accessory cusp reflects the expected intermediacy of Central Asian populations compared to East Asia and Western Eurasia. This region is intermediate in trait expression for shoveling, enamel extensions, cusp 6, protostylid, three-rooted LM1, and four-cusped LM2 (Heim et al., 2016). It has been postulated that this position between these two distinct complexes is a result of gene flow associated with the complex migration histories in the central region of Eurasia (Heim et al., 2016), rather than a settlement zone for early modern humans when first moving out of Africa before expanding into Europe and East Asia (Martínez-Cruz et al., 2011). This same pattern is not evident for the distal accessory cusp. Central Asians exhibit higher frequencies of this trait for the third and fourth premolars than both Western Eurasians and East Asians.

The lowest frequencies for DAC and MAC are found in Western Eurasian populations, particularly in North Africa and South Asia. North Africa is the only group to lack either of these traits on any tooth, though sample size is small. South Asia, represented by India, does not exceed 2.0% for either trait on UP3 or UP4. European populations typically exhibit low frequencies of these traits. This corresponds to the general pattern of simplification of the dental crowns in these populations (Scott et al., 2018).

The MAC frequencies indicate a close relationship between Southeast Asia, Polynesia, and Micronesia for the third premolar, but between Southeast Asia, Polynesia, and Melanesia for the fourth premolar. Additionally, for DAC, the closest similarities are between Southeast Asia, Melanesia, Polynesia, and Australia and between New Guinea and Micronesia for both premolars. While these are univariate comparisons, it is evident that if taken together, these populations exhibit slight clinal variation from their place of origin in Southeast Asia. A mean measure of divergence global analysis of 21 crown traits and six root traits also found a greater similarity between Polynesians and Melanesians than between Polynesians and Micronesians (Scott et al., 2018). The differences between trait and tooth may be reflective of different underlying genetic inheritance patterns and complex migration histories. For instance, while Melanesia is typically associated with Sahul-Pacific groups (Scott et al. 2018), Melanesia is the origin of the Lapita culture that spread into Polynesia. It is hypothesized that it is from the area surrounding the Santa Cruz Islands, Reef Islands, and Vanuatu (i.e., "Central Island Melanesia") where they migrated in multiple waves to remote Oceania, producing an indistinct biological, cultural, and linguistic boundary (Wollstein, 2010; Burley, 2013; Skoglund et al., 2016).

Previous studies of New Guinea dentition revealed an unexpected similarity to the European dental complex (Scott and Turner, 1997; Scott and Schomberg, 2016). Marginal accessory cusps, however, conform to the pattern of expected biological relationships. Mesial accessory cusps occur in frequencies most like Australians for both the third (A: 5.4%, NG: 6.2%) and fourth (A: 15.1%, NG: 16.2%) premolars. The distal accessory cusps for New Guinea are, however, most like Micronesian populations for both the third (Mic: 10.1%, NG: 9.2%) and fourth (Mic: 16.1%, NG: 14.7%) premolars.

Distal accessory cusps exhibit an interesting pattern where their highest prevalence is in the Pacific and Sub-Saharan Africa. African samples are rather small compared to the Pacific groups included here, so further data collection is required to substantiate this finding. Hanihara (2008) found low frequencies for premolar accessory cusps in a larger sample size of Sub-Saharan Africans; however, different samples and method of analysis (the author combined mesial and distal in a dichotomous presence/absence scale) preclude comparison. In general, the results of the present study are like those of Hanihara (2008), with East Asians exhibiting the highest frequencies of accessory cusps on the third premolar while Micronesian and Sahul-Pacific populations have the highest frequencies on the fourth premolar.

The differences found in the distribution of MAC and DAC in the same global populations suggest these traits should be separated for biological distance analyses. Although DAC occurs in lower frequencies than MAC, and most populations exhibit uniformly low frequencies, the patterns present suggest genetic drift affected the distribution of this trait. The distribution of MAC and its correspondence to known population histories of Sinodont and Sundadont populations indicate this trait may be included as part of the suite of traits characterizing these dental complexes and may be informative in understanding the migration of populations out of East and Southeast Asia.

Previous research has indicated varied rates of intra- and interobserver reliability when scoring this trait. Various studies have exhibited low replicability between observers and by a single observer (Nichol and Turner, 1986; Griffin, 1989; Powell, 1995; Aubry, 2009; Stojanowski and Johnson, 2015; Marado et al., 2017). This is likely due, in part, to the absence of a dentine component of these cusps, which results in the obliteration of the trait given a minimal level of wear (Turner et al., 1991; Scott and Irish, 2017). Other researchers have found significant levels of intra-observer replicability (Hubbard, 2012, Thompson, 2013; Passalacqua, 2015; Maier, 2017). As all individuals included in this analysis were investigated by a single observer (C.G.T. II) using the scoring system in ASUDAS, inter-observer error is not a concern in this study. Turner and colleagues (1991) recommend this trait should not be scored on teeth with significant wear, generally limiting analyses to younger individuals. It is important to remember when scoring accessory cusps that grooves must distinctly separate them from the primary buccal and lingual cusps. If wear precludes the ability to observe these grooves, it is best to not grade the trait.

Conclusions

This study is the first to outline the world variation of mesial and distal accessory cusps on the upper third and fourth premolars. It lays a foundation for better understanding the geographic patterning of this underutilized trait. To a large extent, the variation of these cusps reflects known population histories, particularly regarding the mesial accessory cusp of the upper third premolar. Distinctive trends are evident in the distribution of each trait on UP3 and UP4, indicating their utility in studies of biological relationships. The different geographic patterns between mesial and distal accessory cusps are difficult to explain but may suggest the traits experienced different evolutionary histories. As a result, these traits should be treated separately in biodistance statistics rather than collapsed into a scale that tallies mesial and distal cusps together.

Acknowledgments

The authors acknowledge the extraordinary efforts of the late Christy G. Turner II who collected dental morphological data on 23,000 individuals around the world. Although no longer with us, his legacy lives on.

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Dental Anthropology

Volume 31, Issue 02, 2019

Case Study

Research Article

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