

A brief note on the frequency of maxillary molar cuspules in Southwest Asia

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Abstract: *While many of the traits selected to the Arizona State University Dental Anthropology System can be scored despite slight to moderate wear on the tooth surface, small features on occlusal morphology become unobservable even at lower wear grades, often becoming absent in studies accessing archaeological assemblages. This includes many accessory maxillary molar cuspules which can provide means to investigate phylogenetic origins as well as microevolutionary adaptations.*

Using terminology provided in a previous study, a sample from SW Asia is presented here to generate a more complete global frequency of traits. Dental nonmetric traits were recorded from an archaeological population in Sidon (n=44), Lebanon, dating to the Middle Bronze Age (circa 2000–1500 BCE).

Overall, the presence of accessory cuspules was highly prevalent in the Sidon assemblage. Molar occlusal surface complexity, as measured through the presence of cuspules, decreased from the first to the second molar, following the inhibitory cascade model. The Sidon individuals had some similarities with other populations but none followed the same overall prevalence rate, thus providing a useful reference to SW Asian populations for global comparisons.

Key words: Sidon; dental nonmetric trait

Introduction

The formation of teeth is governed by circa 300 genes in interaction with epigenetic and environmental factors (Ramirez Rozzi 2016; Thesleff 2006; Townsend et al. 2009, 2012). Twin and familial studies have been used to estimate the influence of genetic, epigenetic and environmental factors to phenotypic appearance. Generally, these studies suggest that the correlation of genetic and phenotypic variation is moderate to high, but environmental and epigenetic factors do influence the morphology in varying degrees (Townsend et al. 2009, 2012).

Dental morphological traits have been quantified by recording the presence and absence of accessory ridges, tubercles, styles and cusps in crowns and deviations in

root numbers using the Arizona State University Dental Anthropology System (ASUDAS; Turner et al. 1991). Genetic data and dental nonmetric traits collected using ASUDAS standards have found significant and meaningful correlations between dental nonmetric and aDNA biodistance analyses (Delgado et al. 2019; Hubbard et al. 2015).

While many of the traits selected to the ASUDA system can be scored despite slight to moderate wear on the tooth surface, small features on occlusal morphology become unobservable even at lower wear grades. This includes marginal ridge tubercles, recorded mainly from the maxillary first molar, which seldom appear among reported nonmetric trait frequency studies. There are also other molar cusps which, to date, have been most comprehensively published by Kanazawa et al. (1990) who refined prior terminology and generated frequency tables for seven regionally diverging populations from Japan, Europe, Africa and North America. Using the terminology provided by this study, a sample from SW Asia is presented here to generate a more complete global frequency of traits. Traits were recorded on both sides whenever possible from both first and second maxillary molar, providing some further clues into the influence of epigenetics.

Material and methods

Dental nonmetric traits were recorded from an archaeological population in Sidon, Lebanon, dating to the Middle Bronze Age (c. 2000–1500 BCE). From the cemetery consisting of over 200 individuals, 44 were appropriate for the current study due to age-related dental wear (Table 1). Dental wear is common among pre-industrial populations (Mays et al. 2022). In Sidon, wear on the molar cusps was observed soon after teeth came to occlusion, resulting in a sample of individuals in the early to late childhood age category. As sex estimation is not reliable on subadults, the sample represents (likely) both males and females. A full set of dental nonmetric traits

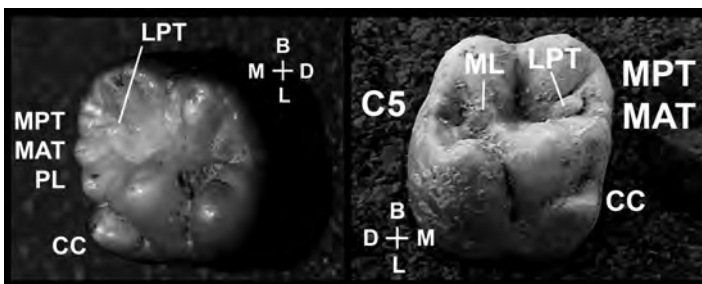


Figure 1. Maxillary molar of individuals 93 (left) and 167.2 (right). A graph of trait location is provided in the Supplementary Material 1.

