Morphogenetic Fields and Variation in Deciduous Tooth Crown Size

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ABSTRACT Does variation in deciduous tooth crown size and variation agree with expectations predicted by morphogenetic fields (MGF) as documented for morphometric attributes of permanent teeth? Published literature on deciduous tooth crown size permits analysis of a large dataset. Are expectations of MGF theory evident in size and patterns of variation within and between deciduous tooth classes? Thirty-five reports of deciduous tooth crown size have a global distribution, are ethnically diverse, and geographically widespread. Analysis centers on mesiodistal (MD) and buccolingual (BL) dimensions, crown areas (CA), coefficients of variation (CV) and rank order of variability across populations and dental arcades. Mean crown size, CAs and CVs follow expectation: a) udi1is larger and less variable than udi2, b) a gradual decline in mean CVs from dc to dm2 is evident, c) in rank order of decreasing CV dm2 is the least variable, and incisors are most variable. The udi1 and dm2s exhibit attributes of key teeth. In size, measures of variability, and rank order variation across teeth, results are consistent with expectations based on MGFs in permanent teeth. This confirms the likely existence of morphogenetic-like fields in deciduous teeth during dental development. The diverse groups and different modes of analysis ensure confidence in the results that may have value for clinical purposes and evolutionary studies.

This study analyzes variation in deciduous tooth crown dimensions within the context of morphogenetic developmental fields. Do patterns of variation in deciduous odontometic data conform to expectations predicted by morphogenetic fields (MGF) in a manner analogous to morphometric variation in permanent teeth? Morphogenetic developmental fields have been proposed to explain morphometric attributes of meristic dental elements in the post-canine teeth of mammals (Butler, 1939). The concept was initially adapted to explain variation in expression of morphological attributes of the permanent dentition of modern humans by Dahlberg (1945, 1950, 1951). More recently the morphogenetic field concept in the human dentition has been integrated with clone and homeobox code models of dental development to better understand anomalies of tooth number and size (Townsend et al., 2009). A field-like mechanism proposed to predict the size of mammalian and hominin teeth is known as the inhibitory cascade, an activator–inhibitor mechanism that affects relative tooth size (Evans et al., 2016; Kavanaugh et al., 2016). Analysis of patterns of variability in crown dimensions of permanent teeth in humans and non-human primates were summarily critiqued by Kieser (1990), who reviewed approaches to odontometric variability giving attention to evidence of developmental and occlusal influences, group variation theory, and coefficients of variation. He concluded that the exact causes for patterns of metric variability in permanent teeth are poorly understood. Analyses of deciduous dental variability are far fewer with significant assessments by Harris (2001; Harris and Lease, 2005) for mesiodistal data and by Riberio et al. (2012) for mesiodistal (MD) and buccolingual (BL) diameters, crown height, and intercuspal distances of same-sex mono- and

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di-zygotic twin pairs. An atlas depicting the development and eruption of deciduous and permanent dental elements clarifies the ontogenetic relationship of the two dentitions (AlQahtani et al., 2010; https://www.qmul.ac.uk/dentistry/atlas/).

Interestingly, Dahlberg (1945, 1951) did not define fields within the primary dentition and, without any comment, he added a premolar field to Butler's (1939) three-field paradigm for permanent teeth (Townsend et al., 2009: S35). This observation was reiterated seven years later, "Neither Butler nor Dahlberg commented specifically on the application of dental field theory to the deciduous dentition" (Hemphill, 2016). While generally correct, these comments overlook the many instances in which patterns of metric variation in deciduous tooth crown dimensions have been interpreted to be consistent with expectations of morphogenetic field theory. This opinion may be stated simply with little elaboration, for example, "The variability in the MD and BL measurements follows the field concept" (Axelsson & Kirveskari, 1984: 343). Before this, Hanihara (1974) used factor analysis to identify influences controlling variation in deciduous tooth crown size in four groups (Japanese, Australian aboriginals, Native American Pima, and Caucasians) and found three factors influencing size and shape. The tendency for the second molar to be less variable in size than the first in a Dominican sample was noted to be in accord with the field concept which considers deciduous second molars as anterior members of a molar tooth field and therefore particularly stable in their morphology (Garcia-Godoy et al., 1985). Farmer & Townsend (1993: 681) note that although distinct morphogenetic fields have not been defined in the deciduous dentition, South Australian children of European descent appeared to show a gradient of decreasing size variability from anterior to posterior, with the second deciduous molar being particularly stable. Gradients in variation of deciduous tooth measures of recent children from Spitalfields Cemetery, London show the greatest variability in anterior teeth and stability in second molar teeth (Liversidge and Molleson, 1999), in accord with the MGF concept. That the second deciduous molar is the key (most stable) tooth in the molar field is supported by stability in size variation and asymmetry of dm2 in the Spitalfields sample and by expression of the protostylid noted by Dahlberg (1950). The differential patterning of coefficients of variation (CV) in deciduous teeth of male Japanese singletons and twins is almost the same as in the permanent dentition, suggesting the existence of three MGFs in the deciduous dentition (Mizoguchi, 1998). Though exceptions exist, this assessment is based on the presumption that the pattern of CVs reflects the extent of MGF control of crown size. The validity of Dahlberg's field hypothesis for the deciduous dentition requires further research into local environmental factors and concrete variables including inducing substances and homeobox genes (Mizoguchi, 1998). While reports of deciduous tooth crown size (DTCS) allege that observed variation is consistent with MGF theory, these reports are few in number, population-specific, and include exceptions. A wider review of data is essential to determine the degree to which the field concept applies broadly and consistently to DTCS in ethnically and geographically diverse populations.

