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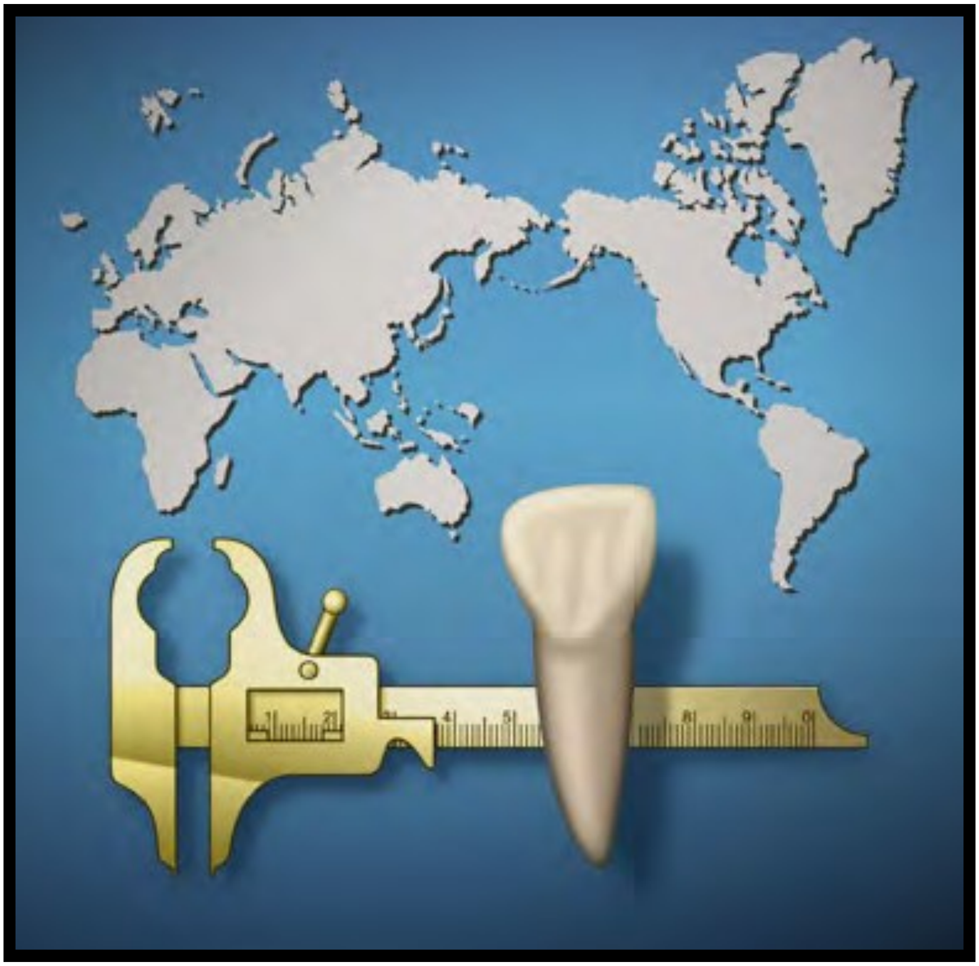

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1400 East Hanna Ave, Indianapolis, IN 46227 U.S.A.
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Department of Anthropology, University of Oregon
Condon Hall, Eugene, Oregon 97403 U.S.A.
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The development of the mammalian dentition as a complex adaptive system

Alan H. Brook[1,2], Toby E. Hughes[1], Grant C. Townsend[1], Richard N. Smith[3] and Matthew D. Brook O'Donnell[4]
[1]*School of Dentistry, University of Adelaide,* [2]*School of Dentistry, Queen Mary University of London*
[3]*Dental School, University of Liverpool,* [4]*Annenberg School for Communication Studies, University of Pennsylvania*

Keywords: Complex Systems, Networks, Dental Development

ABSTRACT General characteristics of Complex Adaptive Systems include self-adaptation and organisation, emergence, multitasking, robustness, critical phases, diversity and compatibility with such statistical models as Thresholds and Scale Free Networks. The aim was to investigate whether dental development exhibits the general and statistical characteristics of a Complex Adaptive System, by examining data on normal and abnormal dental development. The findings were that self-adaptation and organisation occur while interactions between genes, epigenetic and environmental factors lead to the emergence of cells, tooth germs and mineralised teeth. Multitasking occurs as signalling pathways act simultaneously and reiteratively during initiation and morphogenesis. Tooth germs that do not attain a critical threshold during development may undergo apoptosis. Diversity is evident in tooth number, size, shape and mineralisation. Statistical investigation shows that males have significantly larger teeth and higher prevalences of megadontia and supernumerary teeth ($p<0.05$), supporting Brook's Threshold Model which is further developed here to include shape. Image Analysis of tooth dimensions showed they followed a Power Law distribution, with the first 8 of 34 factors in upper lateral incisors accounting for 94.4% of the total variation. In conclusion, the development of the dentition shows the general and statistical characteristics of a Complex Adaptive System.

Complex Systems are widespread in biological systems and communities. Interacting adaptive entities produce dynamic patterns and structure. In a biological complex adaptive system the interaction of lower level components leads to the emergence of high level phenomena and structures. Such systems have the general characteristics of self-adaptation, self-organisation, emergence, multitasking, robustness, critical phases, diversity and compatibility, with such statistical properties as Thresholds and Scale Free Networks (Barabasi, 2003; Camzine et al., 2003; Mitchell, 2009). The aim of this study was to investigate whether development of the dentition exhibits the general and statistical characteristics of a Complex Adaptive System by examining data on normal and abnormal dental development.

DENTAL DEVELOPMENT

Key characteristics of dental development are that it is multi-levelled, has multiple interactions, is multi-factorial, is multidimensional and is progressive over time (Brook, 2009). The core components of this process are summarised in Table 1 and are illustrated in Figure 1.

THE DENTITION AS A COMPLEX SYSTEM

The next step is to examine the components of dental development against the key characteristics of complex systems.

Self-organisation and emergence are evident as tooth germs emerge from molecular level interactions (Lesot and Brook, 2009)and then progressively develop and grow in size and shape until they commence calcification and form mature teeth. The initiation of tooth germs occurs at specific sites within a field and they progress to form different shapes and sizes, so that the calcified macroscopic teeth which emerge are discrete but organised into groups that have different shapes and functions around the dental arch.

Correspondence to:
Alan Brook, School of Dentistry, University of Adelaide,
Adelaide, South Australia, 5005
Email: alan.brook@adelaide.edu.au
Telephone: +61 (0)8 8313 2910

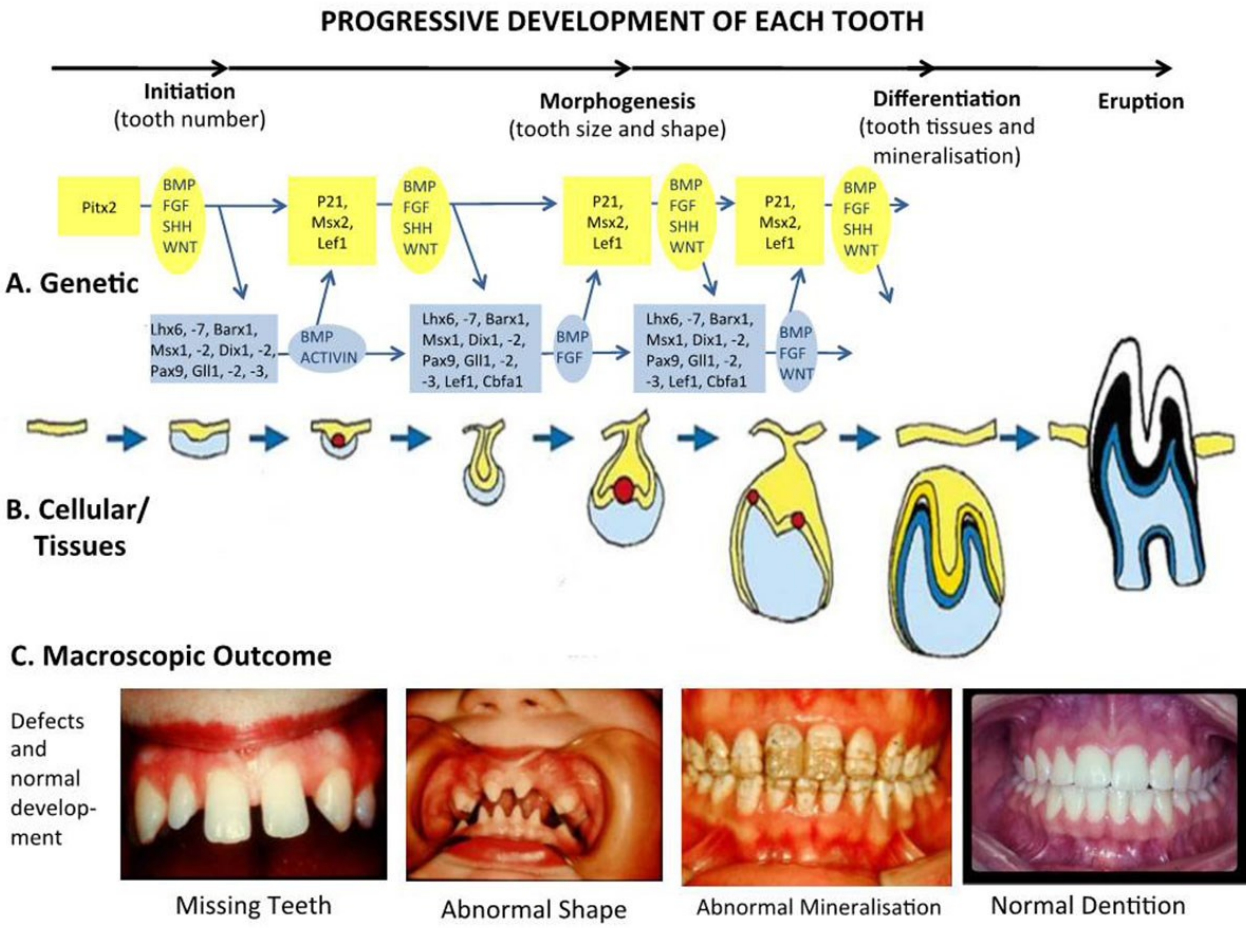

Fig. 1. The multilayered developmental process of tooth formation illustrating the molecular changes within the cells and tissues and the macroscopic outcomes (part of figure from http://bite-it.helsinki.fi/).

TABLE 1. The key characteristics and components of dental development

Characteristic	Components
Multilevel	Mature tooth Cells, tissues, tooth germs Molecular
Multiple interactions	Tooth germ – Tooth germ Cell – Matrix Cell – Cell Gene – Epigenetic – Environment Gene – Gene
Multifactorial	Environmental – local / systemic Epigenetic – narrow / broad Over 300 genes
Multidimensional	Spacial – x, y, z dimensions Time
Progressive over time	Each dentition Tooth type / morphogenetic field Each tooth

The outcome is an integrated, balanced, complex system. It is a major characteristic of a complex system that the mature units bear no resemblance to the precursor entities.

Self-Adaptation is demonstrated by the within -species and between-species diversity that is found. In humans, variations in the number, size, shape and mineralisation of teeth occur frequently (Brook et al., 2009; Townsend et al., 2009). Between species variation in these parameters is also extensive (Hillson, 1986).One of the factors to consider is the adaptive interaction that can occur between developing tooth germs, with the timing of development of each being important. Timing is also significant in the critical phases of dental development. For progression from the initial phase to morphogenesis (Fig. 1), transcription factors in the Msx, Dlx and Lhx families are required. The tooth germ may undergo apoptosis if this progress does not occur at this critical time. Similarly, if the matrix proteins are not removed during enamel calcification, defects in mineralisation result.

Robustness in the development of the dentition comes from the satisfactory functioning of the system even in the presence of variations and moderate developmental defects. Mature teeth have some ability to self-repair and continue to develop in response to environmental challenges, a property akin to self-awareness. This robustness is also associated with excess capacity: genes are switched on and off and function reiteratively in multiple tissues; genes can also be up-regulated, down-regulated and, if their function is defective, other genes sometimes function to produce the necessary product; genes in function can be alternatively spliced and the products varied in amount and nature.

Multitasking adds to this robustness as signalling pathways act simultaneously and reiteratively. Similarly, the ameloblasts control the secretion and later removal of the enamel matrix proteins, as well as the deposition of the minerals.

STATISTICAL MODELS

Based on epidemiological and clinical data, Brook (1984) developed a model to explain the relationship between the prevalence of dental anomalies of number and size. This model is based on a normal distribution on which thresholds are superimposed beyond which microdontia, hypodontia, megadontia and supernumerary teeth occur. Here the model is further developed to include shape (Fig. 2). As tooth size moves closer to the thresholds that determine variation in tooth number, teeth tend to display abnormal shape as well as size. An example is the diminutive perma-

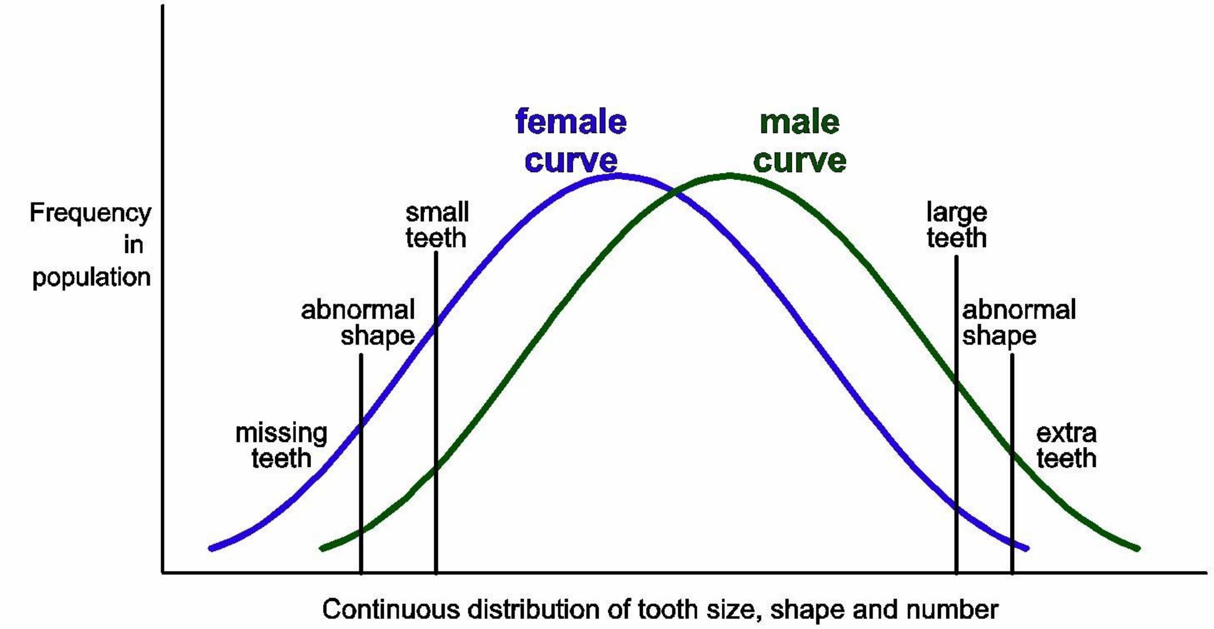

Fig. 2. This development of the Threshold Model of Brook (1984) now incorporates the shape changes seen at the extremes of tooth size.

nent upper lateral incisor which is often 'peg-shaped' as well as being very small. The developmental process underlying these clinical findings and modelling has been elucidated in molecular genetics and histological studies (Brook, 2009; Lesot and Brook, 2009).

The Scale Free Network model reflects findings that when the frequencies of each of the components in some systems are plotted, the result is a Power Law Distribution (Fig. 3).

This distribution occurs when a few components occur with a high frequency and the large majority occur with lower frequency. In a Principal Component Analysis of 34 dimensions in upper incisor teeth, 94 per cent of the total variance was accounted for by 7 dimensions (Khalaf et al., 2009), thereby displaying the properties of a Scale Free Network.

CONCLUSIONS

The dentition exhibits the characteristics of a Complex Adaptive System, both in development and in its mature form. During evolution it has become adapted to different environments. It serves as a valuable model for investigating how genetic, epigenetic and environmental factors interact during somatic development.

ACKNOWLEDGMENTS

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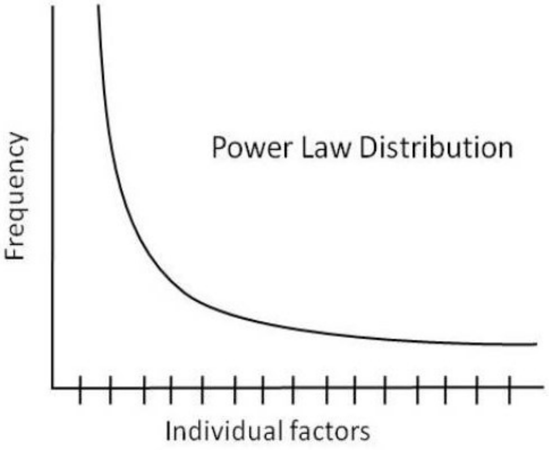

Fig. 3. A typical power law distribution where a few factors occur frequently in a system

Geographic patterns of Early Holocene New World dental morphological variation

Christopher M. Stojanowski[1], Kent M. Johnson[1], William N. Duncan[2]

[1] *Center for Bioarchaeological Research, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287*
[2] *Department of Sociology and Anthropology, East Tennessee State University, Johnson City, TN 37614-1702*

Keywords: New World, Dental Morphology, Paleoindian, Paleoamerican

ABSTRACT Dental anthropology played a seminal role in early studies of the peopling of the New World, and was a foundation of the early three wave model proposed by Greenberg, Turner and Zegura. In recent years, however, developments in anthropological genetics, craniometry, and archaeological discoveries have largely omitted dental anthropology from debates regarding Native American origins. Here we consider this situation and reassert dental anthropology's relevance to the topic by presenting an inter-individual analysis of Paleoindian and Paleoamerican dentitions. A small set of dental morphological variables was used to estimate Gower similarity coefficients between individual specimens. The resulting similarity matrix was ordinated using multidimensional scaling; all analyses were performed in Clustan v. 7.05. While results should be considered preliminary, patterns of variation suggest morphological similarity along both coasts of North and South America with a somewhat distinct grouping of North American Paleoindians deriving from more inland portions of the continent. This pattern is consistent with recent genetic scenarios, notably the bicoastal model presented by O'Rourke and Raff (2010), which indicates that Paleoindians may have taken multiple migration routes from Beringia, moving along both coasts as well as through the ice free corridor. Future studies may build on this work to reintegrate dental data and analysis into research concerning the peopling of the New World.

Dental morphology played a key role in the development of the tripartite model of New World population origins (Greenberg et al., 1985, 1986; Turner, 1971, 1983, 1984, 1985a, b, 1986). While this model still provides a viable explanation for the settlement of the Western Hemisphere (Estrada-Mena et al., 2010; Reich et al., 2012), recent advances in anthropological genetic sampling protocols, amplification techniques, and analytical approaches have provided more nuanced understandings of New World population structure. These include models that propose a single origin from an Asian source population isolated in Beringia prior to colonization of the Americas (Estrada-Mena et al., 2010; Fagundes et al., 2008; Kitchen et al., 2008; Mulligan et al., 2008; Schroeder et al., 2007, 2009; Tamm et al., 2007; Wang et al., 2007), dual origin models (Gilbert et al., 2008; Rasmussen et al., 2010), and more complex scenarios involving one or more migrations from a heterogeneous source population – possibly via different migration routes – followed by bidirectional gene flow between Asia and the Americas that lasted several thousand years (González-José and Bortolini, 2011; Kumar et al., 2011; Mazières, 2011; O'Rourke and Raff, 2010; Perego et al., 2009, 2010; Ray et al., 2010; Rubicz et al., 2010; Tamm et al., 2007). In addition, recent archaeological discoveries have largely supplanted the "Clovis First" model which dominated Paleoindian research for several decades (e.g., Adovasio and Pedler, 2004; Dillehay, 1997; Goebel et al., 2008; Waters et al., 2011) and which coincided strongly with the predictions of the tripartite model. Discoveries of Early Holocene skeletal material from South America, combined with advances in phenotypic data analysis better grounded in evolutionary processes, have also generated new views on the peopling of the Americas (e.g., de Azevedo et al., 2011; Gonzalez et al., 2010; González-José and Bortolini, 2011; González-

Correspondence to:
Christopher M. Stojanowski
900 S. Cady Mall
School of Human Evolution and Social Change
Arizona State University
Tempe, AZ 85287
cstojano@asu.edu

José et al., 2001, 2008; Mena L. et al., 2003; Neves et al., 2004, 2005; Perez et al., 2007, 2009; Pucciarelli et al., 2003, 2006, 2008, 2010).

Despite the historical importance of dental anthropology in the First Americans debate, recent synthetic surveys of the literature (e.g., Dillehay, 2009; Fiedel, 2004; Goebel et al., 2008; González-José and Bortolini, 2011; Mazières, 2011; O'Rourke, 2011; O'Rourke and Raff, 2010; Pitblado, 2011) indicate that dentition has lost its relevance in these discussions. In fact, the most recent literature review fails to include a single citation for papers using dental morphology as a basis for inferring New World population history (Pitblado, 2011). There are many reasons why this may be. However, one inescapable fact is that genetic, archaeological, and craniometric specialists have adopted new research approaches and methods over the last decade, including more sophisticated types of data capture and analysis, which increase the specificity and nuance of their interpretations. This is evidenced by the incorporation of inferential analyses that access more complex evolutionary models in the analysis of phenotypic size and shape. Dental anthropology on the other hand has largely maintained a focus on population-based frequency analyses and, in particular, the sinodont/sundadont dichotomy (see Turner, 1990).