following ASUDAS and Scott and Irish (2017) has been recorded from the Sidon assemblage and reported elsewhere (Maaranen et al. 2023). Here, the focus is on the maxillary molar cuspules (Table 2, Figure 1). Carabelli's cusp, a larger accessory cusp located on the lingual surface of the protocone, was included in the exploratory phase of the study.

Table 1. Sidon individuals (n=44).

ID	Age group	Burial type	Interment	Disturbance
1	Early/Late childhood	jar	primary	disturbed
2	Early/Late childhood	jar	mixed	uncertain
4	Early childhood	stone-lined	primary	disturbed
8.1	Early/Late childhood	pit	uncertain	uncertain
8.2	Infant/Early childhood	jar	primary	uncertain
13	Early childhood	mudbrick	primary	undisturbed
14	Adolescent	jar	primary	undisturbed
17	Early childhood	jar	primary	disturbed
18	Early/Late childhood	jar	primary	undisturbed
19	Late childhood	stone-lined	primary	undisturbed
24	Early/Late childhood	jar	primary	uncertain
28	Late childhood	pit	primary	undisturbed
33	Early/Late childhood	jar	primary	uncertain
39	Early childhood	jar	primary	disturbed
43	Early childhood	jar	primary	undisturbed
45	Infant	jar	primary	undisturbed
46	Early childhood	jar	primary	undisturbed
49.1	Infant	jar	primary	uncertain
49.2	Early/Late childhood	jar	secondary	uncertain
51	Early/late childhood	mudbrick	secondary	disturbed
52	Early/Late childhood	pit	primary	undisturbed
54.2	Early childhood	jar	secondary	uncertain
55	Late childhood	mudbrick	primary	undisturbed
59	Early/Late childhood	pit	primary	disturbed
62	Adolescent	pit	primary	undisturbed
63.2	Middle adult	jar	primary	uncertain
65	Adolescent	pit	primary	disturbed
67	Early/Late childhood	stone-lined	mixed	uncertain
69	Late childhood	stone-lined	primary	undisturbed
93	Early/Late childhood	jar	primary	disturbed
97	Early childhood	jar	primary	undisturbed
116	Early/Late childhood	pit	primary	disturbed
119	Early/Late childhood	jar	primary	undisturbed
120	Early childhood	pit	primary	undisturbed
125	Late childhood	stone-lined	primary	undisturbed
132	Early/Late childhood	pit	primary	disturbed
133	Late childhood	stone-lined	primary	undisturbed
139.3	Late childhood	NA	fill	uncertain
143	Early/Late childhood	jar	primary	undisturbed
144.1	Adolescent	stone-lined	primary	undisturbed
144.2	Early/Late childhood	stone-lined	primary	disturbed
164	Early/Late childhood	jar	primary	undisturbed
167.1	Late childhood	jar	secondary	uncertain
167.2	Early/Late childhood	jar	primary	undisturbed

Table 2. Descriptions and abbreviations of maxillary molar traits used in this study. MPT, MAT and PL are gathered as Marginal ridge tubercles in ASUDAS.