Materials

This analysis emanates from original research on deciduous dental attributes in prehistoric and living samples from India and Indonesia. These studies included variability in crown dimensions (Lukacs 1981, 2016, 2019, 2022; Lukacs et al., 1983; Lukacs and Kuswandari, 2022), non-metric dental morphology (Lukacs and Walimbe, 1984; Lukacs and Kuswandari, 2009, 2013), developmental enamel defects (Lukacs, 1991; Lukacs and Walimbe, 1998; Lukacs et al., 2001a, 2001b), and diachronic change in deciduous dental traits (Lukacs and Walimbe, 2005; Lukacs, 2007). Collectively this research gives deeper insight into biological relationships and health in otherwise understudied regions of the world. The recent re-analysis of Indonesian DTCS and inter-group variation in sex dimorphism in the deciduous dentition led to this study (Lukacs and Kuswandari, 2022). This study is designed to determine if patterns of deciduous dental variation within and between populations are consistent with MGFs in a manner analogous to developmental fields in the permanent dentition.

A search of the scientific literature (Anthrosource, Medline, Web of Science) revealed the rapidly increasing growth of reports on DTCS among widespread populations. The thirty-five samples in this study have a global distribution, are ethnically diverse, and geographically widespread (Table 1). Criteria for selecting studies to include in this analysis focused on the presence of: descriptive odontometric statistics including CV or data from which CV could be computed (mean, standard deviation), a protocol ensuring reliability of tooth crown measurement methodology (repeat measures, evaluation of measurement error), and broad geographic and ethnic distribution of study samples. Studies that did not present data by sex and/or were based on small samples were excluded, such as Moss and Chase's (1966) analysis of Liberian children (n= 21), for example. Indigenous and modern samples from all continents are included. Four Indigenous groups include the Bunun (Taiwan); Pima (native North America), San, Kalahari (South Africa), and Warlpiri Yuendumu (central Australia). Though global in origin, samples are unevenly distributed with a bias toward East Asia (China, Japan; n=8) and Europe (n=6), and underrepresentation of other groups (middle East, South America). A shortcoming not evident from this list is that crown dimensions are not reported for all teeth in all groups (see Table 1). For example, incisor dimensions were not included in Adler and Donlon's (2010) analysis of Australians of European descent, and only measurements for deciduous molars were reported for the Indian (Puducherry; Sujitha et al., 2021) and Spanish (Madrid; Barberia et al., 2009) samples. Buccolingual dimensions of incisor and canine teeth were not part of Kaul and Prakash's (1984) description of Jat odontometrics. Yet more commonly, BL dimensions are not reported at all or especially for anterior teeth, thus precluding computation of

Table 1. Global distribution and data source of samples included in study (n = 35)

Region	Location	Group	Data	Data Source
Africa (n=4)	AfroAmerican	Tennessee	all	Vaughn & Harris, 1992
	sub-Saharan	Kalahari San	all	Grine, 2009
	sub-Saharan	South Afr Black	all	Grine, 1986
	sub-Saharan	Nigerian	all	Egibobo et al., 2010
American (n=5)	EuroAmerican	Burlington White	all	DeVito, 1988
	EuroAmerican	Michigan White	all	Black, 1978
	Native	Pima	all	Alvrus, 2000
	Dominican	mulatto	all	Garcia-Godoy et al., 1985
	South	Colombian	MD	Botero et al., 2015
Asia – East (n=9)	Chinese	Taiwan 1	all	Tsai, 2000
	Chinese	Taiwan 2	all	Liu et al., 2000
	Indigenous	Taiwan 3	MD	Lee, 1978
	Japan	Japan 1970	MD	Makiguchi et al., 2018
	Japan	Japan 2000	MD	Makiguchi et al., 2018
	Japan	various	MD	Ooshima et al., 1996
	Japan	Nagoya	all	Yamada et al., 1986a, b
	Japan	Tokyo	all	Tsutsumi et al., 1993
	Korea	south	all	Baik et al., 2002
Asia - South (n=4)	India	Puducherry	inc	Sujitha et al., 2021
	India	Gujarat	all	Lukacs et al., 1983
	India	Jat	inc	Kaul & Prakash, 1984
	India	Wardha	all	Chaudhury et al., 2011
Asia - Southeast (n=2)	Indonesia	Malay	all	Lukacs & Kuswandari, 2022
	Vietnam	native	all	Huynh et al., 2020
Australia (n=4)	Indigenous	Warlpiri-Yuendumu	all	Margetts & Brown, 1978
	European	southern White	all	Farmer & Townsend, 1993
	Melanseia	Nasioi	all	Bailit et al., 1968
	Sydney	white	inc	Adler & Donlon, 2010
Europe (n=6)	Iceland	modern	all	Alexsson & Kirveskari, 1984
	London	Spitalfields	all	Liversidge & Molleson, 1999
	Poland	Medieval	all	Zadzinska et al., 2008
	Portugal	NMNH, Lisbon	all	Cardoso, 2010
	Spain	Granada	all	Viciano et al., 2013
	Spain	Madrid	inc	Barberia et al., 2009
Middle East (n=1)	Jordan	Irbid	all	Hattab et al., 1999

compound variables like Crown Area (MD x BL). Mesiodistal dimensions are clinically relevant to issues of spacing and occlusion and some reports comprise only MD data. Examples include, Colombian (Medellin; Botero et al., 2015), Japanese (Ooshima et al., 1996), Javanese (Kuswandari and Nishino, 2004), and the Indigenous Bunun of Taiwan (Lee, 1978). Hence, MD crown dimensions were selected for a worldwide analysis of temporospatial variations and sex dimorphism by Harris (2001, Harris and Lease, 2005: 594); BL measurements were less frequently and consistently reported.