Our purpose here is not to engage existing debates about the utility of the sinodont/sundadont model or the relationship between specific Paleoindian or Paleoamerican specimens and the morphological complex associated with sinodonty or sundadonty (e.g., Chatters, 2000; Haydenblit, 1996; Lahr and Haydenblit, 1995; Powell, 1993, 1995, 2005; Sutter, 1997, 2005; Turner, 2002). Here, we adopt a more paleontological focus that recognizes the relative dearth of existing Early Holocene material from North and South America and the singleton status of much of the North America Paleoindian record. Our primary goal in this paper is to move the field forward by demonstrating that fragmentary specimens and small data sets can be used to consider hypotheses about the temporal and spatial structure of New World phenotypic variation using a research approach distinct from frequency-based assessments. We make no claims that one approach is necessarily better than the other. We only demonstrate the potential of different approaches for complementing one another and engaging new models of interpretation that add nuance to the literature.

MATERIALS AND METHODS

Using existing morphological data, our purpose in this paper is to determine whether Early Holocene (Paleoindian and Paleoamerican) inter-individual dental morphological variation is geographically structured. That is, we consider whether inter-individual patterns of affinity reproduce geographic spatial structure, and if so, whether dental variation corresponds with recent hypothesized migration scenarios into the New World, such as the bi-coastal model proposed by O'Rourke and Raff (2010), which accommodates multiple, possibly contemporaneous migration routes from Beringia through the ice-free corridor and along both coasts. We mined published raw dental morphological data from confirmed Paleoindian and Paleoamerican dentitions (see Chatters, 2000; Jenks, 1937; Owsley et al., 2010; Potter et al., 2011; Powell and Rose, 1999; Turner, 1992; Young, 1988) and verified the Early Holocene age of these specimens (> 7500bp). These data are summarized in Table 1. Raw trait scores were used to generate inter-individual similarity statistics using Clustan v. 7.05 (Wishart, 2004). Gower coefficients were used because they allow for missing data (obviating data imputation) and mixed scale data types (ordinal and binary). Similarities were ordinated and visualized using multidimensional scaling in two dimensions set at 500 runs and iterations. Variables were removed from the final analysis based on frequency of observation (variables that were too sparse were removed) and if the variable demonstrated insufficient trait score variability among individuals. Those variables that demonstrated no inter-individual variation or were autapomorphic were removed from the raw dataset prior to the calculation of similarities. In addition, traits that were clearly redundant (for example, Carabelli's scores for maxillary M1s and M2s) were reduced, where the trait that was kept was largely decided based upon data density rather than notions of key tooth representation. Individual Paleoindian or Paleoamerican dentitions were omitted if they preserved too few recorded scores, although we note the rarity of North American specimens required more consideration of trait exclusion to maximize the coverage of the

TABLE 1. Early skeletal remains from North and South America[a]

Sample/site	Age (^{14}C years BP)	*N*
North American skeletal remains included in the present analysis		
Warm Mineral Springs, FL	10260 +/- 190	1
Arch Lake, NM	10220 +/- 50; 8870 +/- 40	1
Horn Shelter, TX	9875 +/- 110 (average)	2
Gordon Creek, CO	9455 +/- 110 (average)	1
Tehuacán Valley (Tc50), Mexico	ca. 8500-7000	1
Kennewick, WA	8410 +/- 60 (average)	1
Pelican Rapids, MN	7840 +/- 70	1
Additional North American skeletal remains not included in the present analysis		
Upward Sun River, AK	~11500	1
Arlington Springs, CA	10960 +/- 110; 10080 +/- 810; 10000 +/- 310	1
Peñón Woman III, Mexico	10755 +/-75	1
Anzick, MT	10680 +/- 50 (average)	2
Buhl, ID	10675 +/- 95	1
Wilson-Leonard, TX	10500-10,000	1
Chimalhuacán, Mexico	ca. 10500	1
Mostin, CA	10470 +/-490	1
Tlapacoya I, Mexico	10200 +/-65	1
Marmes, WA	10130 +/- 300; 9840 +/-300; 9820 +/-300	3
Midland, TX	ca. 10000	1
White Water Draw, AZ	10000-8000	1
J.C. Putnam, TX	-[b]	1
49-PET-408 (On Your Knees Cave), AK	9730 +/- 40 (average)	1
Grimes Point Burial Shelter, NV	9470 +/-60	1
Spirit Cave, NV	9415 +/- 25 (average)	1
Wizard's Beach, NV	9225 +/- 60 (average)	1
Browns Valley, MN	9049-8790 +/- 110/82	1
La Brea, CA	9000 +/- 80	1
Metro Balderas, Mexico	ca. 9000	1
Cueva de Tecolote, Mexico	ca. 9000-7000	1
Koster (Horizon 11), IL	ca. 8500	9
Renier, WI	ca. 8500-6000	1[c]

TABLE 1., Cont'd

Fishbone Cave, NV	8370 +/- 50; 8220 +/- 50	1
La Jolla, CA	8350 +/-90	2
Gore Creek, BC	8250 +/- 115	1
Hourglass Cave, CO	8170 +/-100; 7944 +/-84; 7714 +/-77	1
Stick Man, WA	8125 +/-50 (average)	1
Windover, FL	8120-6990	168
L'Anse Amour, Labrador	7530 +/-140	1
Texcal Cave, Mexico	7480 +/-55	1
Shifting Sands, TX	-	1
<u>South American skeletal remains included in the present analysis</u>		
Cerca Grande 6 and 7, Lagoa Santa, Brazil	ca. 11000-8000	44
Cuchipuy, Chile	8070-6105; ca. 8000-6000	3
<u>Additional South American skeletal remains not included in the present analysis</u>		
Lapa Vermelha IV (Luzia), Brazil	11680 +/-500 – 10200 +/-220; 9330 +/-60 (minimum age)	1
Pampa de Fosiles 13, Peru	10250 +/-180	2
Sueva 1, Colombia	10090 +/-90	1
Quiqche Cave Tomb 1, Peru	9940 +/-200[d]	1
Toca dos Coqueiros, Brazil	9870 +/-50	1
Tequendama, Colombia	9740 +/-135	9
Toca da Janela da Barra do Antoniao, Brazil	9670 +/-140	1
Santana do Riacho Burial XII, Brazil	9460 +/-110	1
Guavio 1, Colombia	9360 +/-45	1
Piuquenes Cave, Chile	8990 +/-40	3
Acha-2 and Acha-3, Chile	8970 +/-255	5
Baño Nuevo-1 Cave, Chile	8890 +/-90; 8880 +/-50; 8850 +/-50	5
Capelinha Burial II (Luzio), Brazil	8860 +/-60	1
Santo Domingo Tomb 1, Peru	8830 +/-190	1
Pali Aike, Chile	ca. 8800	4
Santana do Riacho, Brazil	8280 +/-40; 8185 +/-110	40
Las Vegas, Ecuador	8250-6600	192
Huentelauquén-2, Chile	8080 +/-70	1
Intihausi, Argentina	8060 +/-100; 7970 +/-100	6

TABLE 1., cont'd

Tres Ventanas Tomb 1, Peru	8030 +/-130	1
Sumidouro Cave, Lagoa Santa, Brazil	>8000	29
Monte Hermoso 1-2, Argentina	7866 +/-75	1
Arroyo Seco, Argentina	7805 +/-85 – 7580 +/-50	5
Checua, Colombia	7800 +/-60 – 6800 +/-40	4
Santo Domingo Tomb 2, Peru	7740 +/-85	1

a References for early American skeletal remains are listed in Stojanowski et al. (2013).
b Associated with stratum thought to date to the Late Pleistocene (Young 1988).
c The small quantity of calcined bone fragments is suggestive of a single individual (Mason and Irwin 1960).
d Date is from the level underlying the skeletal remains.

Fig. 1. Map of North and South American showing the location of Paleoindian and Paleoamerican specimens used in this analysis: 1. Arch Lake; 2. Gordon Creek; 3. Horn Shelter No. 2; 4. Kennewick; 5. Pelican Rapids; 6. Tehuacán (Tc50-2); 7. Warm Mineral Springs; 8. Cuchipuy; 9. Lagoa Santa.

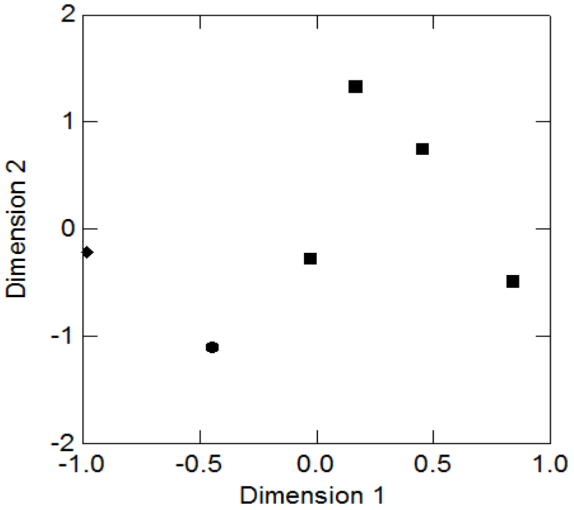

Fig. 2. Multidimensional scaling of Gower similarity coefficients calculated from eight dental morphological traits for confirmed North American Paleoindians. Icons represent geographic divisions: circle = western North America (Kennewick), square = central North America, diamond = eastern North America (Warm Mineral Springs).

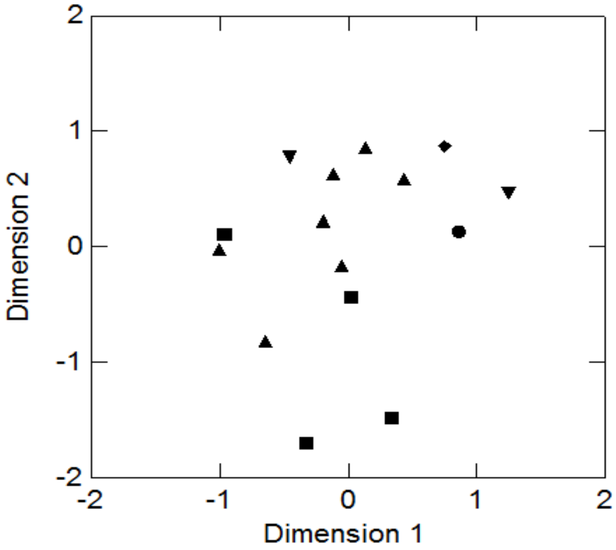

Fig. 3. Multidimensional scaling of Gower similarity coefficients calculated from six maxillary dental morphological traits for confirmed North and South American Paleoindians and Paleoamericans. Icons represent geographic divisions: circle = Mexico, diamond = eastern North America, square = central North America, upward triangle = eastern South America, downward triangle = western South America.

continent so that assessments of geographic structure were possible.

RESULTS

Because the majority of South American dentitions lacked paired maxillae and mandibles we first consider patterns of inter-individual variation among North American Paleoindian specimens. Despite the number of possible Paleoindian specimens (see Table 1) we were only able to include data from six individuals: Pelican Rapids, Gordon Creek, Warm Mineral Springs, Arch Lake, Horn Shelter 2, and Kennewick. These six dentitions range from Washington to Florida with most samples deriving from the middle of the continent (Figure 1). Based on data preservation, we included eight dental morphological traits in the calculation of Gower similarity coefficients (UI1 shoveling, UM1 hypocone, UM1 Carabelli, UM1 enamel extension, UP1 root number, UM2 root number, LM2 cusp number, and LM2 root number). Results of the multidimensional scaling are presented in Figure 2. There is some evidence for geographic patterning. For example, the four central North American samples (non-coastal) form a weak cluster in the upper right quadrant while both coastal samples plot in the negative half of both axes. This could be consistent with a single population bifurcating and migrating quickly down the Atlantic and Pacific coasts of North America with a distinct population colonizing the middle of the continent.

Inclusion of South American Paleoamerican dentitions required using only six maxillary traits (UI1 shoveling, UM1 hypocone, UM1 Carabelli, UM1 enamel extension, UP1 root number, and UM2 root number). The sample included the same Paleoindian specimens as above (with the exception of Kennewick which had to be excluded), a single individual from Mexico (Tehuacán Tc50-2), two individuals from western South America (Cuchipuy), and seven individuals from eastern South America (Lagoa Santa). Results are presented in Figure 3. Although the clustering tendency was more abstract there does appear to be some geographic patterning evident in this figure. For example, the dentitions from western South America, eastern South America, Mexico, and eastern North America dominate the positive half of the dimension two axis, while dentitions from non-coastal North American Paleoindians dominate the negative half of the dimension two axis. Another way to consider this is that coastal samples from both North and South America cluster in the positive half of the dimension two axis while interior samples (all from North America) plot in the negative half of the dimension two axis. Remarkably, the overall pattern of variation does not change with the addition of South American data. These analyses, therefore, may reflect a possible bi-coastal migration of Early Holocene populations along both the Pacific and Atlantic coasts of North and South America with a somewhat distinct population inhabiting the interior of North America (perhaps involving the ice-free corridor), consistent with O’Rourke and Raff’s (2010) model.

CONCLUSION

Recent advances in archaeology, anthropological genetics, and human craniometry have enhanced our understanding of New World population origins and migration dynamics within the Western Hemisphere. For a variety of reasons, dentition has figured less prominently in recent First American debates to the point that the most recent literature review of this expansive literature ignores dentition entirely (Pitblado, 2011). This is unfortunate. Here we have tried to demonstrate that a specimen-specific approach to Paleoindian and Paleoamerican dental morphology may have some merit. In particular, using a small series of dentitions and morphological traits our results suggest a similar dental phenotype among coastal populations of the Early Holocene New World with a somewhat distinct morphology among central, non-coastal North American dentitions. Here, we have emphasized population structure and evolution as the primary explanatory mechanism; however, differential selection pressures related to distinct coastal/inland diets should also be considered. In closing, we want to stress how preliminary these results are. As indicated in Table 1 there is now an abundance of Paleoindian and Early Archaic period sites and specimens in the Americas and our analyses utilize only a small number of traits for a small number of individuals. Nevertheless, we hope our results show enough promise to justify a more comprehensive survey of dental morphology in these specimens, including the use of recent developments in three-dimensional data capture and incorporation of evolutionary developmental principles in the assessment of evolutionary signatures of human dentition.

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A fool's mission? A test of three common assumptions in dental metric analyses

Brian E. Hemphill
Department of Anthropology, 405A Bunnell Hall, University of Alaska, Fairbanks, Fairbanks, AK 99775-7720

Keywords: Morphogenetic Fields, Ontogenetic Canalization, Sex Dimorphism

ABSTRACT Three aspects of metric variation in the permanent dentition of humans are often simply accepted as true. The first is that formation of the permanent dentition occurs within morphogenetic fields broadly associated with tooth type and jaw. The second is that dental development of among females is characterized by a higher degree of ontogenetic buffering relative to males. The third is that expression of sex dimorphism in permanent tooth size is expressed uniformly among well-nourished human populations. This study tests these assumptions through an examination of mesiodistal and buccolingual dimensions of all non-canine permanent teeth, except third molars, among 2,709 living individuals of 15 ethnic groups from South Asia. With sexes pooled, only one in four contrasts of variance among key versus distal teeth within dental fields are significantly heterogeneous, while one in four contrasts yield higher levels of variance among key teeth relative to their distal counterparts within a dental field. Such results weaken considerably orthodox applications of Butler's dental field theory. When samples are the unit of analysis, male samples are marked by fewer dental fields with significantly heterogeneous levels of variance between key and distal members, while males and females are affected equally by significantly heterogeneous variation between key and distal members when dental fields are the unit of analysis. Such results suggest males and females are equally buffered against environmental perturbations that affect odontometric variation. One-way ANOVA indicates that a tooth's position within a dental field accounts for 15.5% to 23.1% of the observed variation in tooth size, while two-way ANOVA reveals that when sex is added as a second factor, the percentage of variance in tooth size explained increases from 16.7% to 30.8%, an improvement of 27.2%. Such results indicate sex dimorphism in tooth size varies in both patterning and in magnitude among these samples, thereby explaining why discriminant functions developed for one population often perform more poorly when applied to other populations.

Over the last 70 years a consensus has emerged that dental development in humans is characterized by a series of developmental fields that correspond broadly to tooth type by jaw (Butler 1939; Dahlberg 1945, 1951), that odontogenesis is marked by a greater degree of developmental buffering, or "canalization," among females relative to males (Garn et al. 1965, 1966; Nichol et al. 1984; Niswander & Chung 1965), and that expression of sex dimorphism is uniformly expressed across adequately nourished human populations (Kieser et al. 1985). This study tests these assumptions through assessment of mesiodistal and buccolingual dimensions of all non-canine permanent teeth except third molars among 2,709 living individuals of 15 ethnic groups from South Asia.

MATERIALS AND METHODS

Dental casts were collected from 2,709 living individuals with informed consent of 15 ethnic groups from the Hindu Kush/Karakoram Highlands of northern Pakistan, the northern periphery of the Indus Valley of Pakistan, Gujarat State of northwestern peninsular India, and Andhra Pradesh State of southeastern India (Fig. 1). Of these, some 2,455 individuals (1,087 Females, 1,368 Males) are represented by casts for both upper and lower dentitions. Mesiodistal tooth lengths and buccolingual tooth breadths were measured for all teeth, except third molars using standard odentometric procedures (Moorrees, 1957). Kolmogorov-Smirnov tests were used to determine whether

Correspondence to: Brian Hemphill, Department of Anthropology, 405A Bunnell Hall
University of Alaska, Fairbanks, AK 99775-7720
bhemphill@alaska.edu

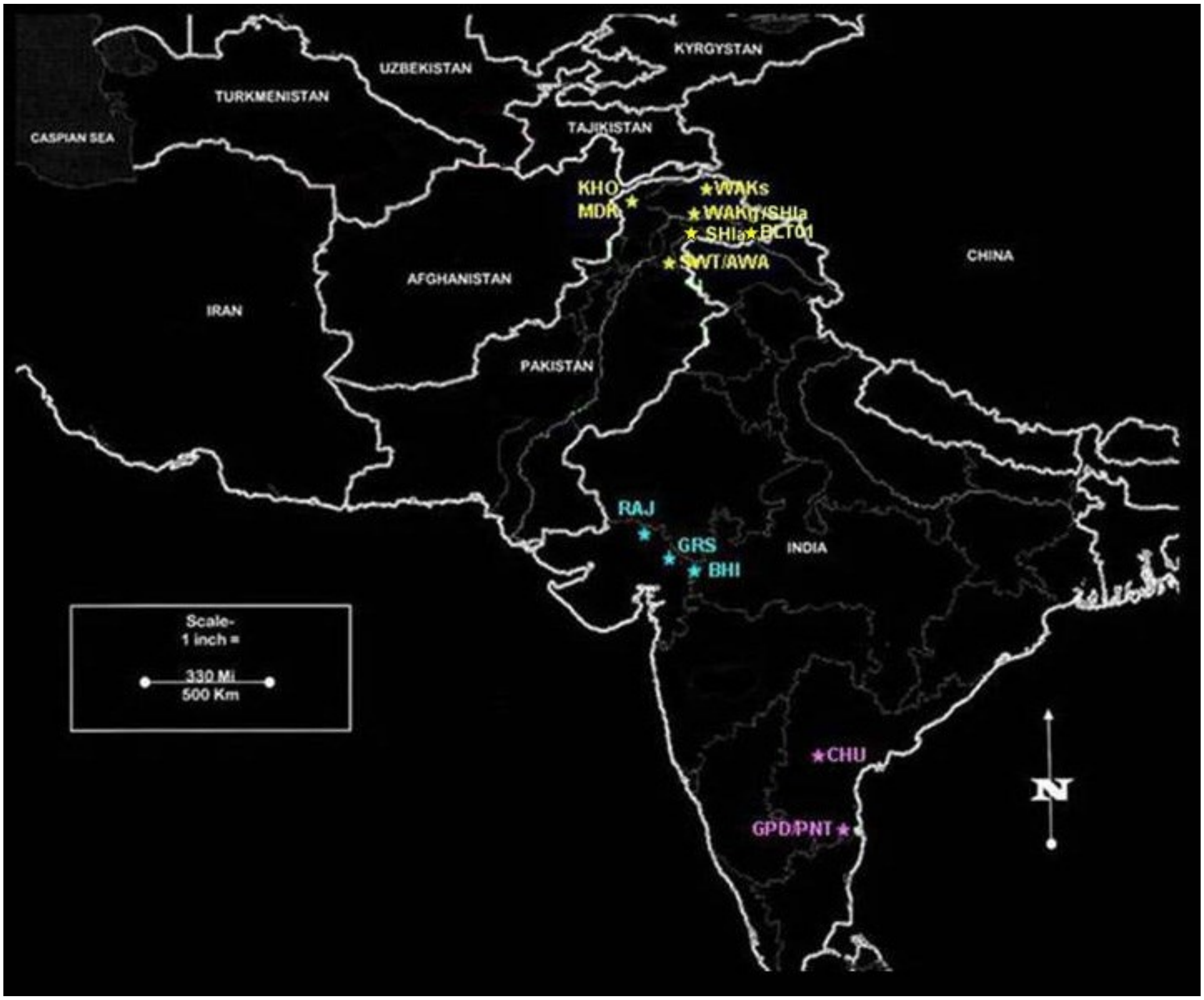

Fig. 1. Location of the samples used in the study. Abbreviations are from Table 1.

variable distributions by sex and by sample depart significantly from normality. Antemortem tooth loss, dental pathology and casting defects preclude some measurements from being collected. EM estimation (Dempster et al., 1977) was used to estimate missing values by sex and by sample. No more than three of the 28 variables (10.7%) were estimated by individual. Teeth within incisor, premolar and molar dental fields were separated into "key" and "distal" members by jaw. Standard descriptive statistics were calculated for each variable. Heterogeneity of variance between key and distal members was tested with Bartlett's chi-square (Snedecor and Cochran, 1989) and variances were compared to test for the expected pattern of higher variance for the distal member within each morphogenetic field, except for the mandibular incisors for which Dahlberg (1945, 1951) maintained that the morphogenetic field was reversed, such that LI2 is considered the key tooth and LI1 the distal tooth. One-way ANOVA was used to test for the impact of position within a dental field upon tooth size in both sex-pooled and sex-segregated samples by ethnic group. Sex-pooled samples were further tested with two-way ANOVA to determine the impacts of position and sex by ethnic group. Relative contributions of sex to position were rank ordered to illustrate differences between samples in the expression of sex dimorphism.