Feature	Abbr.	Location	Recording	ASUDAS
Carabelli's cusp	CC	On the lingual surface of the protocone	Grade	yes
Cusp 5	C5	Between the metacone and hypocone on the distal aspect	Grade	yes
Mesial paracone tubercle	MPT	Marginal ridge tubercle attached to the paracone	Presence/absence	yes
Mesial accessory tubercle	MAT	Marginal ridge tubercle between the paracone and protocone	Presence/absence	yes
Protoconule	PL	Marginal ridge tubercle attached to the protocone	Presence/absence	yes
Metaconule	ML	On the oblique ridge between the metacone and hypocone	Presence/absence	no
Lingual paracone tubercle	LPT	Distal to the marginal ridge tubercles (MPT, MAT, PL)	Presence/absence	no

Some cuspules, i.e., cusp 5 and marginal ridge tubercles, are included in ASUDAS. The presence of additional cuspules, the metaconule and the lingual paracone tubercle, was also recorded. Though these are not part of ASUDAS, Alt and Türp (1998) and Alt (1997) have included these as rare dental anomalies that can be useful for ontogenetic, evolutionary and kinship studies. A brief description of each recorded cuspule is provided here as the nomenclature around these features has been inconsistent.

Cusp 5 (C5), as it is known in ASUDAS, is located distally between the metacone and hypocone and is distinguished from these two cusps by vertical grooves running parallel to the distal margin (Scott & Irish 2017). The feature has, however, been referred to by other names, most commonly “metaconule”—e.g., Harris and Bailit (1980) based their identification of the metaconule or “C5” on previous descriptions and illustrations (Osborn 1907). There are some discrepancies in this nomenclature pointed out by Kanazawa et al. (1990) as the exact placement of the feature varies slightly in the publication illustrations, from the margin or posterior aspect between the metacone and hypocone (Harris & Bailit 1980) to the oblique ridge connecting the metacone and hypocone (Osborn 1907; Osborn & Wortman 1892); the latter, according to Kanazawa and colleagues, is a separate feature.

Marginal ridge tubercles are observed on the mesial margin on the first upper molars, and can consist of a varying combination of three cuspules, referred to by Kanazawa et al. (1990) as mesial paracone tubercle (MPT), mesial accessory tubercle (MAT) and protoconule (PL). An earlier observation of these cuspules was published by Remane (1960) who used slightly different names for the former two; small oc-

clusal tubercle (kleiner Kauflächenhöcker) and accessory marginal tubercle (Randleistenhöcker), respectively. There is currently no consensus whether there is a phylogenetic difference between a marginal ridge, described by Selenka (1898) as *accessorium anterius internum*, and the marginal ridge tubercles (Kanazawa et al. 1990; Korenhof 1966).

Lingual paracone tubercle (LPT), referred to as “mesial tubercle” by Hanihara (1956), *crista nova* by Remane (1960) and lingual paracone ridge by Korenhof (1966), is located distal to the marginal ridge tubercles. According to Kanazawa and colleagues, it co-occurs particularly with the MPT and MAT but also independently of both, possibly due to a different phylogenetic origin.

The terminology provided by Kanazawa and colleagues was utilised to maximise recording resolution regardless of the possible phylogenetic origin(s) of the different cuspules. Aside from the Carabelli’s cusp and cusp 5 which were recoded additionally by their degree of expression, traits were recorded as present and absent. Additional notes were made based on the appearance of the marginal ridge tubercles.

Due to the limited sample number, no significance testing was applied on the data; instead, descriptive statistics, i.e., frequencies, were produced to propose some tentative patterns. Bar charts and density plots were produced using ggplot2 (Wickham 2016) in program R (2020) to visualise frequencies. All raw data has been provided in the **Supplementary Material 2** for further studies.