Methods

Multiple methods were used to determine if DTCS and patterns of variability meet expectations of MGFs as defined in permanent teeth. Two levels are used to evaluate variability in deciduous tooth dimensions: intra-population and inter-population. First, differences in linear dimensions, ratios, and crown areas of adjacent teeth were evaluated within populations. Data came from individual reports of tooth crown size or were calculated from reported mean values. Analysis within each population compares variability in DTCS by tooth across dimensions (MD, BL) and arcades (maxilla, mandible). Second, inter-population assessment of coefficients of variation for linear dimensions (MD & BL, mm) and crown areas (CA = MD x BL, mm^2) were calculated and assessed. The summary data: mean MD and BL (linear), CV (index) and, and CA (area) from all studies were evaluated for normality using the Shapiro-Wilk (1965) test before computing means across all groups.

The CV is a relative measure of variability that indicates the size of a standard deviation in relation to the mean. A standardized, dimensionless measure, a CV allows you to compare variability between disparate groups and traits. The CV is occasionally referred to as the relative standard deviation. CVs are often used to analyze mammalian odontometric variation as reviewed by Polly (1998). The CVs were taken directly from published reports on deciduous tooth crown dimensions. Since two positively correlated linear dimensions contribute to overall crown size, Crown Area (CA) was computed from reported data for each tooth (CA = mean MD * mean BL; in mm^2) and the CVs of mean CAs across populations were examined. If CVs were not given in a study, they were calculated from mean values and standard deviations for each linear dimension (MD and BL) of each maxillary and mandibular tooth. If standard deviation was not included among descriptive statistics in a report it was calculated from the standard error (CV = std error * $\sqrt{n}$), then the CV was determined. To be clear, mean CVs of linear dimensions (MD, BL) were computed across populations and have an associated standard deviation. However, since CAs are a product of mean MD and mean BL of each dental element in each population there's no way to obtain a mean CV (and standard deviation) for each CA across all populations. Hence the CVs of the mean CA values were assessed for relative variability using Forkman's (2009) F test. Differences in mean CV across populations were evaluated by first applying a test for normality (Shapiro-Wilk), to each variable and if normal, an F-test for equality of variances was conducted before the t-test was run ($\alpha = 0.05$). If data failed the normality test a Mann-Whitney rank-sum test for differences in median values was used with 25% and 75% confidence values. Tooth crown size databases were created and stored in Excel (Microsoft Office 365 ProPlus), statistical analysis was conducted in Excel data analysis and in SAS-PC (ver. 9.3), graphics were prepared using SigmaPlot for Windows (ver. 11.0). Statistical significance of differences in CV were evaluated using Forkman's (2009) approximate F test for equality of CVs in MedCalc (v.20.144; Belgium; www.Medcalc.org).

The CVs for a set of measurements within a population, say MD dimension of maxillary teeth, were ranked from one to five in order of decreasing CV from most to least variable tooth. The tooth with the largest CV was ranked one (most variable), the tooth with the lowest variability was ranked five, the least variable, or the most stable tooth in the set. This procedure was followed independently by jaw and dimension for each tooth in each population resulting in four sets of rankings for each data set (MD-maxilla, MD-mandible; BL-maxilla, BL- mandible). The relative frequency of ranks across all groups was determined for each tooth and dimension to identify patterns of variability, based on CVs, throughout the dental arcade. Which teeth exhibit greater variability? Which teeth are most stable? Can patterns of variability be identified and do they follow expectations of MGFs in permanent teeth? If MGFs, as described for permanent teeth, are expressed in the deciduous dentition, observed patterns of deciduous crown size and variability should reveal a series of specific expectations (Table 2). These are described below.

Morphogenetic fields in deciduous incisor teeth

The concept of dental morphogenetic fields when

Table 2. Crown size and variability expectations for deciduous tooth types based upon the MGF theory as described for permanent dentition (Butler, 1939; Dahlberg, 1945, 1951)

Arcade	Expectations: deciduous teeth Size	Variability	Basis for Expectations: permanent teeth
Maxilla	$di^1 > di^2$	$di^1 < di^2$	I^1 is a polar tooth, larger and less variable than I^2
	$dm^1 > c > di^2$	$dm^1 < c < di^2$	based on tooth position and development
	$dm^1 < dm^2$	$dm^1 > dm^2$	M^1 developmentally more stable than M^2 or M^3
			dm^2 and M^1 are developmentally closely related with both arising from the same dental lamina with developmental timing that overlaps but with dm^2 initiation preceding M^1
Mandible	$di_1 < di_2$	$di^1 > di^2$	I_1 is smaller and more variable than I_2
	$dm^1 > c < di^2$	$dm^1 < c < di^2$	based on tooth position and development
	$dm_1 < dm_2$	$dm_1 > dm_2$	same reasons as for maxilla

applied to the pattern of metric variation in permanent incisors has several components and is different for upper and lower incisor teeth (Dahlberg, 1945, 1951). Initially, the description of MGFs applied to human permanent teeth focused on morphometric attributes of Native Americans in a comparative perspective. In upper incisors: the central incisor is the key or polar tooth and is larger and more stable (less variable) than the lateral incisor. By contrast, lower permanent incisors exhibit a reversed morphogenetic field, opposite that expressed in upper incisors. In MD size the ldi1 is smaller and less stable (more variable) than ldi2, which is the polar tooth and is larger and less variable. After assessing variability in incisor crown size, patterning of coefficients of variation is evaluated across the deciduous dental arcade.

Results

A brief description of the data used in this analysis precedes presentation of results. Sample sizes varied across dental elements and studies, but mean sample sizes (n) varied from 80 to 106 for MD (34 studies) and from 50 to 75 for BL dimensions (29 studies). Sample sizes for mean crown dimensions, mean CVs, and mean CAs analyzed in this analysis represent means across studied groups (e.g. inter-population) from which data were derived. Shapiro-Wilk tests of normality revealed the majority of variables match a pattern expected if drawn from a population with a normal distribution; 90% of sample means (8/10 - MD, 9/10 - BL, 10/10 CA) passed, and 80% of coefficients of variation passed (6/10 - MD_CV, 9/10 - BL_CV, And 10/10 - CA_CV) with $\alpha = 0.05$. Thus, skewness and kurtosis are unlikely to impact this analysis of deciduous dental variability.

