Tooth Size, Crown Complexity and the Utility of Combining Archaeologically-derived Samples with Living Samples for Reconstruction of Population History

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Abstract

In recent years biological anthropologists have expressed considerable reluctance in employing contrasts of differences in the allocation of tooth size across the permanent dentition for reconstruction of population histories, favouring instead contrasts of differential frequencies of non-metric morphological features of the tooth crown. This research seeks to address two important questions: 1) Are systemic biases introduced when prehistoric archaeologically derived samples are considered in the same analysis of biological distance as samples of contemporary living individuals?; and 2) Does variation in tooth size allocation yield results consistent with analyses based upon dental morphology trait frequencies? The results obtained here from comparisons of 2298 and 2242 prehistoric and living individuals of 23 and 22 samples from the Hindu Kush highlands, Indus Valley, Iran, Central Asia and peninsular India, respectively, indicate that no systemic biases are introduced when prehistoric individuals are considered alongside living individuals. Further, results obtained from assessment of tooth size allocation yield consistent, but different patterns of biological distances from those identified by dental morphology analysis. Since there is no reason to assume that one system of biological variation is more important or more sensitive than the other, both should be employed when attempting to reconstruct the biological histories of past and present populations.

Introduction

Biological anthropologists have been wary of using dental indicators of biological affinity to trace patterns of relatedness among ancient and living populations because it is well-known that both tooth size and crown complexity have changed in the post-Pleistocene era. Numerous studies have found that overall tooth size has decreased since the Upper Palaeolithic and this reduction has been documented in Europe (Brabant, 1967, 1971; Frayer, 1977, 1978, 1980, 1984; Meiklejohn et al, 1984; P. Smith, 1979, P. Smith et al, 1984; y'Edynak, 1978, 1989; y'Edynak & Fleisch, 1983), the New World (Hinton et al., 1980; Ryan and Posner, 1975; Sciulli, 1979; F. Smith et al., 1980), East Asia (Brace, 1978; Brace and Nagai, 1982; Brace et al., 1984; Suzuki, 1969), and even in South Asia (Lukacs, 1982, 1984, 1985a,b; Lukacs and Hemphill, 1991). Although the specific cause of this reduction has been the subject of much debate, early suggestions of a "probable mutation effect" (Brace, 1962, 1963, 1978; Brace and Mahler, 1971; Brose and Wolpoff, 1971; McKee, 1984) or some kind of a "somatic budget effect" to reduce costs for developing and maintaining complex structures that no longer confer an adaptive advantage (Greene, 1970, 1972) have been discarded in favor of explanations that invoke directional selection (Frayer, 1977, 1978, 1980, 1984).

The assertion is that as technology improved in the post-Pleistocene era, more extensive premasticatory food preparation resulted in consumption of softer foods that required less vigorous chewing and a reduction in overall tooth wear. This led to a disadvantageous situation in which large teeth were increasingly misaligned in small jaws (Carlson, 1976a,b; Carlson and Van Gerven, 1977; P. Smith, 1979, P. Smith and Shegey, 1988; Calcagno, 1986). Then, with the change in subsistence from hunting and gathering to agricultural production, the resultant increase in soft, sticky carbohydrates led to a tremendous increase in carious lesions (Brothwell, 1963). These carious lesions not only tended to be located in the myriad nooks and crannies formed by misaligned teeth, but also in the fissures and pits that accompany greater crown complexity (Anderson and Popovich, 1977:383-4; Armelagos, 1968; Dirks, 1965; Grainger et al, 1966; Mayhall, 1972, 1977a,b; Paynter and Grainger, 1962; Pedersen, 1949; Van Reenan, 1966:711). Thus, commensurate with positive selection for a reduction in overall crown size (Calcagno and Gibson, 1988) would have been selection favoring a reduction in crown complexity as well, for it is known that within a population morphological complexity is positively associated with size

(Anderson and Popovich, 1977; Armelagos, 1968; Dirks, 1965; Garn, 1977; et al, 1966a,b; Grainger et al, 1966; Greene, 1970; Harris, 2007; Hsu et al, 1997; Keene, 1968; Kondo and Townsend, 2006; Lombardi, 1975; Noss et al, 1983; Reid et al, 1991, 1992; but see Garn et al, 1966c).