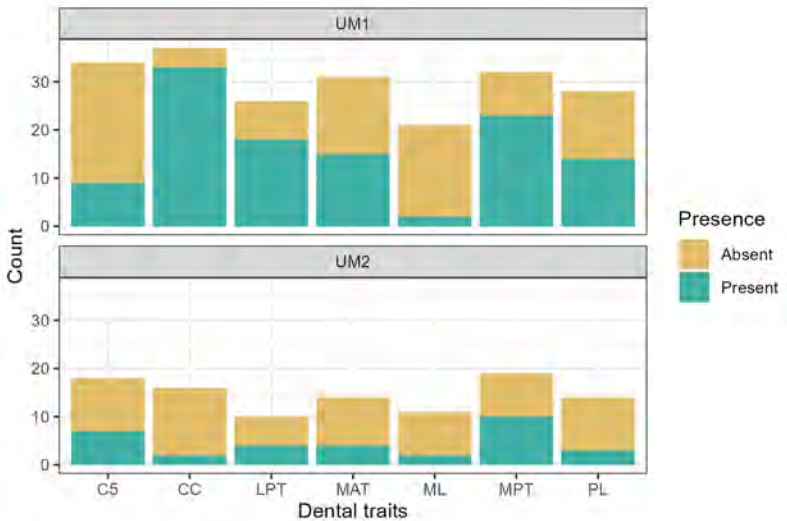


Figure 2. Bar plot showing the presence of traits based on count.

Results

A total of 325 observations, 600 when accounting cusp 5 and Carabelli’s cusps, were recorded from 44 individuals. Both left and right side were recorded, while overall prevalence rates were plotted using the right side which had a marginally higher overall number of observations (Figure 2, Table 3).

Table 3. Maxillary first (UM1) and second (UM2) molar trait frequencies (%).

Trait	Side	N	n	%
UM1				
C5	L	31	8	26%
	R	34	9	26%
CC	L	35	32	91%
	R	37	33	89%
LPT	L	23	11	48%
	R	26	18	69%
MAT	L	31	17	55%
	R	31	15	48%
ML	L	22	5	23%
	R	21	2	10%
MPT	L	34	28	82%
	R	32	23	72%
PL	L	27	20	74%
	R	28	14	50%
Total		412		
UM2				
C5	L	18	7	39%
	R	18	7	39%
CC	L	16	2	13%
	R	16	2	13%
LPT	L	11	7	64%
	R	10	4	40%
MAT	L	12	7	58%
	R	14	4	29%
ML	L	9	1	11%
	R	11	2	18%
MPT	L	12	8	67%
	R	19	10	53%
PL	L	8	2	25%
	R	14	3	21%
Total		188		

Carabelli’s cusp was the most prevalent trait in first molars, the recommended tooth for recording this trait in ASUDAS; conversely, cusp 5 was more prevalent in the second molar, rather than the first. Marginal ridge tubercles were frequent in both first and second molars, with the mesial paracone tubercle being the most prominent. The second-most prevalent tubercle of the trio differed by tooth. Though all three tubercles were typically present, alternative configurations were also noted (Table 4). The lingual paracone tubercle, prevalent in the collections, exhibited a similar pattern

in both first and second molars. The tubercle often co-occurred with marginal ridge tubercles, particularly the mesial paracone tubercle, but it was observed independent of these as well (**Supplementary Material 2**). It was often bilateral, though some exceptions were noted (e.g., individual 13). The metaconule was rare in both first and second molar (c. 10–20%). Some fluctuation in overall prevalence rates was noted by tooth and side, likely resulting from the small sample size.

Table 4. Correlation test with b value higher than 0.49. Full correlation table in **Supplementary Material 2**.

Traits		b	n	p
MPT UM1	MAT UM1	0.509	21	0.02
MPT UM1	PL UM1	0.859	17	0.00
MAT UM1	PL UM1	0.567	19	0.01
C5 UM1	ML UM1	0.522	12	0.08
C5 UM1	PL UM2	1.000	4	0.00
C5 UM1	C5 UM2	0.548	7	0.20
CC UM2	PL UM2	0.612	5	0.27
MPT UM2	PL UM2	0.707	6	0.12
MAT UM2	C5 UM2	0.548	7	0.20

Asymmetry, measured by total presence or absence of traits, was investigated for the whole sample (**Figure 3**) and each individual (**Supplementary Material 1**). Again, Carabelli’s cusp and cusp 5 were most commonly bilateral, while the smaller cuspules