Results are presented in two sections. The first focuses on patterning of variability in incisor teeth. The second addresses the results of three different approaches to patterns of variability in deciduous tooth crown metrics. Is the pattern of metric variation observed in the deciduous dentition concordant with expectations based on MGFs in permanent incisors? Analysis of results focused initially on incisor teeth because reversed fields have been described for upper and lower permanent incisors. In relative MD and BL size, the observed pattern is that udi1 exhibits attributes of a polar or key tooth. Table 3 shows that in size the udi1 is larger and less variable, has a lower SD and CVs than udi2 in both dimensions. By contrast, mandibular incisors reveal a mixed pattern, not fully consistent with field theory expectations. The lateral incisor is significantly larger in MD and BL dimensions than the central incisor as expected ($p<0.0001$), and consistent with expectation, ldi2 is less variable than ldi1 in BL dimension. Yet in MD diameter the lower lateral incisor is more variable than ldi1, an observation inconsistent with MGF patterning in permanent lower incisors. The pattern of odontometric variation in size and variability of deciduous upper incisors follows expectations based on the description of morphogenetic fields in permanent maxillary incisor teeth. In mandibular incisors the size differential is consistent with field expectations - lateral incisors are significantly greater in MD and BL dimension than centrals, however, ldi2 is less variable than ldi1. However, CV is greater for the MD dimension of ldi2 than ldi1, an unexpected result not compatible with reduced variation expected of a polar or key tooth.

Table 3. Mean crown dimensions (n, mean, sd, min, max) and mean coefficient of variation ($\bar{x}$CV, sd) across populations (males only; see Fig. 1)

Variable	n	Mean	sd	$\bar{x}$CV	sd	min	max
mesiodistal							
udi1	31	6.59	0.28	**6.32**	1.14	5.80	7.35
udi2	31	5.38	0.25	6.78	1.22	4.91	6.00
udc	32	6.83	0.20	5.93	0.93	6.48	7.41
udm1	34	7.40	0.29	6.16	1.28	6.69	8.25
udm2	34	9.22	0.41	**5.40**	1.27	8.58	10.55
		F=0.6354;			*p=0.2060*		
ldi1	31	4.21	0.22	7.50	1.42	3.86	4.97
ldi2	31	4.69	0.17	**7.89**	1.80	4.25	5.01
ldc	32	5.94	0.18	6.26	1.69	5.68	6.48
ldm1	34	8.12	0.25	5.62	1.24	7.43	8.54
ldm2	34	10.16	0.35	**4.93**	1.45	9.39	10.89
		F=0.3919;			*p=0.0098*		
buccolingual							
udi1	25	5.04	0.21	7.07	1.60	4.48	5.47
udi2	25	4.76	0.25	**8.10**	1.76	3.87	5.24
udc	26	6.03	0.28	7.61	1.64	5.39	6.61
udm1	29	8.65	0.34	5.52	1.62	7.73	9.17
udm2	29	9.95	0.3	**5.00**	1.20	9.44	10.65
		F=0.3825;			*p=0.0158*		
ldi1	25	3.83	0.18	**7.91**	1.86	3.53	4.33
ldi2	25	4.28	0.19	7.35	1.62	3.95	4.75
ldc	26	5.52	0.21	7.08	1.39	5.13	6.05
ldm1	29	7.33	0.42	6.41	1.73	6.17	7.98
ldm2	29	9.09	0.37	**5.18**	1.65	8.54	10.02
		F=0.4303;			*p=0.0336*		

N = sample size; SD = standard deviation; CV = CV for mean for all samples; min = minimum; max = maximum; **Bold =** largest and smallest CV by dimension and arcade; F=test for equal CVs, *p*-value, α=0.05

Variability in deciduous teeth across the arcade: metric and rank analyses

To determine if patterns of deciduous odontometric variability follow expectations predicted by patterns documented by MGFs in permanent teeth (see Table 2), three analyses were conducted. The first examines the expression mean CVs by tooth and dimension across the arcade and across populations. The second investigates relative size of mean CAs and their associated CVs. The third quantifies the rank order of CVs from di1 to dm2 by jaw and dimension across populations.

Descriptive statistics for mean CVs for males are presented in Table 3. Mean crown dimensions (n, mean, sd, min, max) and mean coefficients of variation ($\bar{x}$CV, sd) across populations are provided. Figure 1 provides a graphic representation of data that allows easy visualization of differences in CV by tooth and dimension. Results for females exhibit the same pattern as males and are not presented. The overall result follows expectations in that dental elements exhibit a gradation of decreasing variability (or increased stability) from anterior to posterior elements of the dentition (from di2 to dm2). More specifically: a) the upper central incisor (udi1) is less variable, than the upper lateral incisor (udi2) in MD and BL dimensions, b) all second molars (dm2) have lower mean CVs than first molar teeth in upper and lower arcades, and c) the lower lateral incisor (di2) is more stable (lower CV) than the central incisor (di1) in BL dimension. The relative amount of variability in anterior (incisors) and posterior (molars) teeth were tested with an assessment of significant differences in mean CV. The largest $\bar{x}$CVs in a dental quadrant (bold values) are consistently found in incisor teeth and the smallest $\bar{x}$CVs (bold values) occur in dm2s. In three of four comparisons (see Table 3) the difference between largest and smallest $\bar{x}$CVs were found to be significant using Forkman's (2009) F-test: ldi2_MD *vs.* ldm2_MD (F=0.3919, p=0.0098); udi2_BL *vs.* udm2_BL (F=0.3825, p=0.0158), and ldi1_BL *vs.* ldm2_BL (F=0.4303, p=0.0336). However, this difference is non-significant in one quadrant (udi2_MD *vs.* udm2_MD; F=0.6354, p=0.2060). These observations are all consistent with expectations of MGF as described for permanent teeth. The only exception is in the MD dimension of the lateral incisor (di2) which has a greater mean CV than the central incisor (di1). These results show that for maxillary and mandibular molars, dm2s consistently exhibit lower $\bar{x}$CVs than dm1s. Most comparisons of mean CVs are consistent with MGF expectations with one exception.