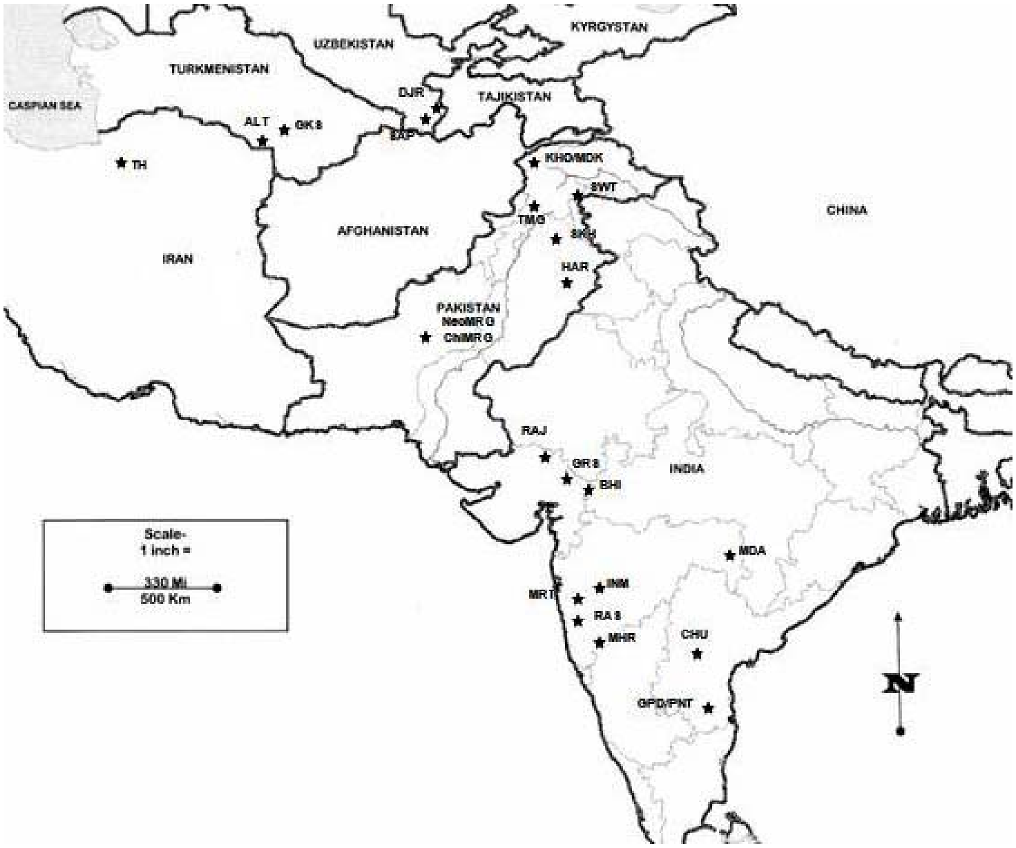

Figure 1. Map of odontometric samples.

Since dental changes likely involve a large battery of genes (Alvesalo and Tigerstedt, 1975; Biggerstaff, 1976; Dahlberg, 1971; Dempsey et al, 1995; Dempsey and Townsend, 2001; Garn et al, 1965; Goose, 1971; Jernvall and Jung, 2000; Keene, 1982, 1991; Lundström, 1963, 1967; Mitsiadis and Smith, 2006; Nichol, 1989; Osborn, 1978; Potter et al, 1968, 1976; Scott and Potter, 1984; Townsend and Brown, 1978, 1979; Townsend and Martin, 1992; Townsend et al, 2009), it is expected that these changes occurred gradually, rather than instantaneously, as those individuals who possessed smaller teeth with less complex crowns enjoyed better dental health and greater overall health. Logically, one would expect that populations with the shortest history of ceramic technology and agricultural production should possess the largest tooth sizes and greatest crown complexities, while those with the longest histories of ceramic technology and agriculturally-based diets should possess the smallest teeth with the simplest crowns (Dahlberg, 1960, 1963; Greene, 1970:278, 1972:322; Lukacs, 1982, 1985a; but see Bailit and Friedlaender, 1966; Garn et al, 1969; Sciulli, 1979). If this relationship holds true, analyses of tooth size and dental morphology merely reflect a specific population's history of improvements in technology that affect pre-masticatory food preparation and their respective dietary consumption. Thus, systemic bias, due to differences in antiquity and hence differences in the length of exposure to agriculturally-based foods and such innovations as ceramic technology enters into any comparison involving ancient and living populations. Consequently, due to these impacts, it would appear that assessment of both tooth size and crown complexity of prehistoric individuals offers little potential for providing a meaningful diachronic foundation for reconstructing the population history of contemporary populations.