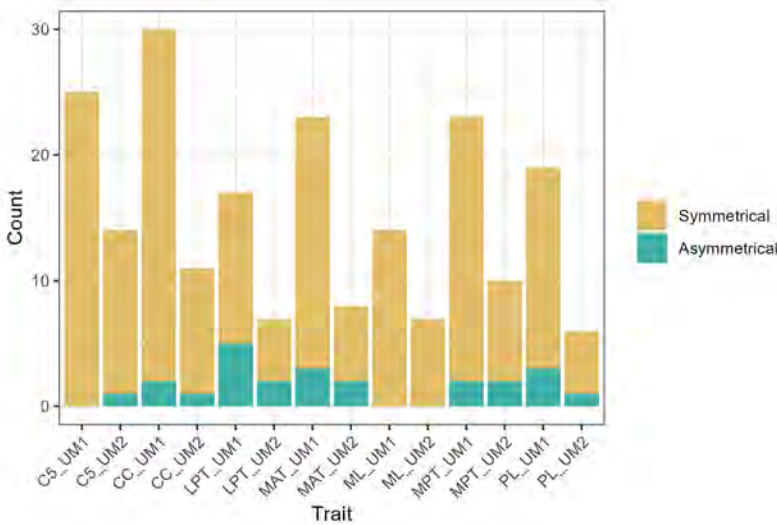


Figure 3. Bar plot showing the asymmetry in the sample based on total presence/absence of traits. Individual plots available in **Supplementary Material 1**.

exhibited more asymmetry. As the comparison requires bilateral observations, only 36 individuals had good enough preservation to produce at least one example. From these, 15 individuals had at least one unilateral trait out of those 9 had two. The 15 individuals do not share any apparent aspects of their biological profile or contextually

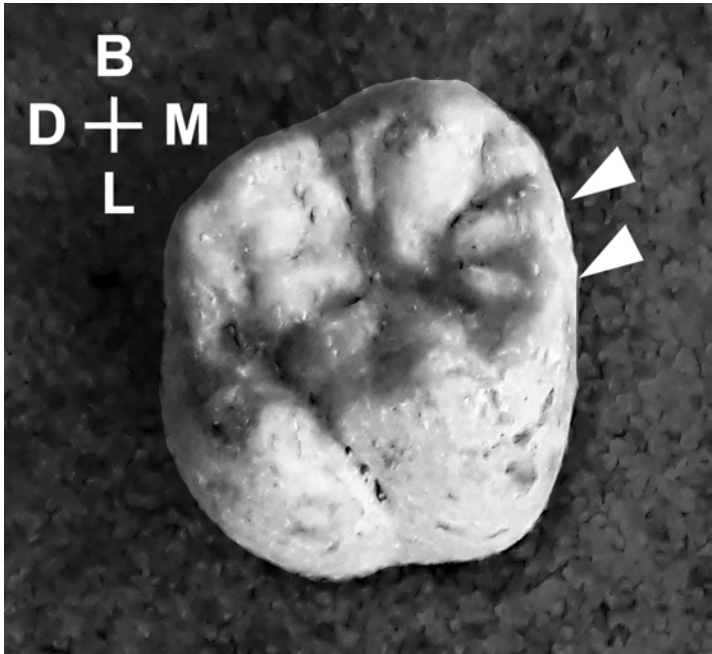


Figure 4. Marginal ridge tubercles (MRTs) with an elongated appearance.