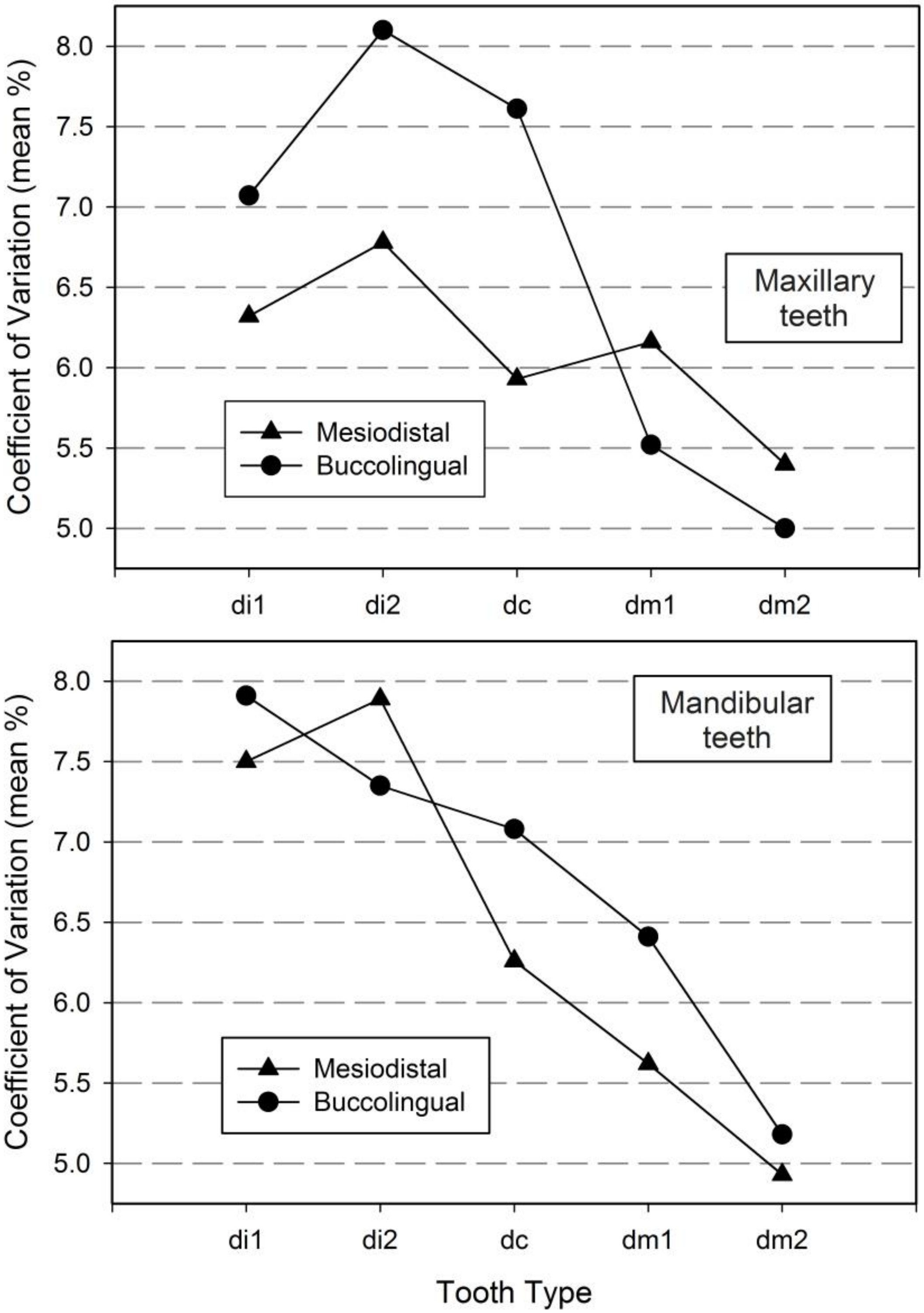

Figure 1. Mean Coefficients of Variation (CV) for mean tooth crown size (maxillary - upper panel, mandibular - lower panel, mesiodistal - MD and buccolingual - BL; see Table 3).

The second approach focuses on variability in CAs across the dental elements. Covariation of MD and BL dimensions varies among elements of the dental arcade, hence CA (mm²) provides an approximate overall estimate of tooth size. For this reason, CVs for each mean CA were calculated and plotted. The results include mean CAs, associated CVs, and descriptive statistics (Table 4, Figure 2). Are key teeth less variable? Do they have lower CVs than non-key dental elements? In four comparisons of adjacent teeth, (upper and lower incisors; upper and lower molars) prospective key teeth have lower CVs than non-key teeth, thus exhibiting patterns of variation consistent with field theory expectations. The CV comparisons consistent with field theory include: udi2 > udi1, ldi1 > ldi2, udm1 > udm2, and ldm1 > ldm2. An F test for significant differences between largest and smallest CVs (Forkman, 2009) shows that incisors (udi2, ldi1) are more variable than second molars (udm2, ldm2) (see Table 4). The CV for crown area of the udc is intermediate between values for upper incisors and upper molars, while the CV for ldc falls between the lower incisors and dm2.