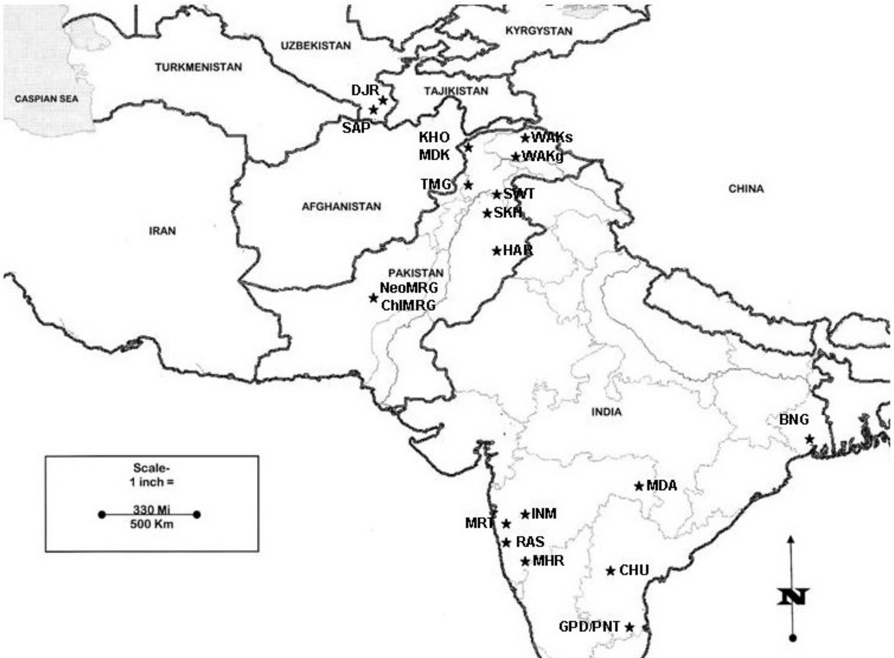

Figure 2. Map of dental morphology samples.

Relative Proportionality, Tooth Size Gradients, Allocation of Permanent Tooth Size

In recent years, largely as a consequence of the influential work of Christy Turner II, researchers interested in understanding patterns of human microevolution in the post-Pleistocene era have largely focused their attention on assessment of differing frequencies of dental morphology traits. Far less common have odontometric data been used for the same purpose (T. Hanihara, 2008; Harris, 1998; Harris and Harris, 2007; Harris and Rathbun, 1989, 1991; Hemphill, 1991, 2008, 2009b; Hemphill et al, 1992, in press). Multivariate studies consistently demonstrate that isometric scaling accounts for a large proportion of the observed variation in tooth dimensions across populations (Harris, 1998; Harris and Rathbun, 1991; Hemphill 1991; Hemphill et al., 1992). In fact, so great are such differences in overall tooth size and so extensive is the evidence for tooth size reduction in the post-Pleistocene era that many researchers have concluded that odontometric data are of little utility for investigating microevolutionary questions among modern humans (e.g., Pedersen, 1949; Thomsen, 1955; Lasker and Lee, 1957; Cadien, 1972; O'Rourke and Crawford, 1980; Harris and Bailit, 1987).

Nevertheless it has also long been known that isometric scaling is not the only form of odontometric variation found among modern humans. Human groups also differ in proportional tooth size within and among tooth types (de Terra, 1905; Campbell, 1925; Pederson, 1949; Moorrees, 1957). A particularly well-known example of the former is the ratio of mesiodistal lengths of the maxillary central and lateral incisors in which, due to the possession of large lateral incisors, I^1/I^2 indices are low among Native Americans, while at the opposite extreme are Europeans, who are marked by relatively small lateral incisors and hence possess large I^1/I^2 ratios (Harris, 1998: 304). Indeed a number of studies have demonstrated that contemporary human groups possess dentitions of different shapes in the sense that "shapes" reflect differences in the proportionality of the various dental elements (Rosenzweig, 1970; Garn et al, 1968a, b, 1969, 1971).

Varied patterns of change are also evident from the studies of Garn and coworkers (1968a), who demonstrated that relative tooth sizes differ markedly among populations.

Thus, since the end of the Pleistocene not only have various human groups experienced greater or lesser amounts of overall reduction in tooth size, but the distribution, or allocation, of size differs across the various morphogenetic fields (K. Hanihara, 1976; Harris and Rathbun, 1989, 1991). Following the rationale of Penrose (1954), who noted that it is typically shape rather than size that most effectively distinguishes groups, Corruccini (1973) argued that shape will be the more important determinant of dissimilarity among closely related populations. This view has been confirmed by other metric data (Campbell, 1978; Corruccini, 1978, 1987; Relethford, 1984; Thorpe and Leamy, 1984), as well as from analyses of differential allocation of tooth size throughout the dentition (Groeneveld and Kieser, 1987; Harris, 1998; Harris and Rathbun, 1989, 1991; Hemphill, 1991; Perzigian, 1984).