RESULTS

Kolmogorov-Smirnov tests reveal that mesiodistal lengths and buccolingual breadths for males and females of all 15 samples are distributed normally. Of the 2,455 individuals represented by

TABLE 1. Samples used in the study

Region[1]	Abb.	Group	Locality	Raw_N	Females	Males	Ne	Ne/Raw_N	n	Pct.	n	Pct.	n	Pct.	n	Pct.
NIVP	AWAm	Awan	Mansehra	172	40	110	150	87.2	19	12.7	47	31.3	71	47.3	107	71.3
NIVP	SWTm	Swati	Mansehra	215	68	103	171	79.5	35	20.5	63	36.8	93	54.4	118	69.0
HK	BLT01	Balti	Partuk	184	80	76	156	84.8	28	17.9	53	34.0	84	53.8	119	76.3
HK	MDK	Madakla	Madaklasht	192	94	80	174	90.6	70	40.2	102	58.6	131	75.3	147	84.5
HK	SHIa	Shina	Astore	164	59	83	142	86.6	78	54.9	92	64.8	115	81.0	119	83.8
HK	SHIg	Shina	Gilgit	106	54	50	104	98.1	83	79.8	86	82.7	95	91.3	98	94.2
HK	WAKg	Wakhi	Gulmit	149	62	57	119	79.9	59	49.6	73	61.3	92	77.3	98	82.4
HK	WAKs	Wakhi	Sost	190	67	72	139	73.2	61	43.9	73	52.5	98	70.5	106	76.3
HK	YASa	Yashkun	Astore	175	64	81	145	82.9	43	29.7	66	45.5	94	64.8	110	75.9
SE	CHU	Chenchu	Andhra Pra-	196	86	109	195	99.5	129	66.2	158	81.0	178	91.3	187	95.9
SE	GPD	Madiga	Andhra Pra-	177	78	96	174	98.3	82	47.1	131	75.3	155	89.1	162	93.1
SE	PNT	Pakanati	Andhra Pra-	184	82	99	181	98.4	109	60.2	145	80.1	166	91.7	170	93.9
NW	BHI	Bhil	Gujarat	208	105	103	208	100.0	152	73.1	172	82.7	189	90.9	200	96.2
NW	GRS	Garasia	Gujarat	207	99	108	207	100.0	136	65.7	178	86.0	190	91.8	198	95.7
NW	RAJ	Rajput	Gujarat	190	49	141	190	100.0	114	60.0	156	82.1	172	90.5	189	99.5
TOTAL				1162	499	656	1155	99.4	1198	48.8	1595	65.0	1923	78.3	2128	86.7

[1]. Region abbreviations are as follows: NIVP (Northern Indus Valley Populations), HK (Hindu Kush highlands), SE (Southeastern Peninsular India), NW (Northwestern Peninsular India).

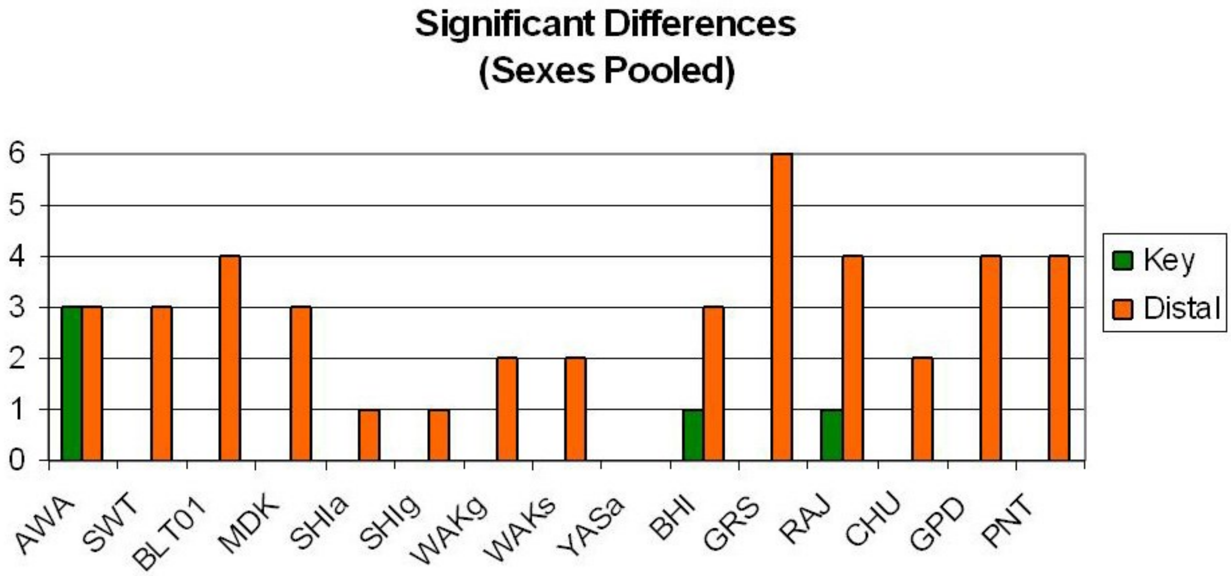

Fig. 2. Number of significant differences in variance between key and distal members of a dental field by position with sexes pooled.

casts for both dentitions only 1,198 (48.8%) are represented by all 28 variables. Estimation of missing values improved the number of individuals with complete data from 1,595 (65.0%), to 1,923 (78.3%), to 2,128 (86.7%) when 1, 2, and 3 variables were estimated, respectively (Table 1).

Bartlett's chi-square reveals that just over one-fourth (47/180= 26.11%) of contrasts of variance between key and distal members of a dental field exhibit significant heterogeneity of variance. The number of significant differences by sample averages 3.13 out of the 12 fields (26.08%) and ranges from a high of six fields among Awans and Garasias to a low of zero among the Yashkuns of Astore. When instances of significant heterogeneity of variance within dental fields are examined to determine whether this heterogeneity is driven by higher variance in key teeth versus higher variances in distal teeth, expectations of dental field theory are resoundingly confirmed. As expected, the vast majority (42/47= 89.36%) of cases involve higher variance for the distal member of a dental field (Fig. 2). In fact, instances of significantly higher variances among key teeth occur among members of only three of the ethnic groups considered here. These include Awans, Bhils, and Rajputs.

A situation in which the amount of variance among key members of a dental field exceed that found among their distal counterparts represents a reversal of dental field theory expectations. Examination of levels of variance reveals some 46 instances of reversal, accounting for just over one-fourth of all comparisons (46/180= 25.56%). The number of reversals runs from a high of seven (58.33%) among Shinas from Gilgit (SHIg) to lows of a single reversal among Garasias (GRS) and Gompadhomptis Madigas (GPD) (Fig. 3). Further examination indicates that while all non-canine dental fields of both jaws are affected, reversals are by far most common among the mandibular incisors (LI2>LI1) where two-thirds of all contrasts yielded reversals (20/30= 66.7%). Reversals are also common among mandibular molars (9/30= 30.0%), are less common among maxillary incisors (6/30= 20.0%) as well as among mandibular (5/30= 16.67%) and maxillary premolars (5/30= 16.67%), and are rarest among maxillary molars (1/30= 3.33%).

Analysis of variance indicates that position within a dental field contributes substantially to the percentage of variance explained in tooth size (Fig. 4). Across all 15 samples position alone accounts for nearly 20% of the variance in tooth size within a dental field, ranging from highs of 23.08% and 22.92% among Bhils and Chenchus to a low of 15.47% among the Wakhis of Gulmit.

Bartlett's chi-square (Fig. 5) reveals that males are marked by a fewer number of dental fields with significantly heterogeneous levels of variance

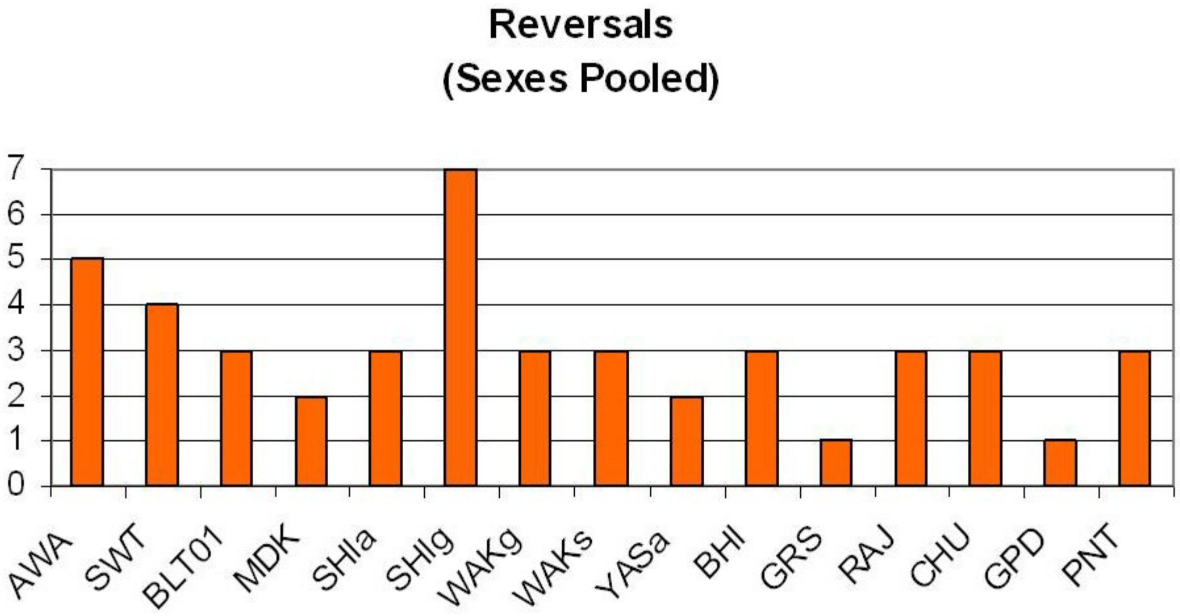

Fig 3. Number of reversals in relative variance between key and distal members of a dental field with sexes pooled.

between key and distal member, for significant heterogeneity occurs in only three of the 15 samples (20.0%), while females are marked by equivalent or higher numbers of reversals in 12 of the 15 samples (80.0%). When heterogeneity of variance is considered by dental field across all samples, Bartlett's chi-square identifies 68 of 360 (18.89%) contrasts as exhibiting significantly heterogeneous levels of variance. Of these, 35 occur among males and 33 occur among females, indicating that males and females are marked by nearly identical numbers of significantly heterogeneous contrasts with regard to variance.

Examination of the patterning of variance among key and distal teeth within dental fields reveals that somewhat more than one-fourth (99/360= 27.5%) are marked by a reversal in which variance is greater among key teeth than their distal counterparts (Fig. 6). When considered by sex, males are more often affected by reversals (31.11%) than females (23.89%). In fact, males exhibit a marked increase (30.23%) relative to that observed among females. When considered by sample, reversal prevalence is greater among males for only six of the 15 samples. This means that, contrary to expectations, males more often exhibit variance reversals than females overall, while in marginal support of expectations, females have a higher or equivalent number of dental fields marked by variance reversals than males in nine (60%) of the 15 samples.

Analysis of variance has already indicated that a tooth's position within a dental field accounts for 15.5% to 23.1% of the variance in size across the 15 samples (Fig. 4). When this relationship is further explored by sex it is clear the influence of sex on the relative size of key and distal members within dental fields differs markedly (Fig. 7). In 11 samples, the average contribution of position is greater among females, while in the remaining four the contribution is greater among males. In some samples, such as the Awans (4.82%) Swatis (6.3%) and Baltis (4.74%) this difference is well-marked, but in others, such as the Bhils (0.01%), the greater contribution of position among females is minimal. In fact, the opposite pattern may also be discerned, where among some samples the difference between the sexes is well-marked, but is greater among males than females, such as among the Wakhis of Gulmit (5.3%), or is but minimal as is the case for Pakanatis (0.14%). Such findings indicate that sex contributes substantially, but differently by sample, to relative tooth size between key and distal members of the same morphogenetic field.

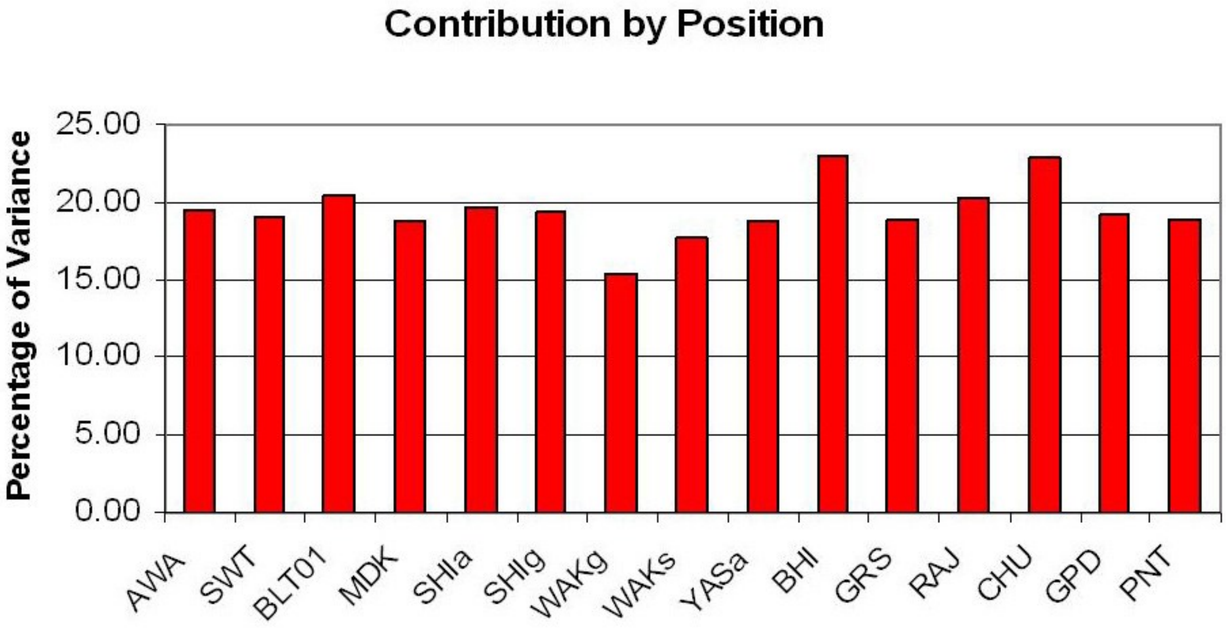

Fig. 4. Average contribution by position in accounting for variance in tooth size between key and distal members of a dental field with sexes pooled.

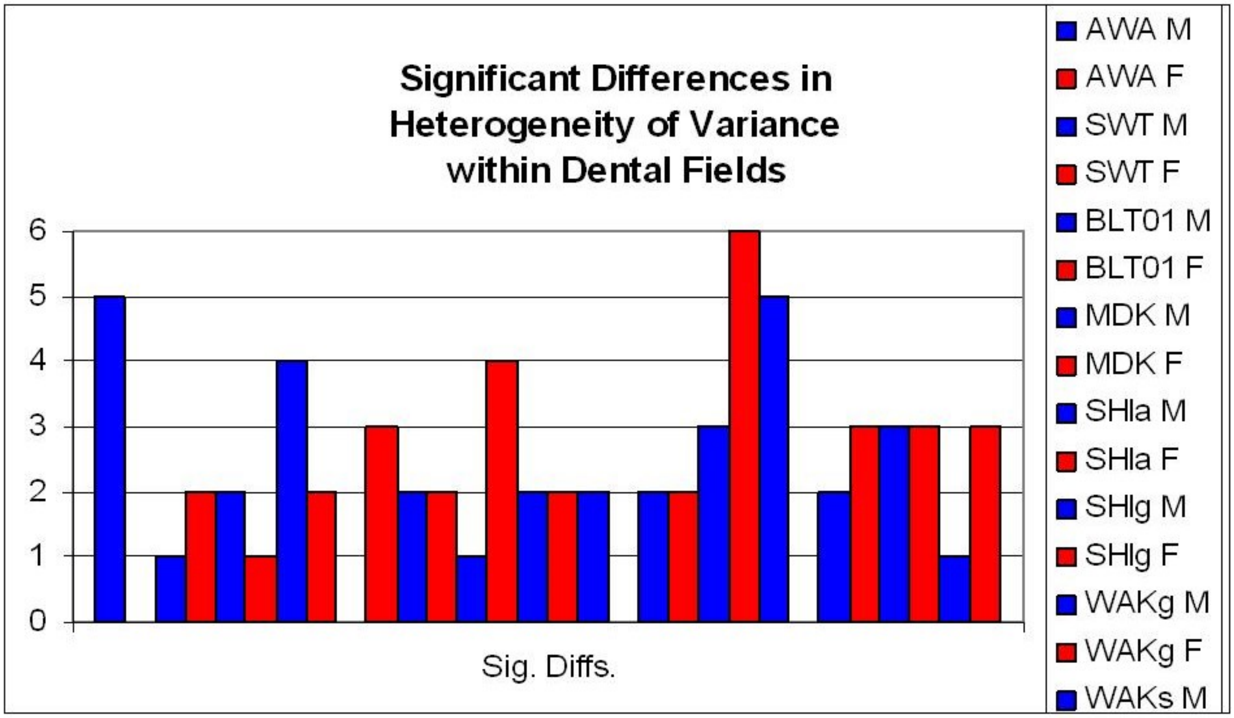

Fig. 5. Number of dental fields in which there are significantly different levels of variance between the key and distal member.

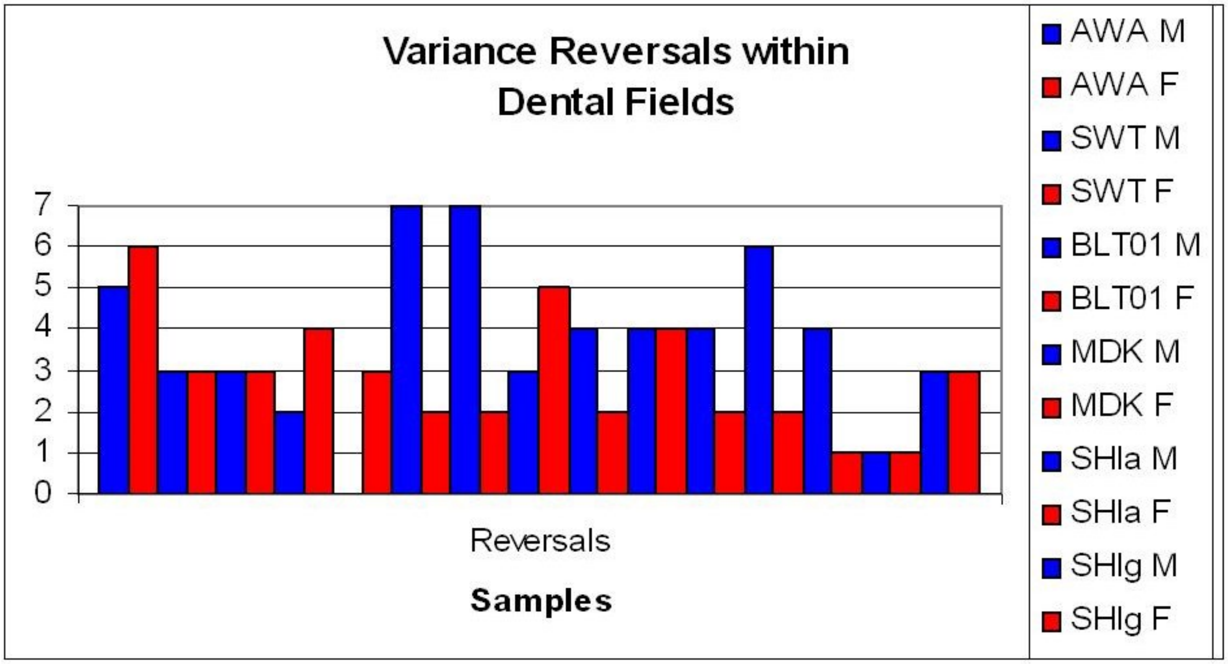

Fig. 6. Number of dental fields in which there is a reversal in the amount of variance expressed by key and distal members.

dental field contributes substantially (15.5%-23.1%) to the determination of tooth size (Fig. 4), but when considered by sex across the 15 samples it is also clear this contribution differs markedly in both magnitude and polarity (Fig. 7). A two-way analysis of variance by sample indicates that when sex is added as a second factor, the percentage of variance explained increases between 16.7 to 30.8%, an improvement of 27.2% over when position is considered alone. The improvement in accounting for the variance in tooth size between key and distal members of a dental field varies widely, from a low of 0.6% among Awans, to a high of 13.2% among Wakhis from Sost. Nevertheless, a paired-samples t-test indicates this improvement is statistically significant (t= 2.764; p= 0.015). Clearly, then, sex, in addition to position, *is* influential in the determination of relative tooth size between key and distal members within a dental field. However, that influence appears to differ markedly across samples.

Rank ordering is used to illustrate differences among samples in the relative contributions played by sex and by position in the relative size of key and distal members of the same morphogenetic field. Ranks were assigned such that those variables in which sex provides a relatively great contribution to the determination of relative size receive high ranks, while those variables in which sex plays a relatively lesser role receive low ranks. Ranks are plotted for maxillary variables in Figure 8, while ranks are plotted for mandibular variables in Figure 9.

Two-way ANOVA reveals that the contribution of sex to relative tooth size of key and distal members of dental fields is greatest for the buccolingual breadths of the premolars and molars in the maxillary dentition, as well as the buccolingual breadths of the incisors and mesiodistal lengths of the premolars in the mandibular dentition. By contrast, the contribution of sex is low for the mesiodistal lengths of both maxillary and mandibular incisors. Nevertheless, despite these overall trends, there is considerable variation among the 15 samples in the contribution of sex for the remaining variables. Indeed, variation in the relative contribution of sex appears especially well-marked for buccolingual breadths of incisors and mesiodistal lengths of premolars in the maxillary dentition, as well as the buccolingual breadths of the incisors and premolars in the mandibular dentition.