The third analysis examines the rank of relative variability in CV for each tooth by dimension and by jaw across populations. Results are presented graphically for MD (Figure 3) and BL (Figure 4) dimensions. Data are presented in summary form in Table 5 and raw data by population in Table 6. Note that not all ranks were observed for all teeth. The BL dimension of maxillary teeth and second molar teeth exhibit fewer than five ranks; ranks not observed are omitted from figures. For example, in the upper BL dimension (see Figure 4, top panel) three ranks (1, 2, 3) were observed and plotted for udi2, and only two ranks (4, 5) were present and graphed for the BL dimension of udm2. Ranks not observed are omitted from the figure and not plotted are indicated by a double dash (--). Close examination of Figures 3 and 4 reveals several patterns: a) ranks one through three have a high frequency in both dimensions (MD, BL) in central and lateral incisors, upper and lower, b) rank five (least variable) has the highest frequency in second molars and is evident in both jaws and both dimensions, c) the first molar is more variable than the second molar with a greater number of ranks observed and with rank 4 attaining highest frequencies, and d) canines display a pattern of ranked variation intermediate between incisor and molar teeth. Rankings of coefficients of variation (CV) by di-

Table 4. Mean Crown Areas ($\bar{x}$CA) and coefficients of variation (CV) across populations (males only; see Fig. 2)

Tooth	n	$\bar{x}$CA	CV	sd	min	max
			maxilla			
di1	25	33.28	8.16	2.71	26.92	40.20
di2	25	25.70	**9.07**	2.33	19.00	31.44
dc	25	41.22	7.20	2.97	36.77	48.98
dm1	25	64.26	5.33	3.42	58.03	70.30
dm2	22	89.55	**5.15**	4.62	81.00	97.29
F=3.0852			*p=0.0113*			
			mandible			
di1	25	16.21	**8.86**	1.44	14.01	19.53
di2	25	20.13	7.30	1.47	17.48	23.80
dc	25	32.88	6.48	2.13	29.55	38.18
dm1	25	59.89	6.56	3.93	50.90	67.11
dm2	22	91.02	**5.46**	4.97	81.51	99.99
F=2.6209			*p=0.0291*			

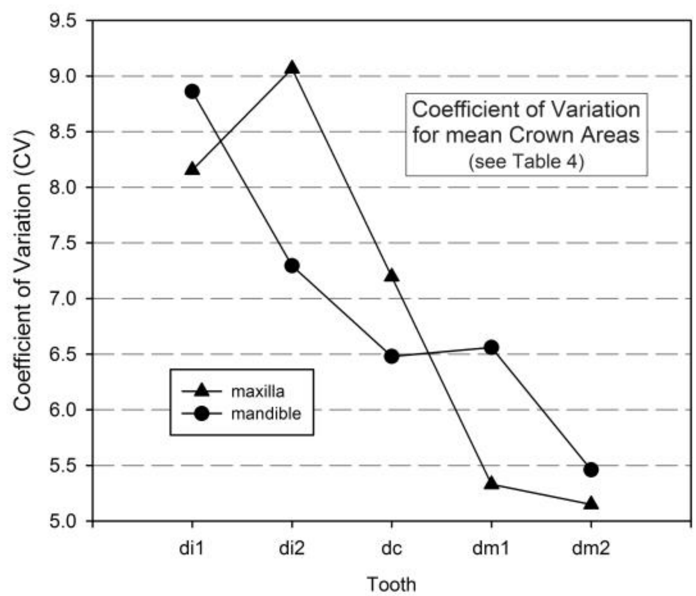

Figure 2. Coefficients of Variation for mean tooth crown areas (CAs; see Table 4).

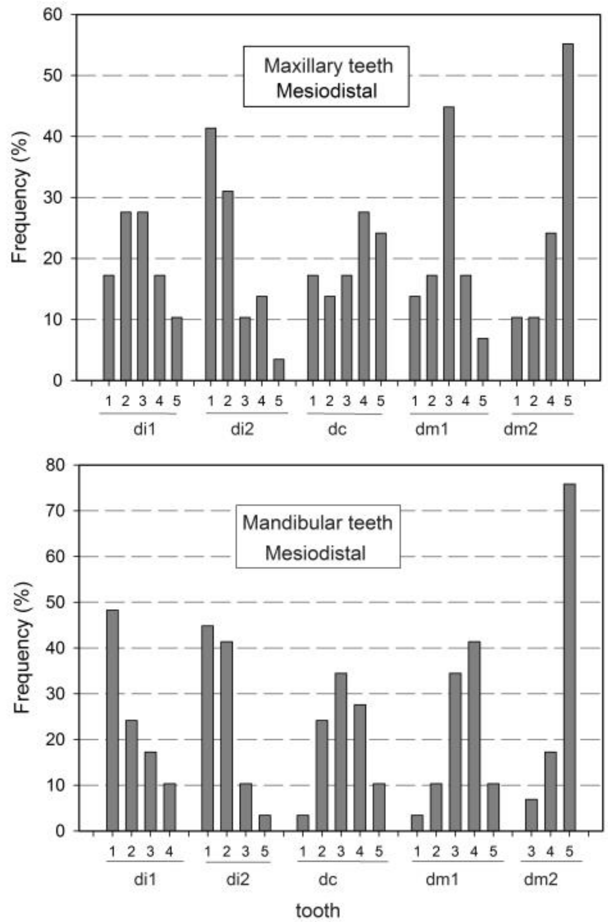

Figure 3. Histogram of CVs in rank order from most (rank 1) to least (rank 5) variable: Mesiodistal dimension (maxillary - upper panel; mandibular - lower panel; see Table 5).