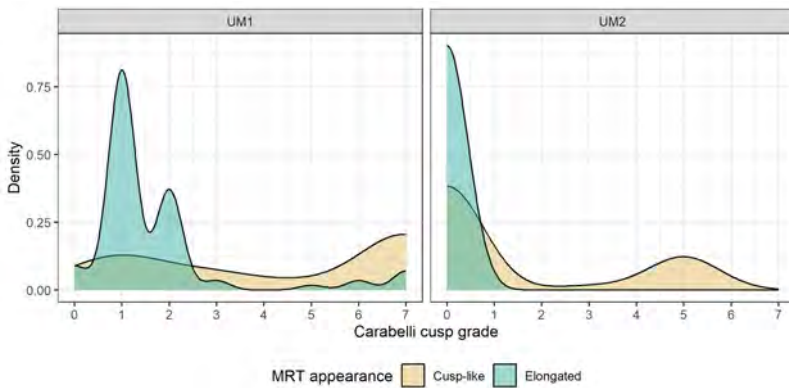


Figure 5. Density plot of Carabelli's cusp (CC), grouped by the appearance of the marginal ridge tubercles (MRT). Teeth with stronger expression of CC also appeared to have more pronounced MRTs.

available information. Though the records are not complete, some observations could be made from some of the individuals (8.1, 13, 19, 33, 49.2, 54.2, 93, 120, 132) who had two asymmetrical features; 8.1 had linear enamel hypoplasia (LEH) lines, 19 had *cribra orbitalia* and LEH, 33 had a marked discrepancy between their dental and skeletal age estimation, 54.2 had further dental asymmetry and extensive periosteal reaction on the endocranial surface. Like 33, 93 had a marked discrepancy between their dental and skeletal age estimation, and 132 (similar to 19) was recorded with *cribra orbitalia*.

Some morphological variation was also observed in the appearance of the marginal ridge tubercles (MRTs). In some cases, the tubercle(s) had a more extended appearance (**Figure 4**) while in others it was more cusp-like (**Figure 1**). Though there is likely some subjectivity in describing the MRTs, a cusp-like appearance was more pronounced in size and observed more often with stronger expressions of the Carabelli's cusp (**Figure 5**) and cusp 5 (**Supplementary Material 1**). When comparing by side, with the exception of two individuals (MPT and PL in UM1 of 13 and MPT in UM2 of 49.2), cuspule appearance remained similar within individuals (**Supplementary Material 1**). Whether stronger cuspule expression correlates with tooth size, remains to be investigated with a larger sample of individuals.

Discussion

Accessory cuspules can provide means to investigate phylogenetic origins as well as microevolutionary adaptations. While many of the traits presented here have appeared in other publications, particularly in regards to mammalian tooth morphology (Osborn 1907; Osborn & Wortman 1892), the investigation by Kanazawa et al. (1990) remains the largest example of maxillary molar cuspules from anatomically modern humans (**Table 5**). Overall, the presence of accessory cuspules was highly prevalent in the Sidon assemblage, an observation which led to their systematic recording in the first place. Like in the prior investigation, the lingual paracone tubercle was noted to occur both with and without marginal ridge tubercles. While this could support the attestation that this feature has a different phylogenetic origin, some singular instances in the Sidon assemblage were noted where an individual had MRTs and LPT on one side and more ambiguous configuration on the other side (Individual 8.1, **Figure 6**).

No other previously recorded group matched the Sidon prevalence rates exactly, however marginal ridge tubercles were similarly common among the Inuit population (between 43% and 64%, depending on the cuspule) recorded by Kanazawa and colleagues. With current sample sizes and the unknown pathways of cuspule formation, it is not advisable to draw any conclusions from population comparisons. Differences in molar morphology, particularly occlusal complexity, increase or decrease based on

Table 5. Prevalence (%) of maxillary molar cuspules from Kanazawa et al. (1990), marked with *, and the Portuguese Coimbra collection (Marado 2014). Sidon frequencies taken from the side with a higher number of observations. Values rounded up to the nearest whole number. MPT, MAT and PL are gathered as Marginal ridge tubercles in ASUDAS.