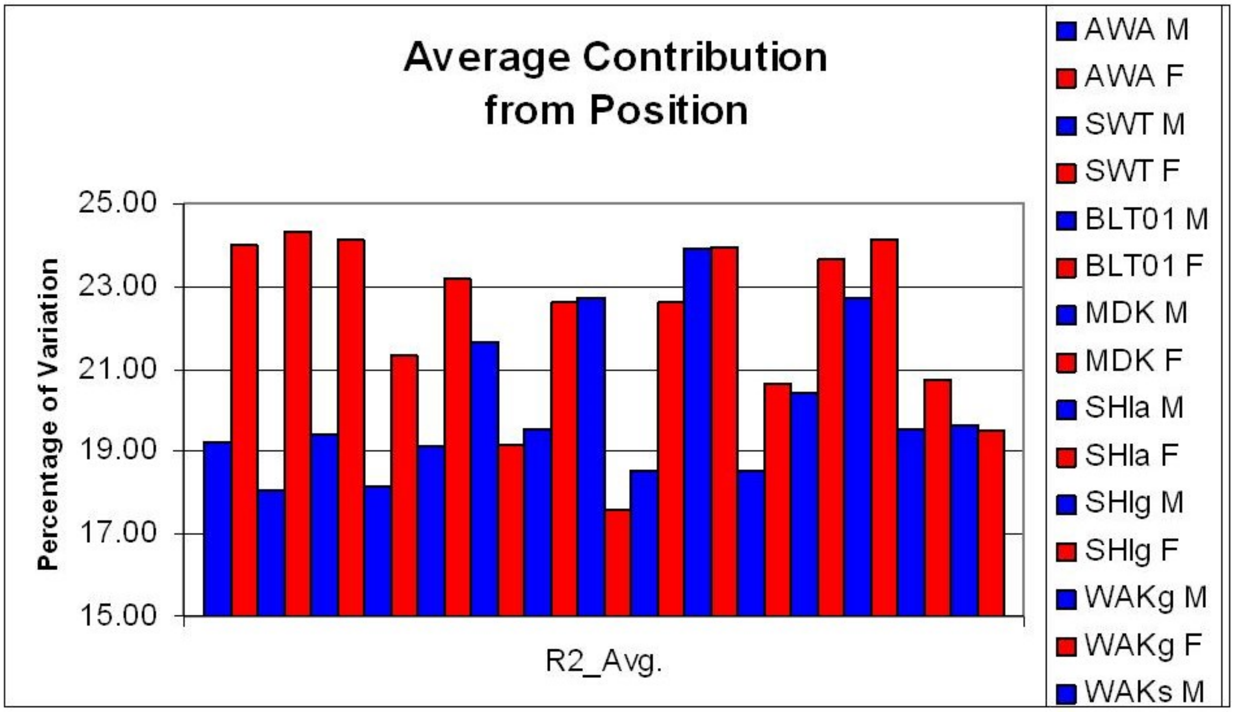

Fig 7. Average contribution by position in accounting for variance in tooth size between key and distal members of a dental field by sex.

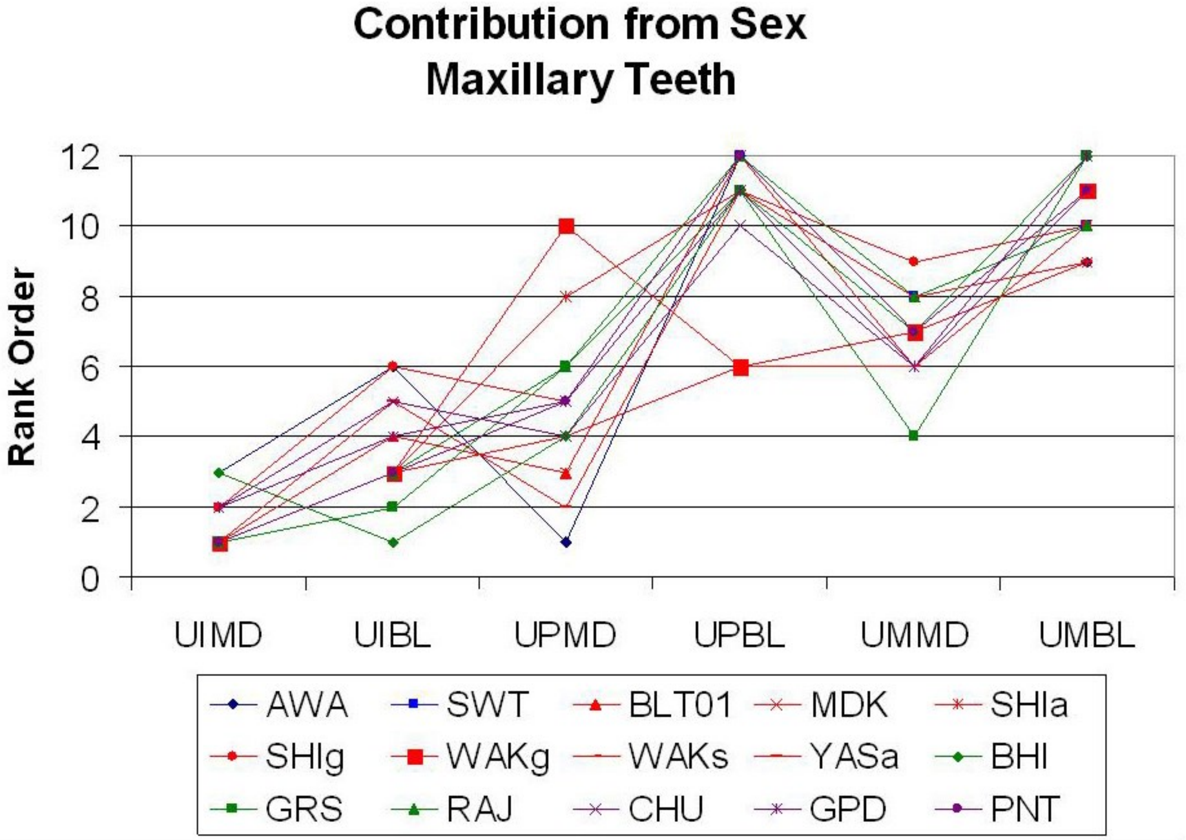

Fig 8. Average relative contribution of sex to position in determination of relative tooth size between key and distal maxillary teeth within a dental field by rank order (ranked by contribution from sex).

When considered by jaw, variation in the contribution of sex to relative tooth size of key and distal members of the same morphogenetic field among the maxillary teeth varies most among the 15 samples for the mesiodistal lengths of the premolars (sd= 2.274), followed by the buccolingual breadths of the premolars (sd= 1.988) and incisors (sd= 1.397). By contrast, variation in rank order is rather low for the mesiodistal lengths (sd= 1.223) and buccolingual breadths (sd= 1.060) of the molars, while variation among samples is lowest of all for the mesiodistal lengths of the incisors (sd= 0.743). Looked at another way, the rank order score for the relative contribution by sex to position for mesiodistal dimension differences between the key and distal members of this morphogenetic field ranges from one among the Awans (where sex contributes the most among the 12 variables considered) to 10 among the Wakhis of Gulmit (where the sex contributes third lowest among the 12 variables considered).

Turning to the mandibular teeth, variation in the contribution of sex to relative tooth size of key and distal members of the same morphogenetic field among the mandibular teeth varies most among the 15 samples for the buccolingual breadths of the premolars (sd= 2.000), followed by the buccolingual breadths of the incisors (sd= 1.668) and the mesiodistal lengths of the molars (sd= 1.624). Variation in rank order is rather low for the buccolingual breadths of the molars (sd= 1.397) and the mesiodistal lengths of the premolars (sd= 1.187), while as in the maxillary arcade, variation is lowest for the mesiodistal lengths of the incisors (sd= 1.183). When the dispersion in rank order scores across samples is considered, the relative sex contribution versus the contribution by position for differences in buccolingual breadths between the key and distal members of the premolars ranges from two among the two Wakhi samples (WAKg, WAKs) to a high of nine among Chenchu tribals of southeastern peninsular India. By contrast, dispersion in mesiodistal lengths of the incisors only ranges from one in three samples (CHU, GPD, SHIg) to five (WAKg).

DISCUSSION

Question 1: Do Developmental Fields exist such that Variance is Less among "Key" Teeth Relative to "Distal" Teeth?

It has often been maintained that the earlier developing members within a morphogenetic field are less affected by environmental factors than later developing members (Alvesalo and Tigerstedt, 1974; Townsend and Brown, 1980) and this has led some researchers who focus on dental morphology to limit considerations of differential trait frequencies found on key teeth only (Scott and Dahlberg 1982; Scott et al 1983; Sofaer et al 1972; Turner 1976). A recent review by Townsend and co-workers (2009) observes that later developing teeth within a morphogenetic field spend a relatively longer period of time in the soft tissue stage prior to calcification during which epigenetic and environmental factors can influence the shape and size of the crown. A similar observation was made by Keene (1982), whose concept of the morphogenetic triangle emphasized the dynamism in the formation of the individual cusps until coalescence among the cusps fuses them in place. Not surprisingly, given these expectations, it has been widely assumed that the key tooth within each morphogenetic field ought to possess the highest heritabilities, while the non-key teeth ought to be marked by lower heritabilities. Indeed, Alvesalo and Tigerstadt (1974) reported such patterning in their data, but other researchers have been unable to confirm such results (Dempsey and Townsend, 2001).

With sexes pooled, only one out of four contrasts of variance between key and distal members within dental fields are significantly heterogeneous, but the overwhelming majority that are significant are due to much higher variance among distal members. While such findings corroborate dental field theory and the findings of other researchers (Harris & Nweeia 1980; Herskovitz et al. 1993; Kieser & Groeneveld 1998; Mayhall & Saunders 1986), it is also the case that one in four contrasts yields higher variance for the key tooth than for the distal tooth within a dental field. A large number of these reversals occur among the mandibular incisors, suggesting that Dahlberg's (1945, 1951) insistence on a reversal of the dental field among mandibular incisors is incorrect. In contrast to expectations of the theory of compensatory tooth size effect (Sofaer 1973; Sofaer et al, 1972a,b), as well as the findings of some researchers with regard to bilateral asymmetry (Harris & Nweeia 1980; Townsend & Brown 1980), no predilection for increased variance was found for mesiodistal over buccolingual dimensions or vice versa. Indeed, one-way ANOVA indicates that position within a dental field only contributes about one-fifth of the percentage of variance explained in tooth size.

Taken together, such results weaken considerably an orthodox application of Butler's field theory. As noted by Townsend et al. (2009), a complicated array of epigenetic and morphogenetic events appears to be involved at different times and to various degrees in crown formation. Further, given more recent research which indicates that secondary enamel knot formation determines the location of cusp tips (Jernvall et al., 1994; Matalova et al., 2005), that knot positioning relative to the margin of the occlusal surface (Moorman et al., 2013) and overall crown size are related to such morphological features of the permanent tooth crown as Carabelli's trait (Harris, 2007), it is clear that crown size and shape are phenomena whose interrelatedness are poorly captured by simplistic developmental models that rely upon morphogenetic fields with key and distal members.

Question 2: Are Females more Genetically Canalized than Males?

The assertion that among humans males are less buffered against environmental stress than females can be traced to Greulich's (1951) study of growth and development among children on the island of Guam who suffered from nutritional stress and other deprivations during World War II. Greulich found than Guamanian boys suffered greater shortfalls in height, weight, weight for height and skeletal maturation than girls when compared to well-nourished U.S. children. Similar results were found among children who survived the atomic bombing of Hiroshima and Nagasaki (Gruelich et al., 1953), as well as children exposed to radiation caused by nuclear testing in the Marshall Islands (Sutow et al., 1965).

In 1969, Stini examined the impacts of malnutrition upon growth and development among boys and girls of Helconia, Colombia. He found skeletal maturation to be delayed in all malnourished children early in life. However, skeletal age among girls was closer to U.S. standards in the earliest years of life and the differences in skeletal maturity between boys and girls increased throughout adolescence such that girls experienced a form of "catch-up" growth to U.S. standards while similarly malnourished boys failed to do so resulting in a reduction of "blunting" of sex dimorphism (Dettwyler, 1992; Eveleth, 1975; Leonard, 1991; Stini, 1972; Tobias, 1972). Similar results have been obtained in studies of the impact of high altitude upon growth and development among Andean populations (Frisancho and Baker, 1970; Pawson, 1977; Stinson, 1980), as well as sex differences in response to infectious diseases (Stini, 1985), parasite loads (Brabin, 1990), and famine (Grayson, 1990). Stini (1975, 1982, 1985) suggested that such sex differences may be the consequence of selection for better environmental buffering in females because of their greater investment in reproduction in supporting pregnancy, lactation and child rearing.

Turning to odontometric variation within the permanent dentition and given the expectations of dental field theory, males ought to express a lesser degree of genetic canalization by exhibiting greater variance among distal members of a morphogenetic field relative to key members. That is, the lesser degree of buffering against environmental perturbations ought to more often result in levels of variance among key and distal teeth that are statistically different. Further, because of lesser buffering and hence greater variation among distal teeth within a morphogenetic field, reversals in levels of variance among key and distal members of the same morphogenetic field ought to be few. By contrast, among females the greater amount of buffering should reduce the relative amount of variance found among the distal members of a morphogenetic field and thereby result in fewer instances in which the levels of variance between key and distal members of a morphogenetic field are significantly heterogeneous. A secondary consequence of greater buffering among females is that greater parity in variance among key and distal members of a morphogenetic field is that reversals ought to be more common due to random chance.

Running contrary to expectations, Bartlett's chi-square indicates that males are marked by a fewer number of dental fields with significant heterogeneous levels of variance between key and distal members, for significant heterogeneity occurs in only three of the 15 samples (20.0%), while females are marked by equivalent or higher numbers of reversals in 12 of the 15 samples (80.0%). When heterogeneity of variance is considered by dental field across all samples, Bartlett's chi-square identifies 68 contrasts as exhibiting significantly heterogeneous levels of variance. Once again running contrary to expectations, males do not exhibit a pattern in which they are affected far more often than females. Instead, with 35 and 33 significant differences affecting males and females, respectively, it appears that members of both sexes are equally buffered against environmental perturbations that affect odontogenesis.

As noted above, an examination of the patterning of variance among key and distal teeth within dental fields finds that a little more than one-fourth (99/360= 27.5%) are marked by a reversal in which variance is greater among key teeth than their distal counterparts. Males are more often affected than females, but when considered by sample, reversal prevalence is equivalent or greater among females than males in nine of the 15 samples. Taken together, these results offer only tepid support for the contention that females are more highly genetically canalized and hence odontogenesis is less affected by environmental factors among females than are males. These finding corroborate those of other researchers who find similar levels of postnatal variability in growth and development among members of both sexes (Frisancho et al., 1980; Martorell et al., 1975, 1984; Stinson, 1985; Yarborough et al., 1975) as well in linear enamel hypoplasia prevalence (Angel et al., 1987; Goodman et al., 1987, 1991; Manzi et al., 1999; May et al., 1993; Santos and Coimbra, 1999; Zhou and Corruccini, 1998). However, as noted by Guatelli-Steinberg and Lukacs (1999), indicators of postnatal stress offer a mixed signal concerning sex differences in response to stress. This is because cultural factors may outweigh and obfuscate the actual levels of stress experienced. Thus, the evidence found here for equivalent levels of variability for males and females may be the consequence of cultural factors that favor care, treatment and feeding of boys over girls. Thus, with regard to greater developmental canalization of females over males, it is clear that if such canalization exists it is not of a sufficient degree to be expressed consistently across the samples analyzed here. Consequently, one cannot assume that females will be less variable odontometrically than their male counterparts.

Question 3: Is Sex Dimorphism Uniformly Expressed across Adequately Nourished Human Populations?

Teeth are considered a useful means for determination of sex (Ghose and Baghdady, 1979; Harris and Nweeia, 1980; Potter et al., 1981; Iscan and Kedici, 2003), especially in cases where remains are highly fragmentary (Anuthama et al., 2011; Prabhu and Acharya, 2009; Vodanovic et al., 2006).

It is usually the case that the canines are the most dimorphic teeth in the permanent dentition (Acharya and Mainali S., 2007; Garn et al., 1967; Iscan and Kedici, 2003; Lund and Mörnstad, 1999; Potter et al., 1981; Townsend and Brown, 1979), but some studies report that other teeth are either the most dimorphic (Garn et al., 1966; Shrestha, 2005) or nearly as dimorphic as the canine in certain populations (Iscan and Kedici, 2003; Kieser and Groeneveld, 1989; Perzigian, 1976; Potter 1972; Potter et al., 1981; Sharma 1983). Indeed, some studies have reported the presence of "reverse dimorphism" in which females possess larger averages for certain variables than males (Acharya and Mainali, 2007; Ghose and Baghdady, 1979; Harris and Nweeia, 1980; Prabhu and Acharya, 2009). In fact, Ghose and Baghdady (1979) report that fully one-third of the variables they examined among Yemenites exhibit such "reverse dimorphism."

Numerous studies report population differences in both the patterning (Anuthama et al., 2011; Ates et al., 2006; Iscan and Kedici, 2003; Prabhu and Acharya, 2009) and magnitude (Anuthama et al., 2011; Iscan and Kedici, 2003; Prabhu and Acharya, 2009) of sex dimorphism in odontometric variables. Such differences also extend to the relative size of key versus distal members of the same morphogenetic field. Designating such differences as "tooth size crown gradients," Harris and Harris (2007) found marked differences between major human groups in which some are marked by "steep" gradients of sharp reductions in size from the key to distal teeth, while others possess "shallow" gradients with similar dimensions across the members of a field.

One-way ANOVA demonstrated that among the 15 samples considered here a tooth's position within a dental field accounts for 15.5% to 23.1% of the observed variation in tooth size within morphogenetic fields. Yet, it is also the case that when

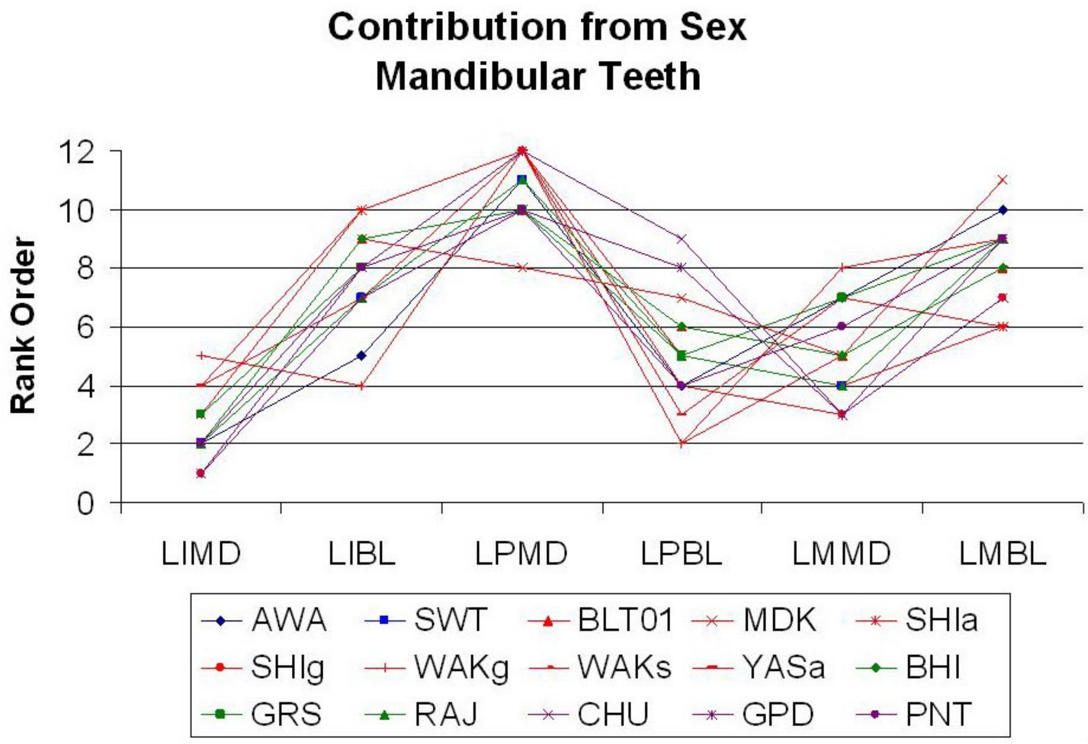

Fig 9. Average relative contribution of sex to position in determination of relative tooth size between key and distal mandibular teeth within a dental field by rank order (ranked by contribution from sex).

variation within dental fields is considered by sex it is clear the contribution from sex differs markedly with regard to both magnitude and polarity. A two-way analysis of variance by sample revealed that when sex is added as a second factor, the percentage of variance explained increases to 16.7%-30.8%, which is an improvement of 27.2% when consideration is limited to position within a morphogenetic field. In accordance with the observations of Harris and Harris (2007), the improvement in accounting for the variance in tooth size between key and distal members of a dental field varies widely. Thus, not only does it appear that sex, in addition to position, is influential in the determination of relative tooth size between key and distal members within a dental field, it is also the case that this influence differs markedly across samples. Such differences in the expression of sex dimorphism were found to mirror differences in tooth size allocation as a whole (Hemphill, 1991) and also explain why discriminant functions developed for determination of sex in one population often predict sex with much lower accuracy when applied to members of other populations (Wright and Hemphill, 2012).

CONCLUSION

Viewed as a whole, this “fool’s mission” appears not to have been at all foolish. Dental field theory offers an inaccurate picture of the true pattern of variation among key and distal members of morphogenetic fields. For while it is the case that key teeth are often less variable than their distal counterparts, reversals are common. Dahlberg’s (1945, 1951) alleged reversal of polarity among mandibular incisors is not supported, nor is Sofaer’s (1973; Sofaer et al, 1972a,b) notion of compensatory tooth size effect. The notion that females tend to be more highly genetically canalized than males and hence are more resistant to environmental perturbations is not confirmed. Males and females were found to exhibit similar levels of relative variability between key and distal members of morphogenetic fields. However, since much of the development of the permanent tooth crown occurs post-natally, potential mitigating cultural factors that favor males over females cannot be ruled out. There is abundant evidence that sex dimorphism is expressed differently, both with regard to patterning and to magnitude across human populations. Drawing from Harris and Harris' (2007) notion of tooth crown size gradients within morphogenetic fields it is clear that among the South Asian ethnic groups considered here, there is considerable variation in the expression of sex dimorphism. Indeed, the very low expression of sex dimorphism among the relatively well-nourished Awans of Mansehra District coupled with the marked expression of sex dimorphism among the isolated high altitude Wakhis of Sost, suggest strongly that these differences cannot be attributed to mere environmentally induced "blunting" of sex dimorphism. Instead, these differences in the degree and patterning of sex dimorphism in permanent tooth size are the consequence of the same population-specific differences in the array of genes that control the apportionment of overall tooth size throughout the permanent dentition. Given that population differences in the expression of sex dimorphism in permanent tooth size are even less likely to be subject to the impacts of natural selection than overall tooth size, patterning in the expression of sex dimorphism in permanent tooth size offers an additional avenue for unraveling the complex histories of human populations on local, regional and continental levels.