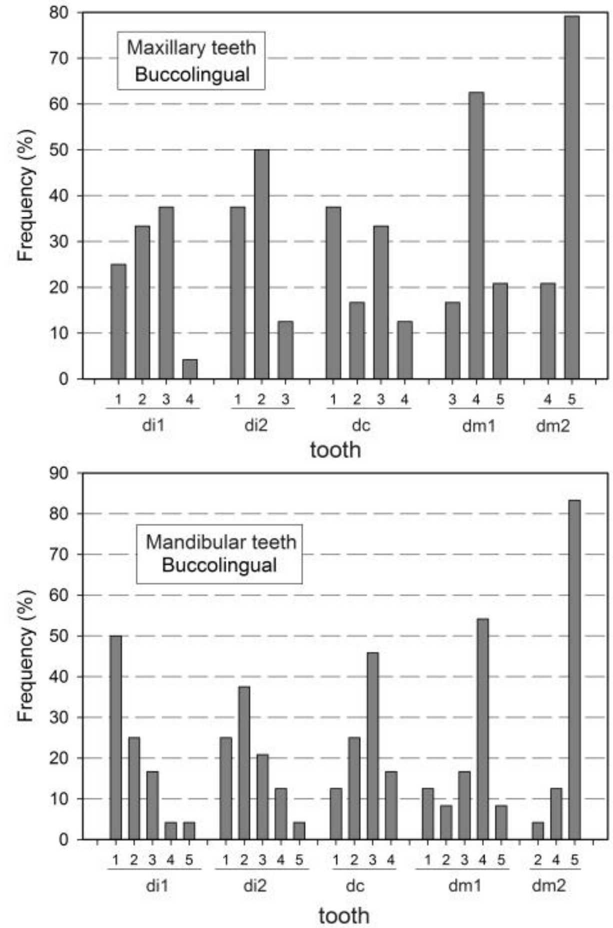

Figure 4. Histogram of CVs in rank order from most (rank 1) to least (rank 5) variable: Buccolingual dimension (maxillary - upper panel; mandibular - lower panel; see Table 5).

Table 5. Frequency (f, %) by rank order of CVs for MD and BL dimensions across populations (raw data by population, Table 6)

	di1		di2		udc		udm1		udm2	
rank	f	%	f	%	f	%	f	%	f	%
	Mesiodistal					maxillary				
1	5	17.24	12	41.38	5	17.24	4	13.79	3	10.34
2	8	27.59	9	31.03	4	13.79	5	17.24	3	10.34
3	8	27.59	3	10.34	5	17.24	13	44.83	--	--
4	5	17.24	4	13.79	8	27.59	5	17.24	7	24.14
5	3	10.34	1	3.45	7	24.14	2	6.90	16	55.17
					mandibular					
1	14	48.28	13	44.83	1	3.45	1	3.45	--	--
2	7	24.14	12	41.38	7	24.14	3	10.34	--	--
3	5	17.24	3	10.34	10	34.48	10	34.48	2	6.90
4	3	10.34	--	--	8	27.59	12	41.38	5	17.24
5	--	--	1	3.45	3	10.34	3	10.34	22	75.86
	Buccolingual					maxillary				
1	6	25.00	9	37.50	9	37.50	--	--	--	--
2	8	33.33	12	50.00	4	16.67	--	--	--	--
3	9	37.50	3	12.50	8	33.33	4	16.67	--	--
4	1	4.17	--	--	3	12.50	15	62.5	5	20.83
5	--	--	--	--	--	--	5	20.83	19	79.17
					mandibular					
1	12	50.00	6	25.00	3	12.50	3	12.50	--	--
2	6	25.00	9	37.50	6	25.00	2	8.33	1	4.17
3	4	16.67	5	20.83	11	45.83	4	16.67	--	--
4	1	4.17	3	12.50	4	16.67	13	54.17	3	12.50
5	1	4.17	1	4.17	--	--	2	8.33	20	83.33

Table 6. Rank order of tooth variability (Coefficient of Variation) by tooth, jaw and dimension (1=largest CV, 5=smallest CV; males only).

jaw	maxilla										mandible									
dimension	mesiodistal					buccolingual					mesiodistal					buccolingual				
source \ tooth	di1	di2	dc	dm1	dm2	di1	di2	dc	dm1	dm2	di1	di2	dc	dm1	dm2	di1	di2	dc	dm1	dm2
Africa_S, Black	1	2	3	4	5	2	1	4	3	5	4	1	2	3	5	2	1	4	3	5
Africa, Kalahari	2	1	4	3	5	1	2	3	4	5	3	1	2	4	5	1	2	3	4	5
AmBlack, TN	3	5	4	2	1	1	2	4	3	5	2	1	3	4	5	1	5	4	3	2
AmWhite, Burl	2	1	4	3	5	3	2	1	4	5	1	2	4	3	5	2	3	1	4	5
AmWhite, MI	3	1	4	2	5	2	1	3	4	5	1	2	3	4	5	1	2	4	3	5
Australia, Warlpiri	3	1	5	2	4	1	2	3	4	5	2	1	4	3	5	3	1	2	4	5
Australia, White	2	1	3	4	5	2	1	3	4	5	1	2	4	3	5	2	1	3	4	5
Dominican	2	3	1	4	5	3	2	1	4	5	3	1	2	4	5	1	2	3	5	4
Iceland	2	1	4	3	5	3	1	2	4	5	2	1	3	4	5	3	1	2	4	5
Japan_1970	5	1	4	3	2	--	--	--	--	--	1	2	4	3	5	--	--	--	--	--
Japan_2000	5	4	2	3	1	--	--	--	--	--	1	2	4	3	5	--	--	--	--	--
Japan, Nagoya	3	1	5	2	4	2	1	4	3	5	1	2	5	3	4	3	2	1	5	4
Japan_Ooshima	1	2	4	3	5	--	--	--	--	--	1	2	3	4	5	--	--	--	--	--
Java, Malay	4	2	1	3	5	3	2	1	4	5	1	2	4	3	5	1	2	3	4	5
India, Gujarat	4	1	5	3	2	4	2	1	3	5	1	2	4	5	3	5	3	2	1	4
India, Jat	1	2	4	3	5	--	--	--	--	--	1	2	3	4	5	--	--	--	--	--
India, Wardha	2	3	1	4	5	1	2	3	4	5	1	3	2	4	5	1	2	3	4	5
Jordan	4	1	2	3	5	2	1	3	4	5	2	1	3	4	5	1	3	2	4	5
Korea, South	4	3	1	2	5	3	2	1	4	5	2	1	5	3	4	1	2	3	4	5
London, Spital	1	2	3	5	4	3	2	1	5	4	1	5	3	2	3	2	4	3	1	5
Pima, NNA	3	2	5	1	4	2	3	1	5	4	1	2	3	4	5	1	4	2	3	5
Melanesia-Nasioi	3	4	5	1	2	3	1	2	5	4	2	1	3	4	5	2	1	3	4	5
Nigeria	4	2	5	3	1	1	2	3	5	4	3	1	2	4	5	2	1	3	4	5
Poland	2	4	3	1	5	2	3	1	4	5	4	3	1	2	5	4	3	2	1	5
Spain, Granada	2	1	3	5	4	3	1	2	5	4	3	1	2	5	4	3	2	1	4	5
Taiwan 1	3	2	1	4	5	3	1	2	4	5	1	2	4	3	5	1	4	3	2	5
Taiwan 2	1	2	5	3	4	1	2	3	4	5	3	1	2	5	4	1	2	3	4	5
Taiwan 3	5	1	2	3	4	--	--	--	--	--	2	3	5	1	4	--	--	--	--	--
Vietnam	3	4	2	1	5	2	3	1	4	5	4	1	3	2	5	1	3	4	2	5