Population	C5	MPT	MAT	PL	ML	LPT
*Japanese	30	64	66	20	5	38
*Inuit	20	64	58	43	1	59
*Bantu	30	30	17	33	3	47
*Bushman	30	23	27	40	0	60
*Indigenous Australians	36	36	20	18	4	78
*Dutch	12	50	46	23	0	50
*Indian	6	38	28	16	0	38
Modern Portuguese		2	1	1		
Sidon-M1	27	69	55	50	23	69
Sidon-M2	39	53	29	21	18	64

the inhibitory cascade model (ICM), a signal received from a previously developed molar (Selig et al. 2021). Many of the molar cuspules observed from M1 were also present in M2 but with overall lower frequency. More similar studies presenting data from the entire molar row, such as the recent study on lower molars by Kenessey et al. (2024), are required.

There is also a possible sampling bias which must be acknowledged. All individuals in the present study were subadults of indeterminate sex, most commonly in their early to late childhood. These individuals were non-survivors which may have had impact on their physical appearance as well, i.e., physiological stress at childhood may have impacted trait expression. This is particularly evident in the five individuals who were

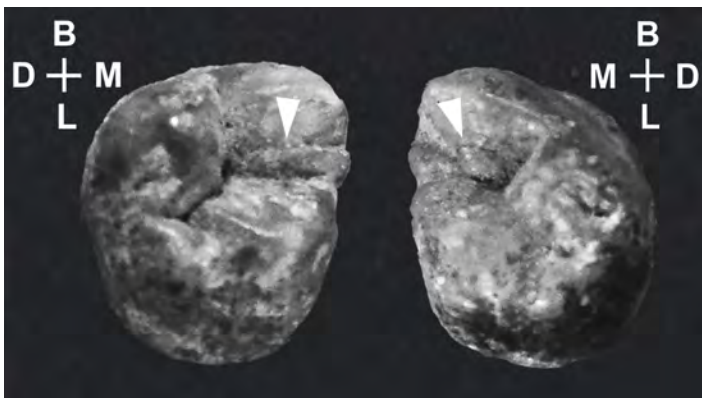


Figure 6. Second maxillary molars of individual 8.1; the presence of the LPT is much more evident on the left UM2 (right side of the image) compared to the right UM2 (right side of the image) where an MPT appears elongated and the presence of the LPT was unclear.

observed with chronic conditions and had a higher level of trait asymmetry. Thus, the Sidon sample may only be reflective of the Middle Bronze Age within this small region and this cohort of young individuals; Further regional investigations representing a range of time periods and age groups could ameliorate this issue.

Due to dental wear in archaeological and palaeontological assemblages, recording more delicate traits is often limited. In the current study, even when minimising wear, distinguishing cuspules could be difficult and resulted in missing (unobservable) data. For maximal recording success, the Moire contourogram utilised by Kanazawa et al. (1990) or a similar imaging method could provide useful. A recent micro-CT study has shown that enamel morphology originates from the enamel-dentine junction (Skinner et al. 2010), which could increase sample sizes to teeth with more extensive enamel wear.

Kanazawa and colleagues also pointed out the challenges caused by non-standardised nomenclature and the mixing of traits expressed on close-by structures, particularly between the C5 (distal accessory tubercle) and the metaconule. Similar issues have been observed from lower molar nomenclature in primate studies (Chapple & Skinner 2003). It is proposed that further studies using these traits provide both descriptions as well as illustrations, or photos to avoid confusion. An illustration has been provided in this work which may be of use (**Supplementary Material**).

In conclusion, recording accessory cuspules, from either upper or lower molars, may be limited in archaeological contexts but they provide a utility beyond the more typical reason (biodistance analysis) that dental nonmetric data is collected for. They offer a macroscopically visible way to investigate odontogenetic theories, epigenesis and possibly thresholds of physiological stress through asymmetry. The increasing availability of imaging techniques, such as micro-CT, may increase the utility of cuspules in biodistance studies as well; as reliance on enamel surface appearance decreases, more individuals with higher rates of dental attrition, i.e., from older age categories, can be included to boost sample sizes and to assess adult data alongside subadults.

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