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Secular change in dental development in New Mexican females

Anna L.M. Rautman[1], Heather J.H. Edgar[1]

[1]*Department of Anthropology and Maxwell Museum of Anthropology, University of New Mexico Albuquerque, New Mexico 87131*

Keywords: Dental Development; Hazards Analysis; Secular Change

ABSTRACT Recent research has indicated a dramatic acceleration of dental development in 20th century European Americans in Tennessee and Arizona, resulting in developmental stages being reached at earlier calendar ages. In order to determine whether this rate change is also observed in New Mexico, radiographs from two cohorts of European American female orthodontic patients with known ages were used to compare age by stage of development. The cohorts date to the 1970's (n=101) and the 1990's (n=93) and were between 5-11 years of age. Dental developmental stages were recorded for five mandibular teeth.

The average calendar age difference between cohorts per tooth and developmental stage combination was less than one month, but varies among tooth/stage combinations by up to 13 months. A Pearson's chi square test found no significant difference between the two cohorts for the 22 tooth/stage combinations. However, Cox Hazards Analysis demonstrated significant differences between the cohorts for five of the 22 tooth and stage combinations. Contrary to previous findings, the calendar age of the 1990's cohort is older for 16 of the 22 tooth/stage combinations than the 1970's cohort. This runs counter to the general trend of acceleration in development observed in multiple systems.

Dental development is generally thought to be a precise method for estimating an individual's chronological age during growth, because it seems to be less affected by environmental variation than long bone length. However, secular change has been documented in the timing of dental development (Nadler, 1998; Cardoso et al., 2010; O'Neill, 2012; Sasso et al., 2012). Secular change refers to non-genetic, directional changes in the timing, rate, and magnitude of development over successive generations, often related to environmental factors (Garn, 1987; O'Neill, 2012). Evidence of secular change has been reported across numerous populations and in many body systems, including height and age of menarche (Cole, 2000; Thompson et al., 2002; Cardoso et al., 2010).

Previous research has shown that children in the United States and Europe are reaching stages of dental development at younger ages then had previous generations (Nadler, 1998; Cardoso et al., 2010; O'Neill, 2012; Sasso et al., 2012). Nadler (1998) noted that patients in Tucson, Arizona in the 1990's who were described as Caucasian and between 8.5-14.5 years were reaching stages of dental development at younger chronological ages than similar patients had in the 1970's. Specifically, he detected a reduction of 1.52 years in the obtainment of dental development stage G (Demirjian et al., 1973) of the mandibular canine in females between two cohorts, 1972-1974 and 1992-1994. Work by O'Neill (2012) also showed an increase in the rate of dental development in patients described as American white from Memphis, Tennessee. This study examined the dental development of all mandibular teeth and found a 1.1-year reduction in chronological age relative to dental age between two cohorts from 1980-1985 and 2005-2010.

Research in Europe has also demonstrated a reduction in age of dental development stage attainment. In Portugal, modern girls were shown to have matured dentally 1.47 years faster than girls from half a century ago (Cardoso et al., 2010). The historic sample was comprised of skeletons of individuals who died between 1903 and 1972, with the majority of the deaths occurring between 1920 and 1950. The modern sample was comprised of dental patients whose radiographs were taken between 1998 and 2006. For both samples, the first seven mandibular teeth were examined. A study in Croatia of seven left mandibular teeth observed an acceleration of 0.83 years in girls' rate of dental development between 1977-1979 and 2007-2009 (Sasso et al., 2012).

Correspondence to: Heather Edgar
Department of Anthropology and Maxwell Museum of Anthropology, University of New Mexico, Albuquerque, New Mexico 87131
Hjhedgar@unm.edu

Given an increase in the rate of dental development observed for Europeans and European Americans, this study examines whether there is evidence for secular change in the timing of dental development in European American females in Albuquerque, New Mexico. The hypothesis was that more recent patients obtained stages of dental development at younger ages than had patients in an earlier cohort.

MATERIALS AND METHODS

The sample consists of 194 radiographs in two cohorts of female patients of European-American ancestry (Edgar et al., 2011) who were less than 11 years old. One orthodontist in Albuquerque, New Mexico saw all the patients. Cohort one included 101 radiographs of patients who were seen between 1973 and 1979. Cohort two included 93 radiographs of patients seen between 1990-1999. While the patients were living in New Mexico at the time of their treatment, how long they had lived in New Mexico was not known.

Through observations of panoramic oral radiographs, one author (ALMR) assigned a dental development stage to every tooth, maxillary and mandibular, deciduous and permanent, using a 13 stage method commonly used in studies of dental development (hereafter referred to as "the Moorrees method”) (Moorrees et al., 1963 a,b; AlQahtani et al., 2010). Because of limited observations, only five teeth, all mandibular, are included in this analysis: the canine, both premolars, and the second and third molars. Although direct scoring of the radiographs was completed using the Moorrees method for dental development stages, scores were converted to stages described by Demirjian (1973, hereafter referred to as "the Demirjian method") so that results from the New Mexico sample could be compared to those reached by Nadler (1998) from Tucson, Arizona and O’Neill (2012) in Memphis, Tennessee. The conversion used the written descriptions of the progress of dental development to match descriptions in the two methods. Details of the conversion are shown in Figure 1.

An intra-observer error test was run on a subset of 40 radiographs, 20 from each cohort. The consistency between the two sets of observations was tested using weighted and unweighted Cohen’s Kappa tests (Cohen, 1960; Viera and Garrett, 2005). The mean and median age and standard deviation were calculated for each developmental stage per tooth for each cohort. Using the mean ages, Pearson’s chi square was used to test for significant differences for each stage per tooth between the cohorts (Gotelli and Ellison, 2004). Cox Proportional Hazards Analysis (Cox and Oakes, 1984; Fox, 2002) was used to analyze individual age differences in survivorship of each stage. In this analysis, the event of interest is the transition to the next development stage. Individual ages represent the time observation. This allows for analysis of relative ages and frequency of individuals who survive to the stage.

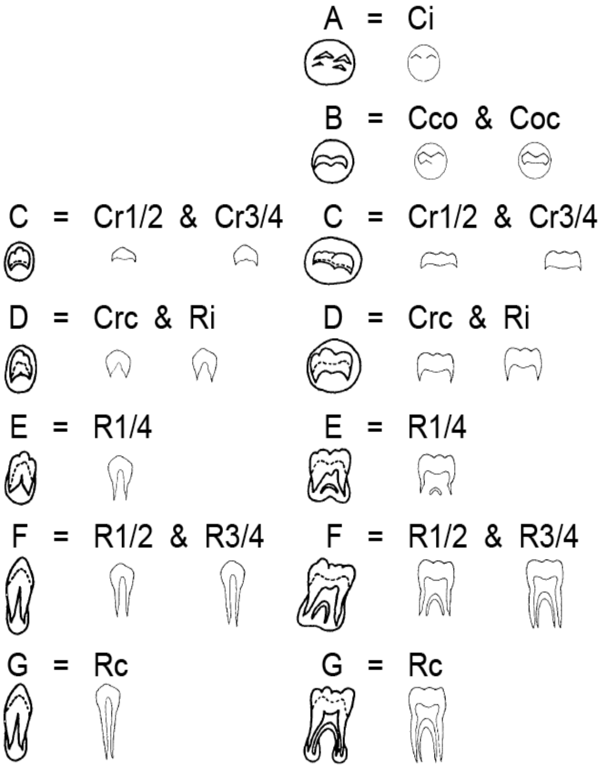

Fig. 1. Conversion between the Demirjian method (A - G) and the Moorree’s method (Ci – Rc) dental development stages. Anterior teeth are pictured on the left, posterior teeth on the right.

RESULTS

Intraobserver Test

The weighted kappa score testing intra-observer error for observations of the five mandibular teeth included in this analysis is 0.917, and the unweighted kappa score is 0.676. Both kappa scores demonstrate agreement between observation, "almost perfect agreement" and "substantial agreement," respectively (Viera and Garrett, 2005). Given the ordinal nature of the development stages, the weighted kappa is more applicable.

Dental Development in New Mexico: The Moorrees Method

The mean age of dental development stages across all five teeth is younger in the 1970's cohort than in the 1990's cohort for the majority of stages. This indicates a slowing of dental development. This difference was usually small, with a mean absolute difference of 3.3 months. However, there are directional differences in which cohort is older for any given tooth/stage combination. Because sometimes the 1970's cohort is older for a given stage of development, and sometimes the 1990's cohort is older, adding all differences between the cohorts together results in the 1990's cohort being on average only 0.2 months older.

Table 1 presents the sample size and frequency per tooth/stage combinations, as well as Pearson's chi square and Cox Hazards Analysis results. Only two tooth/stage combination differences between cohorts were greater than six months: the canine at root one half (10 months) and the crown complete stage in the fourth premolar (13 months). Of the 22 tooth/stage combinations, only six had measurable differences between mean ages older in the 1970's cohort than in the 1990's cohort. Three of these tooth/stage combinations were in the second molar (crown three-quarters, crown complete and root one-half). The other tooth/stage combinations seen at older ages in the 1970's cohort were the canine (root complete), third premolar (root complete), and the fourth premolar (root one-quarter). Of these six tooth/stage combinations, only the fourth premolar (root one-quarter) and second molar (crown three-quarter) had differences greater than one month, 3.81 months and 1.05 months, respectively.

Pearson's chi square and Cox Hazards Analysis disagree about significant differences between the cohorts. No Pearson's chi square result indicates significant differences in the mean or median ages between the two cohorts. This is true for all tooth/stage combinations, and regardless of whether the 1970's or 1990's cohorts showed any particular tooth/stage combination at an earlier age. In contrast, Cox Hazards Analysis detects significant differences between cohorts ($p < 0.05$) in the survivorship of development stages as patients develop out of a given dental stage for five of the 22 tooth/stage combinations. Timing of the canine (root one-half and root three-quarter), both premolars (third: root one-quarter; fourth: root initialized), and the second molar (root initialized) is significantly different between cohorts. Of these five tooth/stage combinations, the mean difference was 5.4 months. The mean age of the 1990's cohort was always older than the mean age of the 1970's cohort.

Dental Development in New Mexico: The Demirjian Method

After conversion of the observed Moorrees method dental development stages to the Demirjian method stages, the difference in mean ages between the two cohorts remains, with the 1990's cohort mean being slightly older. The absolute mean difference is 3.01 months. When directional differences between the two cohorts were considered, the difference is 1.9 months with the 1990's cohort as the older.

Only one tooth/stage combination difference is greater than six months (canine, stage F). Of the 17 tooth/stage combinations considered, only five (canine, stage G; third premolar, stage G; fourth premolar, stage E; second molar, stage F; and third molar, stage C) had mean ages such that younger chronological ages were associated with development stages in the 1990's cohort.

The conversion of dental development scores from the Morrees method to the Demirjian method does not result in any significant Pearson's chi square tests of the mean age differences between the cohorts. Cox Hazards Analysis of the Demirjian method stage data demonstrates four of 17 tooth/stage combinations having significant differences in survivorship of stages between cohorts ($p < 0.05$). These four, canine (stage F), third premolar (stages E and F) and fourth premolar (stage D) have a mean age difference of 4.8 months. In all tooth/stage combinations the mean age of survivorship of the 1990's cohort is older than the 1970's cohort.

TABLE 1. Sample Size Frequencies and P-values for Pearson's Chi-Square and Cox Hazards Analysis

				D	A		B				C				D				E		F				G	
		N total		M	Ci		Cco		Coc		Cr12		Cr34		Crc		Ri		R1/4		R1/2		R3/4		Rc	
		70's	90's		70's	90's	70's	90's	70's	90's	70's	90's	70's	90's	70's	90's	70's	90's	70's	90's	70's	90's	70's	90's	70's	90's
C1	N freq	89	74	M															0.169	0.284	0.337	0.243	0.303	0.149	0.191	0.324
	χ^2			D															0.997		0.891				1	
				M																	0.844		0.919			
	Cox H			D															0.5		**0.01**				0.79	
				M																	**0**		**0.009**			
P3	N freq	97	82	M											0.010	0.049	0.165	0.183	0.371	0.329	0.216	0.098	0.134	0.207	0.103	0.134
	χ^2			D			insufficient data								0.989				0.94		0.936				0.99	
				M													0.91				0.936		0.962			
	Cox H			D											0.89				**0.013**		**0.047**				0.98	
				M													0.6				0.089		0.8			
P4	N freq	93	80	M											0.086	0.138	0.323	0.238	0.323	0.263	0.118	0.200	0.151	0.163		
	χ^2			D											0.936				0.9414		0.9145					
				M											0.768		0.958				0.981		0.962			
	Cox H			D											**0.049**				1		0.88					
				M											0.75		**0.006**				0.42		0.64			
M2	N freq	100	86	M							0.010	0.000	0.050	0.128	0.150	0.163	0.290	0.174	0.340	0.337	0.130	0.174	0.030	0.023		
	χ^2			D							0.943				0.977				0.9491		0.992					
				M									0.982		0.985		0.914				0.997					
	Cox H			D							0.81				0.1				0.23		0.77					
				M									0.91		0.83		**0.018**				0.97					
M3	N freq	34	47	M	0.412	0.234	0.118	0.213	0.206	0.170	0.088	0.170	0.176	0.213												
	χ^2			D	0.932		0.941				0.942										insufficient data					
				M					0.919				0.991													
	Cox H			D	0.47		0.6				0.78															
				M					0.26				0.82													

Arizona, New Mexico, and Tennessee Compared

All tooth/stages are seen at younger chronological ages in New Mexico than in Tennessee (O'Neill, 2012). This difference ranges between 0.7 and 2.52 years, with an average difference of 1.52 years. A similar pattern with less difference between the samples is observed when New Mexico and Arizona are compared (Nadler, 1998).The average difference between the southwest states is 0.69 years, with the Arizona sample older. The range of differences is from the Arizona sample being older by 1.39 years to the New Mexico sample being older by 0.13 years. Figure 2 shows the interquartile range for the New Mexico and Tennessee samples as well as a range of two standard deviations for the Arizona sample, for which interquartile could not be computed.

DISCUSSION

Considering the evidence for secular change seen by previous authors, it was expected that the 1970's cohort would have achieved developmental stages at a later average age than 1990's cohort. However, regardless of the method used to measure dental development, Moorrees or Demirjian, it is apparent that in New Mexico, the 1970's cohort achieved dental development stages at younger ages on average than the 1990 cohort. Our results do not agree with the positive secular trend of dental development as observed previously in Arizona, Tennessee, Portugal, and Croatia. Furthermore, the magnitude of difference in age between cohorts was much larger elsewhere, ranging from 0.83 years in Croatia to 1.52 years in Arizona, compared to the average difference of 0.42 years observed in New Mexico.

Within the New Mexico sample, the significant differences in the Cox Hazards Analysis are primarily seen in eight and nine year olds. This observation raises the question of possible external and/or somatic environmental influences of dental development at that time. This age range generally falls between the mid-growth spurt and the adolescent growth spurt associated with puberty (Eveleth and Tanner, 1976; Bailey, 1991; Bogin, 1999). There is a slower period of body growth between early childhood and puberty. During this lull between the mid-growth spurt and the adolescent growth spurt the energy not used in skeletal growth is allocated elsewhere (Hill and Hurtado, 1996). One possible direction for this energy is social learning (Hill and Kaplan, 1999). At the same time, variation between individuals increases in multiple body systems throughout development (Ogden et al., 2002; Lin et al., 2006). Since the period of greatest variability in dental development is correlated with a lull in skeletal growth, it may indicate that energy not being used in rapid skeletal growth is at least in part being diverted to dental development.

While it appears that the mean age of dental development is not changing in New Mexico, the mean ages in Tennessee are getting progressively younger, getting closer to the early mean age already obtained in New Mexico. This is true for the Arizona sample as well, with one tooth/stage exception (canine, stage G). However, there are differences between the studies from Arizona, New Mexico, and Tennessee in time periods from which cohorts were observed, complicating direct comparison. The first cohort in Arizona and New Mexico was taken from 1970's patient records, while patients in the first cohort from Tennessee were seen in the 1980's. The second cohorts were from the 1990's for Arizona and New Mexico and 2000's for Tennessee.

CONCLUSION

This study finds no evidence of positive secular change of dental development among New Mexican European American females, as had been observed previously in Tennessee and Arizona. In fact, the only significant differences detected show that the more recent New Mexican cohort has less developed teeth at specific chronological ages, exactly opposite of the trend observed by Nadler (1998) and O'Neill (2012).

Causation is often an unexplored issue in studies of secular change. Possible sources of change are external environmental factors such as nutrition, chemical exposure, and disease, as well as somatic environmental effects of energy allocation trade-offs between different body systems (Kieser, 1992; Kieser et al., 1997; Euling et al., 2008; Walker and Hamilton, 2008; Cardoso et al., 2010; Patisaul and Jefferson, 2010). In addition to external and somatic factors, there are genetic factors as well that may contribute to varied rates of dental development. While it is possible that genetic differences are the cause of the observed differences, the fact that all three studies were of European Ameri-

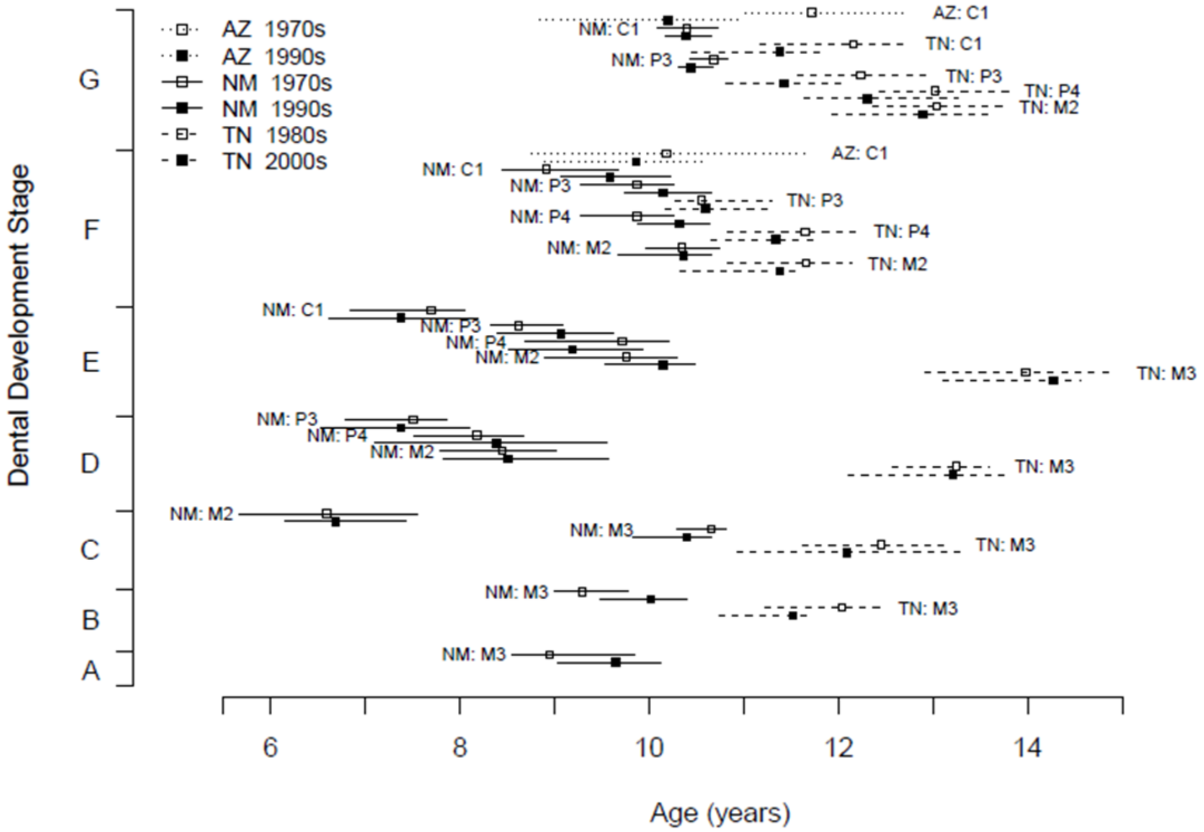

Fig. 2. Age range per stage per tooth.

can females makes this less likely. This would suggest that external and/or somatic environmental factors contribute to the results observed. To address this, a finer scale analysis of when changes in the pace of dental development occur is needed. Such research should consider how the different external, somatic, and genetic factors interact with each other to influence dental development.

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Size does matter: Variation in tooth size apportionment among major regional North and sub-Saharan African populations

Joel D. Irish[1] and Michael W. Kenyhercz[2]
[1]*Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University*
[2]*Department of Anthropology, University of Alaska, Fairbanks, AK 99775-7720*

Keywords: Odontometrics, Prinicipal Components Analysis, Dental Anthropology, Africa, Biological Affinity

ABSTRACT In the 1980s Edward Harris proposed an approach using principal components analysis to compare mesiodistal and buccolingual crown diameters in humans. A major goal was to remove overall "size" from the measurements – which is ineffective for biological affinity. Relative size, however, is important, i.e., to assess how it is apportioned along the tooth rows. To get at such data, Harris utilized three size predictors in multiple linear regression to calculate PC 1 residuals, which were then used with other uncorrected components in analysis.