mension (MD and BL) and by jaw exhibit patterns consistent with the hypothesis that deciduous dental variation is mediated by MGF-like mechanisms during development.

Discussion

The conclusion to Kieser's (1990: 88) chapter on odontometric variability states that, "Dental dimensional variability emerges as a complex phenomenon and will probably require a complex synthesis of ideas for its explanation." The multitude and diversity of hypotheses make some models unfalsifiable using variability statistics (from Butler and Dahlberg's fields, Waddington's epigenetic canalization, Osborn's clones, Pengilly's functional relations, and Grigerich's occlusal complexity). These observations relate to the more thoroughly documented variability observed in the permanent dentition, "The honest answer at the moment is that we do not know the exact cause for the observed patterning of odontometric variability in man" (Kieser, 1990: 88).

This investigation of odontometric variability in deciduous teeth yields insight into important yet unresolved issues. The data presented here for patterns of variability in deciduous tooth crown dimensions are mainly in agreement with predictions based on morphogenetic fields as described for permanent teeth. The pattern of variability in deciduous dentition differs in several ways from that described for permanent teeth: a) three fields -- not four -- are sufficient to explain patterns observed, b) incisor variability follows expectation, with one exception, c) second molars are larger and more stable than first molars, and d) a canine field is implied by variability intermediate between incisor and molar teeth.

Though the findings documented in this report have merit they do not allow confirmation of one or another cause for the observed patterning of variability. We can see that deciduous tooth crown variability adheres to patterns of variation predicted by MGFs to explain variability in permanent teeth. The number of samples and their global and ethnic diversity gives these results a broad empirical base, yet several questions remain. The lower lateral incisor MD is more variable than the central, a deviation from expectation. Does this result suggest that lower incisors do not fully adhere to the reversed MGF of lower incisors in permanent teeth? Additional unanswered questions center on patterns of variability across the transition from deciduous to permanent teeth. Is the deciduous second molar more, or less, stable than the first permanent molar? Which is the key or polar tooth in the molar MGF? How does variability in deciduous molars compare with that of their succedent permanent premolar teeth?

A final question regards causality. Mizoguchi (1998), Farmer and Townsend (1993), Kieser (1990), and others point to the timing of dental development as a potential explanation for the observed patterning of variability. Several studies propose that the time a tooth spends in the pre-calcification, or soft tissue stage of development is a potential explanation. Deciduous incisors are longer in pre-calcification and more variable in crown dimensions, while molars have less time in the soft tissues stage and are more stable odontometrically. Differences in form and development between dm1, dm2 and M1 are notable. Deciduous teeth and the permanent first molar are derived from the same primary dental lamina (Bailey, 2014, 2017), and Butler (1956, 1967) noted these differences are to some extent adaptive. "Dm2 has a much shorter period of function than M1, and it operates in a smaller mouth and shorter jaw. It is a deciduous tooth, whereas M1 is a permanent tooth. From a morphogenetic point of view, however, the two teeth belong to the same series, and their differences may be ascribed to position within the series" (Butler, 1967: 1259). Thus, "…it is tempting to see the deciduous second molar and permanent first molar as representing different stages of the same ontogenetic process" (Bailey et al., 2014: 112). In this analysis dm2 is odontometrically the least variable tooth in the deciduous dentition and its development is closely linked to M1 suggesting that dm2 is the polar or key tooth of the meristic molar series (dm2 thru M3) (Smith et al., 1987, 1997).

Conclusions

Patterns of odontometric variability in deciduous tooth crown size are largely consistent with expectations described for permanent teeth. This correspondence is evident in results from three different analyses and is based on a large and diverse sample of populations. Independent studies of metric variation in deciduous tooth crown measurements have interpreted results consistent with the dental morphogenetic field concept. These studies now have further validation and confirmation from the results reported here. Further analysis of deciduous tooth crown variability in relation to morphogenetic field theory is in progress using statistical procedures for meta-analysis and multivariate methods (e.g., principal components analysis).

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