Here we demonstrate that it is still an effective method, by comparing 32 MD and BL measurements in 12 (n=712) and 18 (n=1251) samples from sub-Saharan and North Africa. Plotting of the first three components (50% of variance) shows clear separation between regions. North Africans are characterized by: 1) small LI1s, and BL dimensions of the UM1, LI2, and LM1, and 2) large MD diameters of the UM2 and LM1, and BL diameters of the LM2 and LM3. Comparisons of North Africans only show the ability to distinguish among samples from the Maghreb, Egypt, and Nubia. In other words, basic crown diameters can be successfully used for affinity estimation, if relative size, a.k.a., "shape" is accounted for.

Over 20 years ago, Edward Harris proposed an approach to compare mesiodistal (MD) and buccolingual (BL) crown diameters that employed principal components analysis (PCA) (Harris, 1997; Harris and Bailit, 1988; Harris and Rathbun, 1991). One major goal, like that of other workers (e.g., Penrose, 1954), was to remove overall "size" -- which is ineffective for biological affinity estimates and phylogenetic analyses. However, relative size is important, i.e., how it is apportioned among crowns along the tooth rows. To get at such data, Harris used three size predictors in multiple linear regression to calculate PC 1 residuals; these and the other uncorrected components were then used in analysis. This approach is called tooth size apportionment (TSA) analysis. It was used by several other researchers (e.g., Hemphill, 1991; Hemphill et al., 1992; Irish and Hemphill, 2001, 2004) to quantify sample differences ranging from global to local in scale -- before its appeal diminished.

Like clothing, analytical methods go in and out of style. When "sexy" approaches involving lasers, aDNA, and stable isotopes emerge, the "old ways" are often forgotten. The purpose here is to show that "old" is not the same as "out-dated;" through TSA, useful results can be achieved with easy-to-obtain odontometric data – all without destructive sampling and at a fraction of the cost.

MATERIALS

Up to 32 MD and BL measurements in the left maxillary and mandibular dentitions of 12 (n=712 inds) sub-Saharan and 18 (n=1251) North African samples for the present study were recorded. Nonmetric findings in these same samples support a known biocultural dichotomy between populations living north and south of the Sahara (Irish, 1997, 1998a,b, 2005, 2006). The names (incl. abbreviations in Figs. 3 and 6), composition, and origins of these 30 samples are presented in the aforementioned publications. Their approximate geographic locations are plotted in Figure 1.

METHODS

Following Harris' [and Hemphill's (1991)] approach, sexes-pooled mean measurements were obtained for each sample (sex dimorphism relates to crown size not shape). Ordinarily, either these data or their z-scores would be submitted to PCA to obtain a rotated (Harris) or unrotated

Correspondence to: Joel D. Irish, Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, Byrom Street, Liverpool L3 3AF, United Kingdom.
j.d.irish@ljmu.ac.uk

(Hemphill) solution. The PC1 size factor would be addressed through use of residuals as noted above. However, this approach was questioned by Jungers et al. (1995), among others, who prefer size correction via Darroch and Mosimann's (1985) geometric mean (GM). Following their lead, the product of all 32 measurements in this study by sample was calculated, the 32nd root obtained, and the resulting GM used as divisor of each measurement to effect correction. These DM values were then submitted to PCA, to yield unrotated PC loadings and factor scores.

RESULTS AND DISCUSSION

To illustrate the effectiveness of DM size correction, the eight sexes-pooled mean MD maxillary measurements for combined samples of North and sub-Saharan Africans are plotted in Figure 2. North Africans exhibit smaller dimensions in all cases. Compare this line graph to that at the top of Figure 5 after size correction. It can be seen that relative between-sample size (a.k.a. shape) varies; that is, it is apportioned differentially along the tooth row: in this example, North Africans have relatively larger UI1, UP4, UM1, and UM3 MD dimensions.

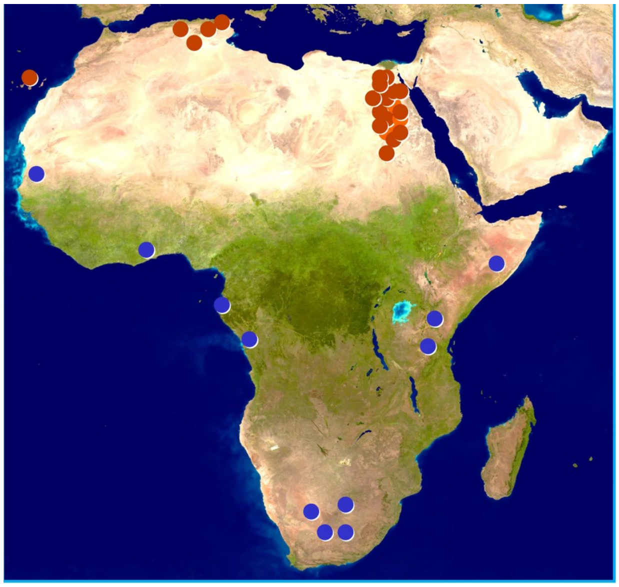

Fig.1. Origins of the 30 North (red dots) and sub-Saharan (blue) samples.

Five components with eigenvalues of >2.0 were retained (see Table 1); they account for >63% of the total variance. Plotting of first three factor scores (<50% of variance) yielded the distribution in Figure 3. The North and sub-Saharan samples show

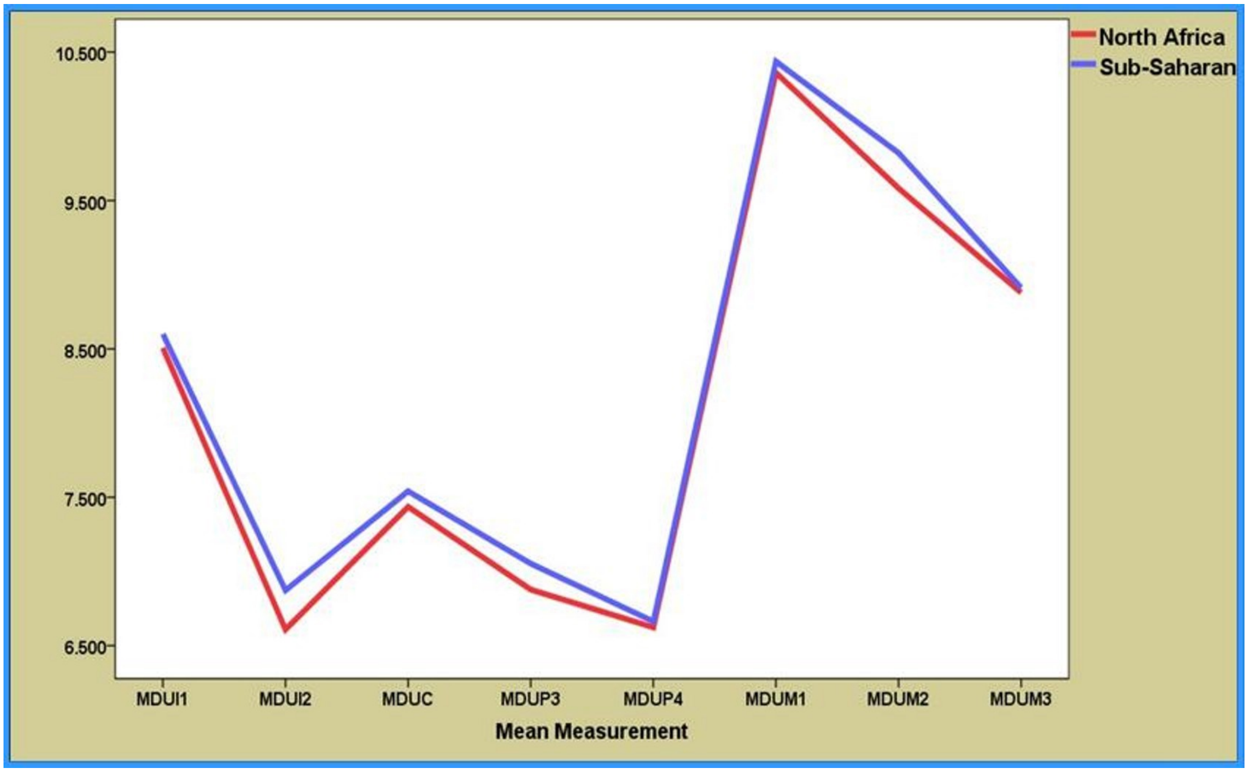

Fig. 2. MD maxillary measurements in pooled North and sub-Saharan samples.

TABLE 1. PCA loadings (high-magnitude values in boldface)

Measure	PC1	PC2	PC3	PC4	PC5
DM_MUI1	-.098	-.246	.123	**.596**	.356
DM_MUI2	**.546**	.466	-.026	-.082	.401
DM_MUC	.151	**-.575**	.234	-.224	.209
DM_MUP3	.429	.343	-.083	.111	**.527**
DM_MUP4	-.294	.138	-.130	.219	.242
DM_MUM1	-.419	.252	.028	-.238	.175
DM_MUM2	.099	**.543**	.467	-.113	-.317
DM_MUM3	-.377	.371	.246	.393	-.407
DM_BUI1	.085	**-.698**	.057	.053	.110
DM_BUI2	.400	-.310	.196	**-.512**	.471
DM_BUC	.429	**-.654**	.115	-.175	.035
DM_BUP3	**.777**	.121	.158	.319	.117
DM_BUP4	.456	-.179	.344	.437	-.073
DM_BUM1	**-.588**	-.170	**.501**	.095	.262
DM_BUM2	.287	-.153	**.784**	-.099	-.328
DM_BUM3	**.600**	.067	.255	.243	-.080
DM_MLI1	**-.512**	-.234	-.023	**.635**	.064
DM_MLI2	-.342	-.265	-.329	**.539**	-.220
DM_MLC	.498	-.078	-.225	-.329	**-.511**
DM_MLP3	**.653**	.323	-.352	.144	-.138
DM_MLP4	-.044	.366	**-.649**	.022	.053
DM_MLM1	-.079	**.523**	-.329	-.013	.346
DM_MLM2	-.479	.432	.079	-.368	.333
DM_MLM3	-.379	.382	.092	-.162	.319
DM_BLI1	**-.684**	-.489	-.162	-.025	-.212
DM_BLI2	**-.645**	-.499	-.257	-.179	-.219
DM_BLC	-.030	**-.659**	-.222	**-.603**	.025
DM_BLP3	**.674**	.068	-.170	-.003	-.292
DM_BLP4	.299	.132	**-.644**	-.081	-.353
DM_BLM1	**-.705**	.402	.088	-.150	-.125
DM_BLM2	-.279	**.517**	.388	-.282	**-.521**
DM_BLM3	-.094	**.628**	.203	-.145	-.019

obvious separation, as previously as identified by dental nonmetric (Irish, 1997, 1998a,b, 2005, 2006) and other biocultural findings. The PC loadings in the table provide specifics on TSA. High magnitude negative PC1 loadings characterize North Africans on the right of the x-axis in Figure 3, i.e., relatively large LI1, and BL-only values for UM1, LI2, and LM1. High positive PC1 loadings for the sub-Saharan samples show a relatively large LP3, MD-only for UI2, and BL-only for UP3 and UM3. The TSA differences on PC2 and PC3 similarly account for sample locations on the y- and z-axes (Figure 3). To utilize information in all five PCs, Ward's cluster analysis was used to classify samples (Figure 4) based on the factor scores derived from DM_values (Figure 5).

Three main clusters are evident in Figure 4: (1) sub-Saharan only, (2) North African only, and (3) North African with four sub-Saharan samples. Interestingly, the latter samples are from regions

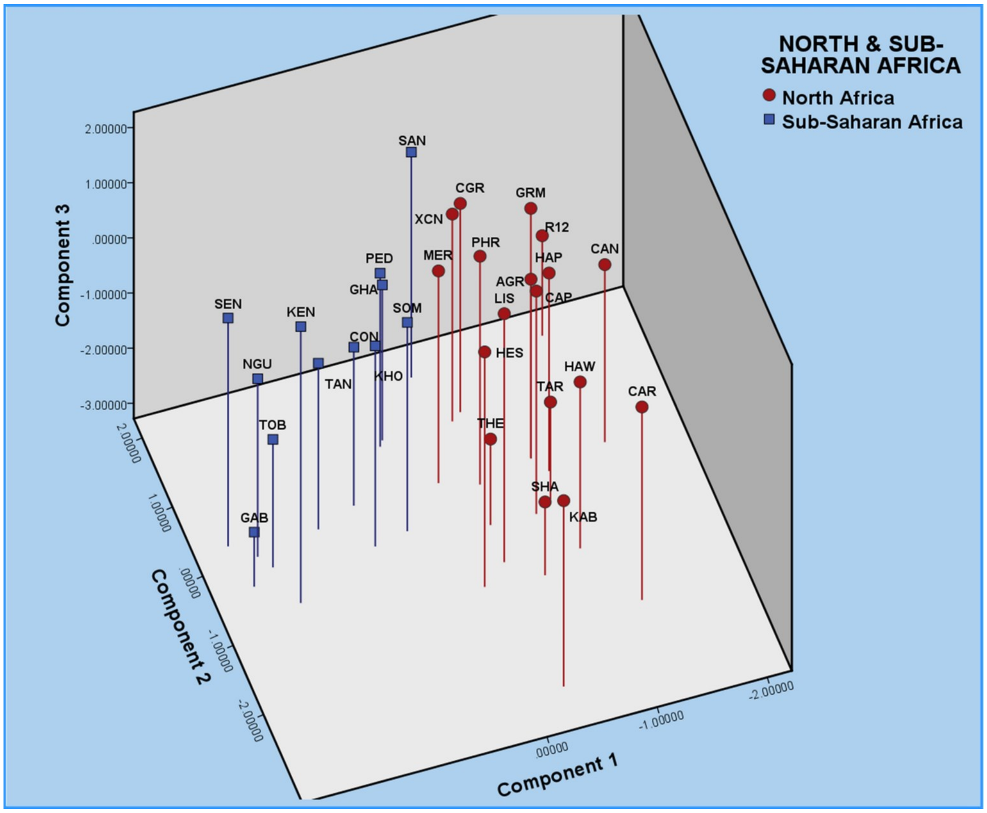

Fig. 3. Samples plot of first three factor scores.

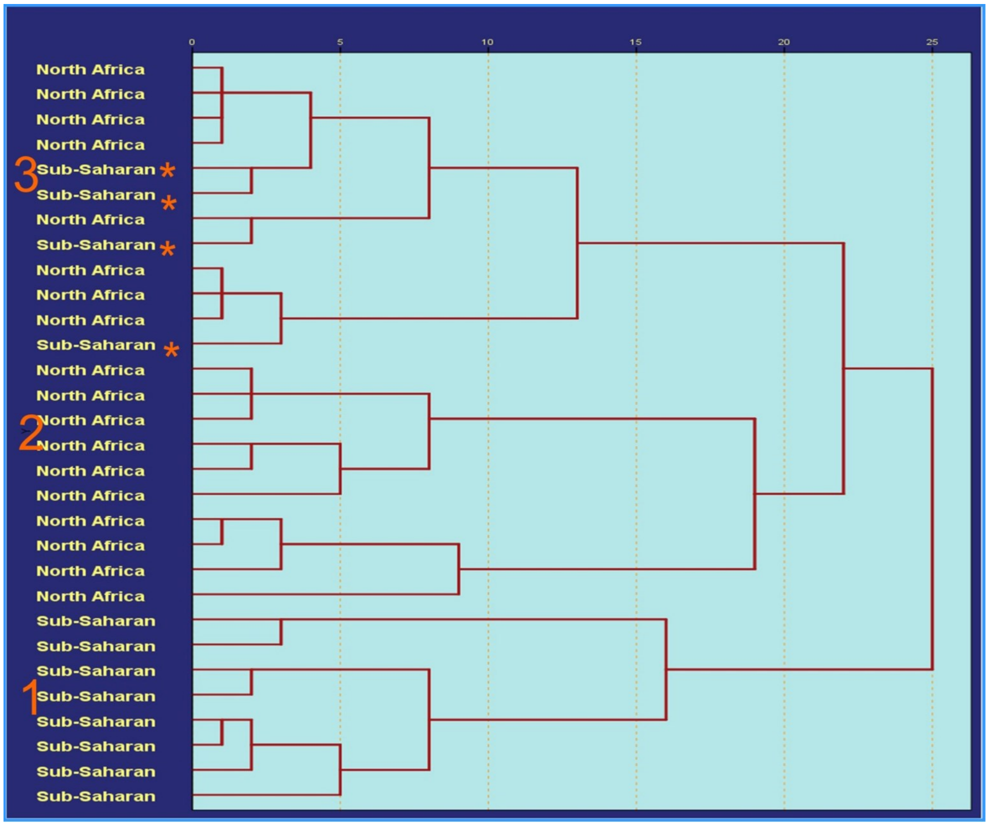

Fig. 4. Ward's cluster analysis of all five factor scores (showing three main clusters as identified in the text).

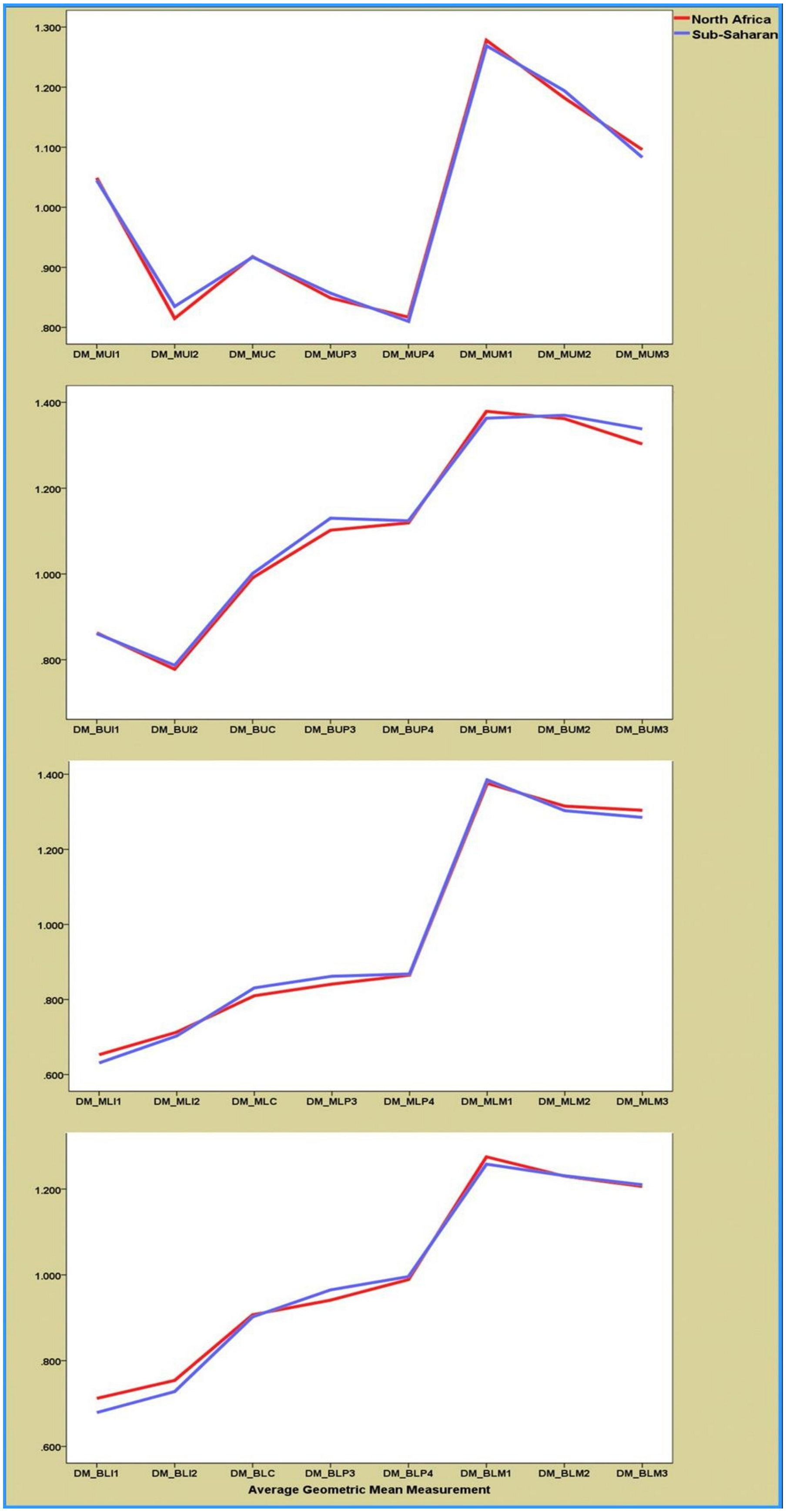

Fig. 5. Average MD and BL DM-values in upper and lower jaws.

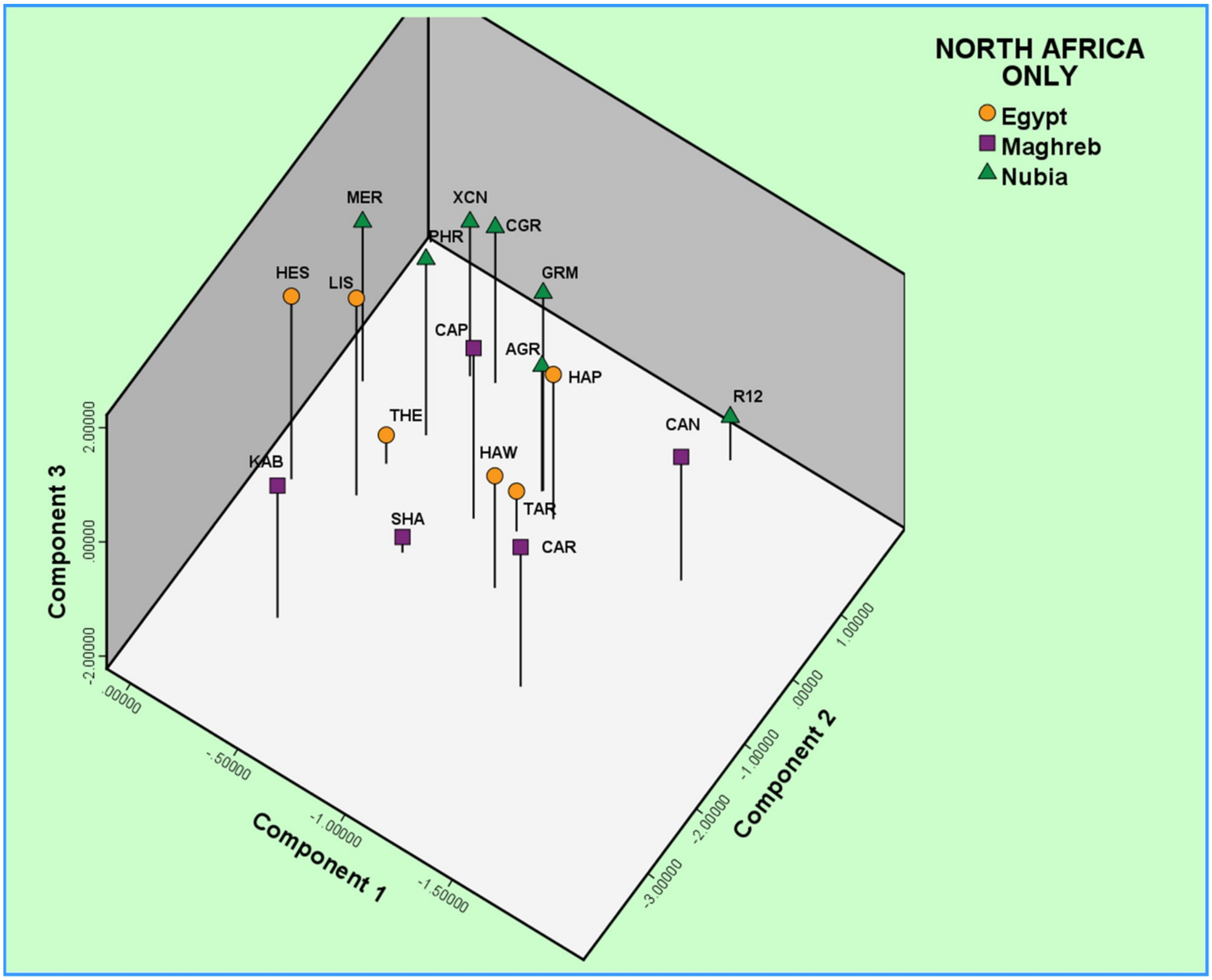

Fig. 6. Samples plot of first three factor scores for North Africans only.

in the proximity of "northern" peoples (e.g., Somalia) -- which may reflect evidence of admixture.

Finally, to demonstrate that TSA analysis can be applied on a regional scale as well, just the 18 North African samples were compared. Figure 6 illustrates that, even at this finer-grained level of study, some differentiation among the Nubian, Egyptian, and Maghreb samples is possible. In other words, the results presented here indicate that an "old" method and basic crown diameter data can be successfully used for affinity estimation, if overall size is accounted for and "shape" is considered. Thus, (relative) size does matter.

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A descriptive study of African American deciduous dentition

Loren R. Lease
Department of Sociology, Anthropology, and Gerontology, Youngstown State University, Youngstown, Ohio 44555

Keywords: Dental Morphology, Biological Ancestry, ASUDAS

ABSTRACT Descriptive studies of the deciduous dentition morphology have been presented as an inclusion in permanent dentition studies, the focus of archaeological populations or on specific traits within modern populations.

The present study describes 25 morphological traits of deciduous dentition in two African American samples from Memphis, TN and Dallas, TX (N= 218), and a European American sample (N=100) from Cleveland, OH. These traits represent the most commonly used traits in population microevolution studies, describing various ancestral groups.

Results indicate trait frequency variation between the two African American samples, as well as in comparison to European American samples. Traits varying in frequency between the two sample populations include maxillary lateral incisor shovel shape trait (69% vs. 46%), canine tuberculum dentale (40% vs. 22%), canine mesial ridge (3% vs. 7%), and maxillary posterior molar hypocone development (76% vs. 92%). Trait frequencies higher than found in previous studies include maxillary central incisor shovel shape trait (38%) and maxillary lateral incisor shovel shape trait (68%), canine tuberculum dentale (40%), maxillary molar complexity (20%), cusp six (33%) and seven (68%), and the Y-groove on the mandibular posterior molar (69%). Trait frequencies seen lower in previous studies include tuberculum dentale trait on both maxillary incisors (8% and 3%) and the hypocone development of the maxillary posterior molar (76%). The level of trait expression is informative when comparing populations, especially the molar traits. For example, Carabelli's pit/fissure is the most common trait expression in African American samples, unlike European American samples.

There have been very few studies focusing solely upon the morphology of the deciduous dentition. Analyses of the deciduous dentition are usually included as part of a larger study of the permanent dentition, (e.g. Aguirre *et al.* 2006) or as an archaeological study (e.g. Sciulli 1998). A few examples of population studies on the deciduous dentition include Jørgensen (1956), Hanihara (1968), Sciulli (1977, 1990, 1998), Harris (2001), Grine (1986) and Lease (2003). Rarely has African American dentitions been described independently.

The present study examines 25 morphological traits of the deciduous dentition in three samples: two African American samples from Memphis, TN and Dallas, TX (N= 218) and a European American sample (N=100) from Cleveland, OH. These traits represent the most commonly used traits in population microevolution studies, describing various ancestral groups. The goal of the study is to provide a description of deciduous trait presence and trait variation within the African American samples.

MATERIALS

Morphological data were collected from a total of 318 individuals from three samples representing two ancestral groups: African and European. The African American children are represented by 117 individuals from Memphis, Tennessee and 101 individuals from Dallas, Texas. The European American children are represented by 100 individuals from Cleveland, Ohio.

Data were collected from two sources: dental stone casts and photographs. Dental casts were the primary resources for the Memphis, TN and the Cleveland, OH samples. The Dallas, TX sample comprises of 5″x7″photographs taken in a professional laboratory (Condon *et al.* 1998).

Casts were included in the study if they met the following criteria: morphological features were

Correspondence to: Loren R. Lease
Department of Sociology, Anthropology, and Gerontology, Youngstown State University, Youngstown, Ohio, 44555
lrlease@ysu.edu

clearly visible, there were clear separations between teeth, there was no stretching of the cast or chipping of the cast and at least one member of the antimere was present (Lease 2003). Photographs were included in the study if the morphology was clearly visible and no caries were present. Edgar (2002) tested the viability of using two different materials and found fewer morphological traits were visible for photographs; intra-observer error is no different than twice observing the same dentition in the same format.

The children (57 females and 60 males) who comprise the Memphis sample were routine dental patients seen during the 1990s at the Pediatric Dental Department of the University of Tennessee, Memphis (Lease and Harris 2001). The majority of the children resided in the "greater metropolitan area of Memphis" which includes suburban and urban areas around Memphis. The socio-economic status was described as middle class and they had access to health care at the University of Tennessee Medical Center (EF Harris, personal communication, 2003). Ancestry identification was determined by parents.

The Dallas, TX sample consisted of 101 children buried in the Freedman's Cemetery, the sex of whom was unknown. Individuals buried at the Freedman's Cemetery were residents of urban Dallas. The cemetery was active from 1867 to 1907, with the majority of excavated burials dating from 1900 to 1907 (Condon *et al.* 1998). Juveniles in the study lived post-slavery (HJH Edgar, personal communication, 2003). All socio- economic statuses available to African Americans at the time are represented.

The European American sample was collected at the School of Dentistry, Case Western Reserve University from the Bolton-Brush Longitudinal Growth Study. Ancestry came from parental determination. Data was collected on 50 males and 50 females born between 1920 and 1945 (Bailey 1992). The children resided in the urban areas of Cleveland, OH and were described as having access to good health care, education and nutrition (Bailey 1992).

METHODS

Morphological data consists of the scores of 25 deciduous traits. These 25 traits represent the most commonly used traits in micro-evolutionary studies and are the basis for creating Dental Morphological Complexes describing various ancestral groups (Jørgensen1956, Hanihara 1963, Hanihara 1966, Hanihara 1967, Grine 1986, Sciulli 1998). A complete description of expressions and traits can be found in Lease (2003).

Morphological data were collected following Sciulli (1998). When present, both the right and left teeth of each individual were scored. If the expression of the antimeres was the same, that score was used as the expression of the tooth. If the score of a trait was different between the antimeres, the more complex expression was used to represent the tooth. If only one tooth was present, that expression was used to represent the tooth. No root traits were collected due to the principle sources (casts and photographs).

In the analysis and discussion of the morphological traits, the use of the term "deciduous molar" reflects the historic or traditional usage in dental anthropology and the scoring procedures (Lease 2003). Ontologically these teeth are premolars (Sciulli 1998).

ANALYSIS

Statistical analyses were performed in SAS version 8.02. The range of variation for each trait was calculated by expression frequencies for each sample. The weighted average expression (W) was calculated for each feature: $W = (Sc_i x_i / Sx_i)$. C_i is the expression value and x_i is the number of individuals with that expression. The weighted average is one method that captures where the range of variation within the sample lies.

For example, the morphological trait of shovel shape for the maxillary central incisor has four expressions: 0, 1, 2, 3. The weighted average for this trait in the Cleveland sample is 1.15.

$$W = (\Box c_i x_i / \Box x_i) = ((0*28)+(1*40)+(2*21)+(3*11))/100 = 1.15.$$

Therefore, dichotomization into absence/ presence frequencies is between the expression class 1 and expression class 2 for the maxillary central incisor.

The second analysis was performed to calculate the dichotomization of frequencies of the morphological traits. Dichotomization (presence/absence) frequencies should reflect the weighted averages for each trait.

TABLE 1. Frequency counts and weighted averages

Trait	Expression	Cleveland N= 100	Memphis N= 117	Dallas N=101
i^1ss	0	28	30	42
	1	40	35	21
	2	21	25	26
	3	11	9	12
	W	1.15	1.13	1.46
i^2ss	0	10	31	31
	1	39	35	23
	2	28	39	31
	3	22	11	15
	W	1.63	1.26	1.30
ucss	0	14	35	38
	1	38	30	26
	2	34	36	25
	3	14	16	13
	W	1.48	1.28	1.13
$i_1$ss	0	91	69	81
	1	5	4	7
	2	4	1	4
	3	0	2	5
	W	0.13	0.16	0.26
$i_2$ss	0	67	80	69
	1	26	17	11
	2	6	4	11
	3	1	2	10
	W	0.58	0.30	0.62
lcss	0	34	48	45
	1	44	36	18
	2	19	17	22
	3	3	12	16
	W	0.91	0.94	1.09
i^1ds	0	99	100	98
	W	0.00	0.00	0.00
l^2ds	0	98	114	97
	W	0.00	0.00	0.00
ucds	0	94	114	98
	1	2	1	1
	2	3	0	1
	W	0.08	0.01	0.03
i^1 interruption groove	0	100	100	98
	2	0	1	0
	W	0.00	0.01	0.00

The presence/absence frequency of a trait was calculated as in the following example using the shovel shape of the deciduous maxillary central incisor:

<u>Shovel shape</u> : ui1
0 Absent: lingual surface smooth
1 Semi-shovel: slight
2 Shovel: marginal ridges present
3 Strong shovel: marginal ridges broad and wide

Expressions 0 and 1 were designated as the absence of the shovel shape trait and expressions 2 and 3 were designated as the presence of the trait in the individuals. The frequency of the trait (presence) in the population can then be expressed at p = 2-3 / 0-3, with 2-3 as the number of individuals having the expression 2 or 3 and 0 to 3 being the total number of individuals scored (Sciulli 1998).

The presence frequencies for the anterior dentition traits among the three samples were tested for significance using Student's T test (Tables 3-5). Expression frequencies for the posterior dentition were tested for significance (Tables 6-8).

RESULTS

Of the original 25 traits, nine traits had minimal variation within the samples (Table 1). These traits were: double shoveling, interruption grooves (for both the maxillary and mandibular central and lateral incisors) and posterior mandibular molar number. These traits were eliminated from further analyses.The remaining 16 traits were dichotomized for each sample either by absence/ presence (i.e. shovel shape) or by the feature expressed (i.e. Carabelli's cusp vs. pit) (Table 2).

Five of the 12 anterior traits (Table 3) are significantly different for the Cleveland and Memphis samples. The Memphis sample has greater percentage for the maxillary lateral incisor and mandibular canine shovel shape trait. The Cleveland sample has greater frequency for the maxillary incisors tuberculum dentale and maxillary canine distal ridge.

The analyses of the posterior traits are found in Table 6. The majority of the traits examined for Cleveland and Memphis indicate that the Memphis sample exhibits higher frequencies for the more complex expressions. Regarding hypocone

TABLE 1., cont'd

Trait	Expression	Cleveland N= 100	Memphis N= 117	Dallas N=101
I^2 interruption groove	0	99	115	97
	W	0.00	0.00	0.00
i^1td	0	78	94	92
	1	17	3	6
	2	3	3	1
	3	0	0	1
	W	0.23	0.09	0.11
i^2td	0	83	110	96
	1	15	3	2
	2	1	1	1
	W	0.17	0.04	0.04
uctd	0	44	69	79
	1	29	13	6
	2	25	33	13
	3	2	0	4
	W	0.85	0.69	0.35
ucmr	0	98	114	96
	1	1	2	4
	2	0	1	2
	3	1	0	1
	W	0.01	0.03	0.11
ucdr	0	88	109	100
	1	9	7	1
	2	1	0	1
	3	1	0	0
	4	1	0	0
	W	0.18	0.06	0.03
lcdr	0	99	112	101
	1	0	1	0
	2	1	3	1
	3	0	1	0
	4	0	0	0
	W	0.02	0.09	0.02

development, Cleveland has higher frequencies for only having the eocone and protocone present (corresponding to Hanihara's (1963) maxillary first molar morphology of 2), Memphis has higher frequencies of 4 and 5 (Hanihara's (1963) 3H and 4 -/4) for the maxillary anterior molar. Similar results are seen for the maxillary posterior molar. The Memphis sample has higher frequencies of the accessory cusps 6 and 7, as well as more cusps on the mandibular anterior molar. In addition, the individuals within the sample have higher frequencies of deflecting wrinkle and a pit/groove for the proto-stylid and the Y-5 molar pattern.

For Carabelli's trait, in the Cleveland sample the trait is more likely to be absent or a cusp, and in the Memphis sample,a pit. With regards to the mandibular posterior groove patterns, the Cleveland sample more often exhibited the + pattern and Memphis the Y pattern.

Comparing Cleveland and Dallas samples

Frequencies of 11 of the 12 anterior traits (Table 4) are significantly different between the Cleveland and Dallas samples. Dallas has higher percentages for maxillary and mandibular central incisor shovel shape trait, mandibular lateral incisor and canine shovel shape trait and maxillary canine mesial ridge. Cleveland has higher presence rates for the maxillary lateral incisor shovel shape, the maxillary incisor and canine tuberculum dentale and the maxillary canine distal ridge.

Similar results are found for the analyses of the posterior traits for the Cleveland and Dallas samples (Table 7) with a few exceptions. Unlike the Cleveland/Memphis analysis of Carabelli's trait, there is no statistical significance between the cusp frequencies for Cleveland and Dallas samples.

Comparing Memphis and Dallas samples

When comparing the two African American samples, four of the 12 traits are significantly different (Table 5). The Memphis sample shows the shovel shape trait more often for the maxillary lateral incisor and canine, while the Dallas samples has higher frequencies of that trait in the mandibular central and lateral incisors.

When comparing the posterior dentition traits (Table 8) for the two African American samples,there are small differences in frequency expressions. The Memphis sample has higher frequencies for the less complex expression for hypocone development for both maxillary molars, while Dallas is statistically significant for the more complex development expressions. Memphis

TABLE 1., cont'd

Trait	Expression	Cleveland **N= 100**	Memphis **N= 117**	Dallas **N=101**
m^{1}hypocone	2	61	16	3
	3 (3M1 & 3M2)	22	22	19
	4 (3H1 & 3H2)	12	57	60
	5 (4- &4)	5	20	20
	W	2.61	3.70	3.95
m^{2}hypocone	3 (3A)	23	15	1
	4 (3B)	34	12	7
	5 (4-)	22	16	17
	6 (4)	11	70	78
	W	3.47	5.76	5.67
m^{2}cusp 5	0	79	110	100
	1	11	4	1
	W	0.12	0.04	0.01
m^{2}Carabelli's trait	0	21	14	13
	1	22	24	44
	2	15	30	6
	3	2	12	2
	4	5	2	8
	5	5	2	6
	6	29	31	22
	W	2.80	2.82	2.53
m$_1$cusp number	3	0	3	5
	4	38	40	27
	5	51	59	54
	6	9	8	15
	7	1	3	1
	W	4.73	4.72	4.80
m$_2$ groove pattern	1 (+)	64	42	23
	2 (x)	2	5	7
	3 (y)	31	60	68
	W	1.66	2.17	2.46
m$_2$ cusp number	1	1	0	1
	2	95	87	68
	3	3	26	26
	W	2.02	2.23	2.26
m$_2$ deflecting wrinkle	0	47	52	52
	1	26	16	4
	2	19	31	25
	3	5	8	18
	W	1.46	0.95	1.09

TABLE 1., cont'd

Trait	Expression	Cleveland **N= 100**	Memphis **N= 117**	Dallas **N=101**
m_2 protostylid	0	90	90	59
	1	0	20	35
	2	5	2	3
	3	4	2	3
	6	1	0	0
	W	0.28	0.26	0.50
m_2 cusp 6 entoconulid	0	89	85	67
	1	6	13	21
	2	1	9	5
	3	0	4	6
	4	0	1	1
	W	0.08	0.42	0.65
m_2 cusp 7 metaconulid	0	39	36	51
	1	15	7	4
	2	30	45	20
	3	15	19	17
	4	1	4	7
	5	0	1	1
	W	1.24	1.56	1.28
m_2 mesial trigonid crest	0	87	88	83
	1	10	16	14
	W	0.10	0.25	0.14

shows a slightly higher frequency for the pit expression while Dallas has a higher cusp expression for Carabelli's trait. Memphis also expresses the + groove pattern more often than Dallas. Dallas has a higher frequency of the Y pattern. Memphis shows a higher frequency for cusp 6 in comparison to Dallas. Dallas has a higher frequency for the mesial trigonid crest.

CONCLUSIONS

The analyses of the three samples indicate that African American deciduous dentition usually has the more complex expression of a posterior trait or has a higher frequency of an anterior trait. In comparison to the European American sample, the African American samples have higher frequencies of:

Shovel shape trait
Mesial canine ridge
Hypocone development on maxillary molars
Carabelli's pit or groove trait
Y posterior mandibular molar groove pattern
Deflecting wrinkle
Pit/groove trait for protostylid
Presence of cusps 6 and/or 7

However, the samples from Memphis and Dallas also have lower frequencies of tuberculum dentale and distal canine ridge traits, as well as the X and + posterior mandibular molar groove patterns in comparison to the Cleveland sample.

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TABLE 2. Dichotomization based on weighted averages

Trait		Absence	Presence	
shovel shape		0, 1	2, 3	
tuberculumdentale	incisor	0	pits/grooves (1)	
	canine		ridge (2)	
maxillary canine mesial ridge		0	1+	
maxillary canine distal ridge		0	1+	
mandibularcanine distal ridge		0	1+	
maxillary anterior molar hypocone				2 = 2, 3M1&3M2 = 3, 3H1&3H2 = 4, 4-and 4 = 5
maxillary posterior molar hypocone				3A = 3, 3B = 4, 4- = 5, 4 = 6
maxillary posterior molar cusp 5		0	1+	
Carabelli’s trait				absence (0), pit (1-3), cusp (4-6)
cusp number of mandibular anterior molar				3 or 4 cusps = 1 5+ =2
groove pattern on the mandibular posterior molar				+ (1), X(2), Y (3)
deflecting wrinkle		0, 1	2, 3	
protostylid				absence (0), pit/groove (1-2), cusp (3-4)
cusp 6		0	1+	
cusp 7		0-2	3-5	
mesial trigonid crest		0	1	

TABLE 3. Results: Cleveland and Memphis samples – anterior dentition

	Cleveland %	Memphis %	$p<0.05$
i^1ss	32	34.4	
i^2ss	51	68.7	0.000
ucss	48	45	
$i_1$ss	4	4	
$i_2$ss	7	6	
lcss	22	38	0.000
i^1td	17	3	0.000
i^2td	15	2.6	0.000
uctd	25	28.7	
ucmr	1	2.6	
ucdr	11	6	0.025
lcdr	1	4.3	

TABLE 4. Results: Cleveland and Dallas samples – anterior dentition

	Cleveland %	Dallas %	$p<0.05$
i^1ss	32	38	0.014
i^2ss	51	46	0.025
ucss	48	37.3	0.001
$i_1$ss	4	9.3	0.025
$i_2$ss	7	21	0.000
lcss	22	37.6	0.000
i^1td	17	6	0.001
i^2td	15	2	0.000
uctd	25	12.7	0.000
ucmr	1	6.8	0.014
ucdr	11	1.9	0.002
lcdr	1	0	

TABLE 5. Results: Memphis and Dallas samples – anterior dentition

	Cleveland %	Dallas %	$p<0.05$
i^1ss	32	38	0.014
i^2ss	51	46	0.025
ucss	48	37.3	0.001
$i_1$ss	4	9.3	0.025
$i_2$ss	7	21	0.000
lcss	22	37.6	0.000
i^1td	17	6	0.001
i^2td	15	2	0.000
uctd	25	12.7	0.000
ucmr	1	6.8	0.014
ucdr	11	1.9	0.002
lcdr	1	0	

TABLE 6. Results: Cleveland and Memphis samples – posterior dentition

		Cleveland %	Memphis %	p<0.0.5
um1 hypocone	2	61	13.9	0.000
	3	22	19	
	4	12	49.6	0.000
	5	5	17.3	0.000
um2 hypocone	3	25.5	13	0.000
	4	37.7	10.6	0.000
	5	24.4	13.8	0.001
	6	12	60.9	0.000
Cusp 5		12	3.5	0.004
Carabelli's Trait	absent	21	12	0.002
	pit	39.4	57.9	0.000
	cusp	39.4	30.7	0.004
cusp number of the mandibular anterior molar	1	38	38	
	2	61.6	68	0.014
groove pattern	+	66	39	0.000
	X	2	4.7	
	Y	32	56	0.000
deflecting wrinkle		24.7	38.2	0.000
protostylid	Pit/ groove	5	19.2	0.000
	cusp	5	1.7	
cusp 6		1	24	0.000
cusp 7		16	21	0.025
mesial trigonid crest		10	5.4	0.025

TABLE 7. Results: Cleveland and Dallas sample – posterior dentition

		Cleveland %	Dallas %	p<0.0.5
um1 hypocone	2	61	2.9	0.000
	3	22	18.6	
	4	12	58.8	0.000
	5	5	19.6	0.000
um2 hypocone	3	25.5	0	0.000
	4	37.7	6.8	0.000
	5	24.4	16.5	0.008
	6	12	75.7	0.000
cusp 5		12	1	0.001
Carabelli's Trait	absent	21	12.9	0.004
	pit	39.4	51.5	0.000
	cusp	39.4	35.6	
cusp number of the mandibular anterior molar	1	38	31.4	0.008
	2	61.6	69	0.008
groove pattern	+	66	23.5	0.000
	X	2	7	0.025
	Y	32	69.4	0.000
deflecting wrinkle		24.7	43.4	0.000
protostylid	Pit/ groove	5	38	0.000
	cusp	5	3	
cusp 6		1	33	0.000
cusp 7		16	25	0.002
mesial trigonid crest		10	14	

TABLE 8. Results: Memphis and Dallas sample – posterior dentition

		Memphis %	Dallas %	p<0.0.5
um1 hypocone	2	13.9	2.9	0.001
	3	19	18.6	
	4	49.6	58.8	0.002
	5	17.3	19.6	
um2 hypocone	3	13	0	0.000
	4	10.6	6.8	
	5	13.8	16.5	
	6	60.9	75.7	0.000
cusp 5		3.5	1	
Carabelli's Trait	absent	12	12.9	
	pit	57.9	51.5	0.014
	cusp	30.7	35.6	0.025
cusp number of the mandibular anterior molar	1	38	31.4	0.008
	2	68	69	
groove pattern	+	39	23.5	0.000
	X	4.7	7	
	Y	56	69.4	0.000
deflecting wrinkle		38.2	43.4	0.025
protostylid	Pit/ groove	19.2	38	0.000
	cusp	1.7	3	
cusp 6		24	33	0.002
cusp 7		21	25	
mesial trigonid crest		5.4	14	0.002

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Accuracy of estimating age from eruption levels of mandibular teeth

Sheryl E. Wilmott[1], Mark P. Hector[2], Helen M. Liversidge[1]
1 Queen Mary University of London, Barts and The London School of Medicine and Dentistry, Institute of Dentistry, Turner Street, London, United Kingdom E1 2AD. 2 School of Dentistry, University of Dundee
Park Place, Dundee, Scotland, DD1 4HN

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ABSTRACT Little is documented on the accuracy of estimating age from alveolar eruption (AE) or partial eruption (PE). The aim of this study was to compare the accuracy of age estimation from eruption levels. Methods tested were Gleiser and Hunt (1955), Garn et al. (1958), Ando et al. (1965), Haavikko (1970) and clinical eruption from Smith et al. (1998). The sample was 946 panoramic dental radiographs from children aged 3-16 years. Left mandibular teeth (excluding third molar) were assessed for eruption level (AE and PE) and root quarters. Methods, teeth and eruption levels were deemed to be accurate if the average difference between estimated and chronological ages was not significant to zero using a t-test (P>0.05). Results show that early erupting permanent teeth were fairly good at estimating age, although there was considerable age variation in eruption. Haavikko incisors and molars at AE and Haavikko and Smith central incisor and second molar at PE estimated age accurately. Root stage of erupting teeth estimated age more accurately than eruption level using Haavikko. These findings suggest that erupting permanent mandibular teeth can be helpful in estimating age.

An 1837 pamphlet by Saunders entitled "The Teeth: a Test of Age" (considered with reference to the factory children) was one of the earliest uses of age estimation from eruption of teeth (Miles 1963). This stated that if the third molar was present in the mouth (i.e. the first permanent molar M1, behind the deciduous molars), the child was likely to be 9 years of age.

The accuracy of estimating age from tooth formation has been well documented, however, the accuracy of estimating age from alveolar or partly erupted or the clinical presence of a tooth in the oral cavity is unknown. Estimating age from a partially erupted tooth is useful if root stage cannot be visualised or has been damaged. The aim of this study was to assess the accuracy of estimated age using several methods that provide mean/median age of tooth eruption levels.

MATERIAL AND METHODS

The sample was panoramic dental radiographs of 946 healthy children of known age attending a dental teaching hospital. Subjects include at least 30 boys and 30 girls of each year of age from 3 to 16 (489 boys, 457 girls, mean age 9.80, age 3.00-16.99). Each year age group was made up similar numbers of children from Bangladeshi and white ethnic origin. Panoramic radiographs were taken with consent in the course of diagnosis and treatment in Paediatric Dentistry and Orthodontics. This is the same sample used to test dental age estimation methods by Maber et al. (2006), Liversidge et al. (2010) and AlQahtani et al. (2014).

Eruption levels of seven mandibular teeth (excluding the third molar) on the left side were assessed by the first author. Eruption levels were defined as developing tooth within bone, cusp tips at or just above the alveolar bone level (AE), cusp tips considerably above the alveolar bone level but not fully erupted (PE), fully erupted. Eruption levels and root fractions are illustrated in Figure 1. Intra-observer reliability of assessing eruption level was calculated from duplicate scoring of 20 radiographs (140 teeth) yielding a Kappa value of 0.96. Tooth formation of seven mandibular teeth on the left side were assessed using tooth stages of Moorrees et al. (1963) as part of a previous study (Maber et al., 2006).

Correspondence to: Dr. Helen Liversidge
Institute of Dentistry
Turner Street, London, United Kingdom E1 2AD
Email: h.m.liversidge@qmul.ac.uk

The number of erupting teeth (AE and/or PE) on the left side of the mandible within an individual was counted.

Age was estimated if a tooth was at AE or PE, using Glesier and Hunt (1955), Garn et al. (1958), Ando et al. (1965) and Haavikko (1970). If a tooth was partially erupted, age was also estimated from Haavikko (1970) and Smith et al. (1998). These values are shown in Table 1. Values for Ando et al. (1965) were calculated in Liversidge (2003) and contain an error M1 in boys. The raw data show that 60% of the youngest age category had reached AE.

Chronological age was subtracted from estimated age by tooth type and eruption level and the difference

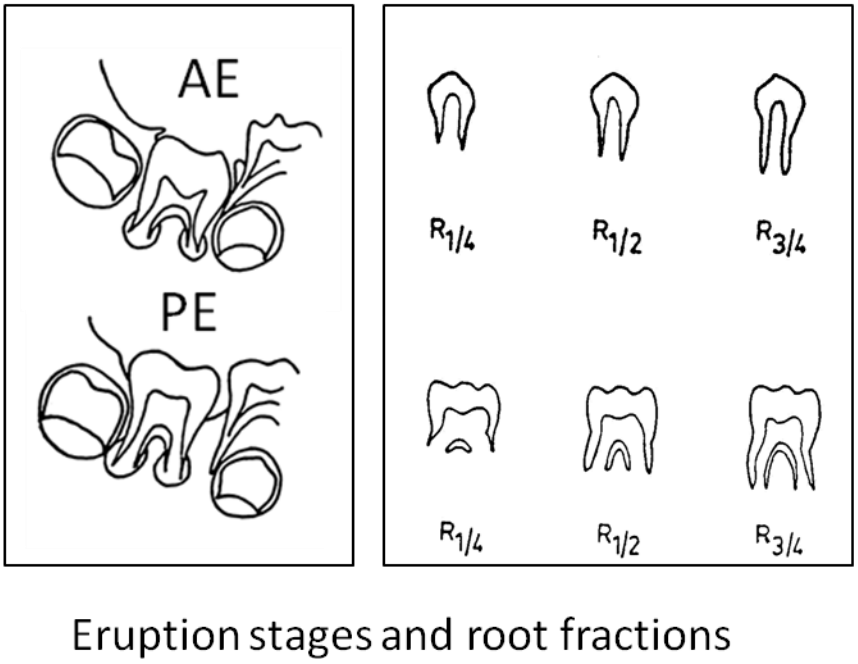

Fig. 1. Eruption levels and root fraction stages used in this study. A molar is shown at stages AE (alveolar eruption) and PE (partial eruption). Root fractions are from Haavikko (1970).

TABLE 1. Methods of age estimation from alveolar (AE) and partial (PE) stages of eruption of mandibular teeth used in this study[1]

Tooth	Sex	Gleiser +Hunt AE	Garn AE	Ando AE	Haavikko AE	Haavikko PE	Smith PE
I1	girls			6.30	**5.8**	**6.2**	**6.15**
	boys			6.28	**5.9**	**6.3**	**6.26**
I2	girls			7.13	**6.5**	6.8	7.24
	boys			7.14	**6.9**	7.3	7.47
C	girls			9.24	8.8	9.2	9.81
	boys			9.54	9.8	10.4	10.71
P1	girls		**9.7**	9.59	9.1	9.6	10.45
	boys		**10.1**	9.61	9.6	10.3	10.89
P2	girls		**10.3**	10.46	9.2	10.1	11.62
	boys		**11.1**	10.54	10.3	11.1	11.96
M1	girls	**5.1**	5.7		**5.0**	6.3	6.27
	boys	**5.4**	5.8		**5.3**	6.3	6.32
M2	girls		10.7	10.86	**9.9**	**11.4**	**11.58**
	boys		11.2	10.98	**10.8**	**12.2**	**12.06**

[1]Methods include mean age from Gleiser and Hunt (1955), Garn et al. (1958), mean age calculated from Ando et al. (1965) tabulated in Liversidge (2003), median age from Haavikko (1970) and mean age of clinical emergence from Smith et al. (1998). Bold values estimated age with no average bias (difference between dental age and chronological age not significant to zero).

compared to zero using a t-test with a significance level of P<0.05. A method, tooth or eruption level was considered accurate if the difference was not significant to zero. The difference between chronological and estimated age for teeth at AE and PE was also split by root fractions and compared to zero if N≥10 per tooth stage.

RESULTS

The number of erupting teeth (AE and/or PE) in the left side of the mandible within an individual ranged from zero to four. Just over half of this large sample (52%) had one or more erupting teeth. This is a reflection of the age range of the sample with most of the youngest individuals having no permanent teeth erupted and most of the older individuals having all seven permanent teeth erupted. The most frequent number of erupting teeth was one erupting tooth and only a small percentage of the sample had three or four erupting teeth.

Accuracy of estimating age from eruption levels showed that generally, early erupting teeth performed better than late erupting teeth. The difference between estimated and chronological age using the methods tested in this study for individual teeth are shown in Table 2. The difference for M1 at AE using Gleiser and Hunt was not significant to zero. The two premolars using Garn also estimated age accurately. No tooth using Ando performed well. Alveolar eruption of incisors and molars and partial eruption of I1 and M2 using Haavikko and Smith estimated age accurately. Most tooth types underestimated age with the canine and premolars considerably under-estimating age at both eruption levels.

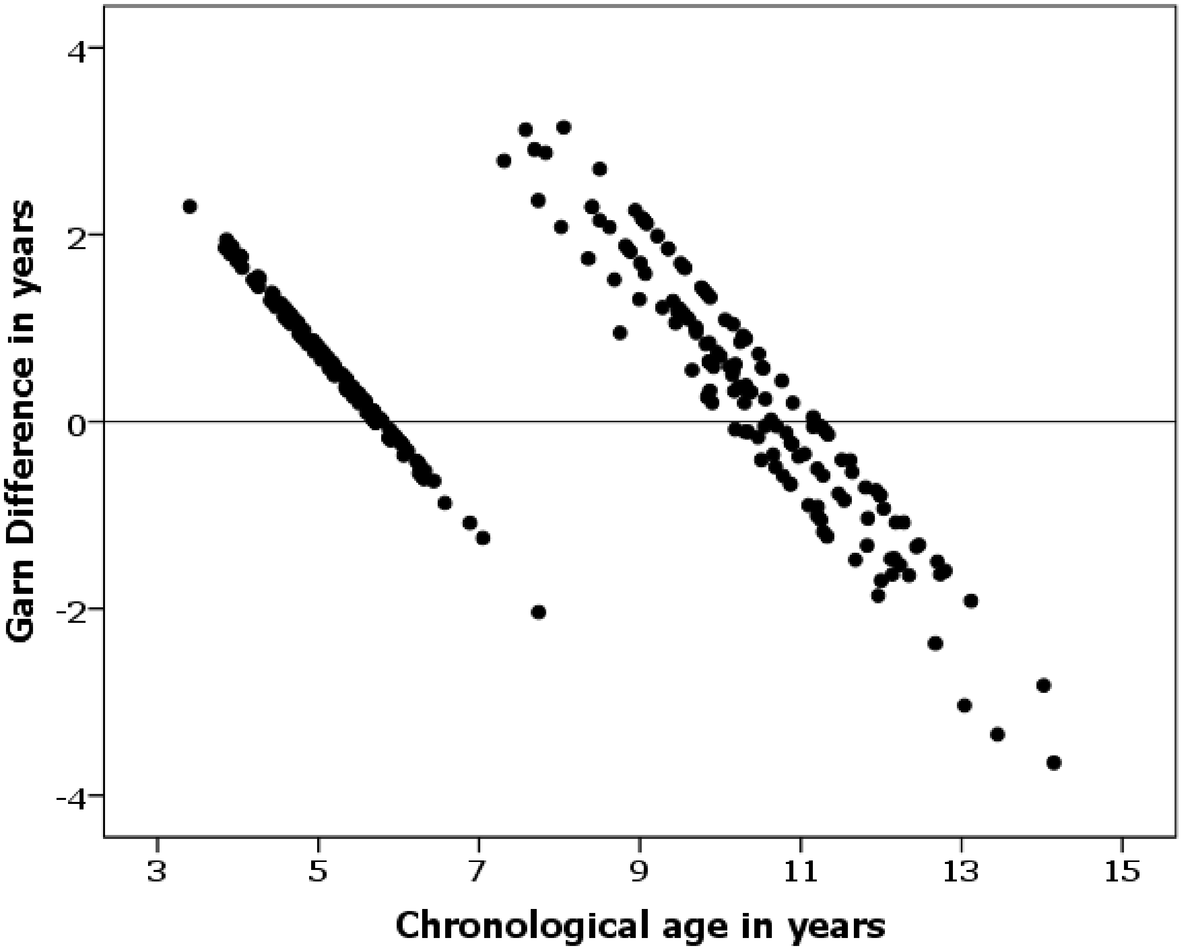

Fig. 2. Scatterplot of estimated age using Garn alveolar eruption and chronological age in years.

TABLE 2. Accuracy of estimating age from alveolar eruption (AE) and partial eruption (PE) using methods of Gleiser and Hunt, Garn, Ando and Haavikko[1]*, and Smith*

Method Eruption level	Tooth	N	Mean difference	SD	P value
Gleiser+Hunt					
AE	M1	106	0.04	0.78	0.62
Garn					
AE	P1	46	-0.32	1.36	0.11
AE	P2	39	-0.28	1.30	0.19
AE	M1	109	0.55	0.79	0.00**
AE	M2	115	0.58	1.25	0.00**
Ando					
AE	I1	59	0.57	0.68	0.00**
AE	I2	48	0.28	0.84	0.03*
AE	C	36	-0.91	1.10	0.00**
AE	P1	46	-0.69	1.32	0.00**
AE	P2	39	-0.42	1.29	0.05*
AE	M2	115	0.56	1.24	0.00**
Haavikko					
AE	I1	59	0.13	0.68	0.14
AE	I2	48	-0.16	0.86	0.20
AE	C	36	-1.10	1.16	0.00**
AE	P1	46	-0.86	1.38	0.00**
AE	P2	39	-1.22	1.35	0.00**
AE	M1	109	-0.02	0.79	0.74
AE	M2	115	-0.01	1.29	0.91
Haavikko					
PE	I1	36	-0.16	0.80	0.24
PE	I2	39	-0.77	1.02	0.00**
PE	C	54	-1.35	1.46	0.00**
PE	P1	54	-1.54	1.46	0.00**
PE	P2	42	-1.78	1.92	0.00**
PE	M1	50	0.29	0.89	0.02*
PE	M2	42	0.02	1.39	0.92
Smith					
PE	I1	36	-0.21	0.80	0.13
PE	I2	39	-0.45	1.00	0.00**
PE	C	54	-0.95	1.59	0.00**
PE	P1	54	-1.12	1.82	0.00**
PE	P2	42	-0.87	2.02	0.01**
PE	M1	50	0.30	0.88	0.02*
PE	M2	42	0.05	1.36	0.82

[1] AE and PE for individual teeth, * P<0.05, ** P<0.01. Mean difference = estimated age minus chronological age in years.

TABLE 3. Individual Haavikko root stages fractions and eruption levels where the average difference between estimated and chronological ages was not significantly different to zero (Mean difference in years, SD standard deviation in years)

Tooth	Stage	Eruption	Method	N	Mean diff	SD	P value
I1	R1/2	AE	Haavikko	25	0.12	0.66	0.38
	R3/4	AE	Ando	10	-0.03	0.57	0.86
I2	R1/2	AE	Haavikko	25	0.09	0.73	0.53
	R3/4	AE	Ando	14	-0.18	0.68	0.35
	R3/4	PE	Smith	20	-0.06	0.55	0.65
C	R3/4	PE	Haavikko	14	-0.44	1.19	0.19
	R3/4	PE	Smith	14	-0.03	1.21	0.94
P1	R3/4	PE	Smith	24	-0.41	1.13	0.09
P2	R3/4	PE	Smith	15	0.16	1.20	0.61
M1	R1/4	AE	Haavikko	77	0.12	0.73	0.15
	R1/2	AE	Garn	28	0.10	0.73	0.46
M2	R1/2	AE	Haavikko	41	-0.30	1.04	0.07
	R3/4	PE	Haavikko	25	0.20	1.12	0.38
	R3/4	PE	Smith	25	0.19	1.05	0.38

Standard deviation values were high for most teeth ranging from 0.68 to just over 2 years. The difference between estimated age using Garn and chronological age is plotted against chronological age in Figure 2. This shows the early (first molar) and late phases of erupting teeth (premolars and second molar) and the age variation for each phase. The zero line indicates individuals whose teeth erupt at average age. Age is overestimated for individuals whose teeth are advanced in eruption and underestimated for individuals whose teeth are delayed in eruption.

Further analyses by Haavikko tooth stage are shown Table 3 with only combinations of root fraction and eruption level with differences not significantly different to zero reported. For both incisors at AE and root stage R1/2 Haavikko and R3/4 Ando estimated age accurately. Haavikko estimated age accurately (not significant to zero) if M1 was at AE and R1/4, but if root stage was R1/2 then Garn estimated age accurately. Two teeth estimated age accurately at PE (Haavikko): the canine and M2 at R3/4. If M2 was AE and R1/2, Haaviko estimated age accurately.

The results of accuracy comparing tooth stage and eruption level using Haavikko root fractions for teeth at AE and PE are shown in Table 4. There were four combinations of eruption level and tooth stage that accurately estimated age using Haavikko (I1 at AE and R1/2, M1 at AE and R1/4, M2 at AE and R1/2 and M2 at PE and R3/4). For all these combinations, the estimated age from root stage was closer to chronological age than estimated age from eruption level. Standard variation for M2 stages were considerably greater than earlier erupting teeth.

DISCUSSION

Tooth eruption has long been thought to be more variable than tooth formation and therefore less accurate at estimating age. Our results show that alveolar eruption and partial eruption (including gingival emergence into the oral cavity) of permanent mandibular teeth can be used to estimate age in the immature dentition when root stage cannot be seen or has been damaged. Alveolar eruption of early erupting permanent teeth (I1, I2 and M1) as well as both AE and PE eruption levels of M2 can estimate age accurately.

The finding that Gleiser and Hunt and Haavikko values of M1 AE could accurately estimate age suggests that there has been no secular change in the eruption process of this tooth.

The use of gingival eruption of individual teeth to estimate age should be interpreted as a minimum age. The position of the cusp tips of a recently erupted tooth in the oral cavity relative to the occlusal level is not well documented and is influenced by local factors and tooth type. Molars probably erupt closer to the occlusal level than later erupting premolars and canines.

The strength of this study was the large sample age range with sufficient individuals prior to AE of M1 as well as sufficient older individuals. These older children, however, were drawn from orthodontic clinics and several individuals were excluded because they appeared to have crowding of teeth that prevented full eruption. Limitations of this study include the definition of partial eruption. Dean (2007) defined erupted stage more carefully with early and late eruption with cusp tips at/below the maximum bulbosity of the adjacent crown. Assessing the process of tooth eruption into our discrete stages appeared to have adequate reproducibility. Further research is needed to assess if our partial eruption level is equivalent to clinical emergence.

CONCLUSIONS

The eruption of mandibular permanent teeth can play a role in estimating age. Accuracy is higher using early erupting permanent teeth I (M1 and incisors) to estimate age compared to later erupting teeth. Gleiser and Hunt for M1 AE and Haavikko I1, I2 and M1 and M2 AE and I1, M2 at PE are recommended to estimate age. If a tooth is erupting and root stage can be assessed, accuracy is higher using root stage.

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TABLE 4. A comparison of accuracy estimating age from eruption level and tooth stage using Haavikko[1]

Tooth	N	Tooth stage	eruption level	Estimated age method	Mean difference	SD
I1	25	R1/2	AE	eruption	0.12	0.66
	25	R1/2	AE	tooth stage	-0.03	0.68
M1	77	R1/4	AE	eruption	0.12	0.73
	77	R1/4	AE	tooth stage	0.06	0.74
M2	41	R1/2	AE	eruption	-0.31	1.04
	41	R1/2	AE	tooth stage	0.03	1.27
M2	25	R3/4	PE	eruption	0.20	1.12
	25	R3/4	PE	tooth stage	0.04	1.25

[1] There were four combinations of eruption level and tooth stage that accurately estimated age using Haavikko (I1 at AE and R1/2, M1 at AE and R1/4, M2 at AE and R1/2 and M2 at PE and R3/4). For all these combinations, the estimated age from the root stage was closer to chronological age than estimated age from eruption level.

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