If one assumes that contemporary variation in tooth size and size proportionality have developed through divergence over time, such divergence may have occurred through the myriad factors noted above (probable mutation effect, somatic budget effect, directional selection), although all of these explanations have been criticized as inadequate (Kieser, 1990; Harris, 1998). It is just as likely these differences may be the consequence of historical contingency (Gould, 1991a,b). That is, intergroup differences in tooth size allocation, while statistically significant (Perzigian, 1984; Harris and Rathbun, 1991), may represent nothing more than incidental repercussions of other evolutionary changes (Lande and Arnold, 1983), or they may simply be reflective of genetic drift and gene flow. If the latter is the case, for there is no inherent reason why a slightly broader lateral maxillary incisor relative to a relatively narrower central incisor should confer an advantage over the reverse, it may be that allocation, or “gradients” (Harris and Harris, 2007) of tooth size across the various morphogenetic fields of the permanent dentition may actually be less subject to the selective pressures that have accompanied technological and dietary changes throughout the Holocene than the dental morphology traits upon which so many recent studies of biological distance are based.

This investigation seeks to address two important questions:

1. Are systemic biases introduced when prehistoric archaeologically derived samples are considered in the same analysis as samples of contemporary living individuals?
2. Does variation in dental morphology trait frequencies yield results consistent with results obtained from assessment of tooth size allocation?

Materials and Methods

Odontometrics

Mesiodistal lengths and buccolingual breadths of all tooth crowns, except third molars, were measured according to the standards of Moorrees (1957) and contrasted among 22 samples that include 2159 living and prehistoric individuals (Table 1, Fig. 1). Tooth measurements were size corrected by standardizing measurements against individual geometric means in samples of living populations and against sample means in prehistoric samples (Jungers et al, 1995) to provide an assessment of tooth size allocation across the permanent dentition (Harris and Bailit, 1988; Harris and Rathbun, 1991).

Table 1. Samples used in the Tooth Size Allocation Comparison.

			Source of		**Source of Archaeological**
Sample	**Abb.**	**n**	**Dental Data**	**Date**	**Context & Date**
Altyn Depe	ALT	25	Hemphill *et al.* (in press)	2500-2300 BC	Kohl (1992)
Bhils	BHI	208	Lukacs & Hemphill (1993)	Living	N/A
Chalcolithic	ChlMR	28	Lukacs &	4500 BC	Jarrige (1984); Jarrige

Mehrgarh	G		Hemphill (1991)		& Lechevallier (1979, 1980)
Chenchus	CHU	196	Hemphill (1991)	Living	N/A
Djarkutan	DJR	48	Hemphill *et al.* (1998)	2100-1950 BC	Hiebert (1994)
Garasias	GRS	207	Lukacs & Hemphill (1993)	Living	N/A
Geoksyur	GKS	64	Hemphill *et al.* (in press)	3500-3000 BC	Kohl (1992)
Gompadhompti Madigas	GPD	177	Hemphill (1991)	Living	N/A
Harappa	HAR	26	Hemphilll *et al.* (1991)	2600-1900 BC	Kenoyer (1998)
Inamgaon	INM	38	Lukacs (1987)	1600-700 BC	Sankalia (1984)
Khowar	KHO	104	Hemphill *et al.* (in press)	Living	N/A
Kuzali	KUZ	31	Hemphill *et al.* (1998)	1950-1800 BC	Hiebert (1994)
Madaklasht	MDK	191	Hemphill (2008); Hemphill *et al.*	Living	N/A

			2010)		
Molali	MOL	52	Hemphill *et al.* (1998)	1800-1650 BC	Hiebert (1994)
Neolithic Mehrgarh	NeoMRG	42	Lukacs (1986)	6500-6000 BC	Jarrige (1984); Jarrige & Lechevallier (1979, 1980)
Pakanati Reddis	PNT	184	Hemphill (1991)	Living	N/A
Vaghelia Rajputs	RAJ	190	Lukacs & Hemphill (1993)	Living	N/A
Mixed Maharashtrans	RAS	70	Hemphill (1991)	Living	N/A
Sapalli Tepe	SAP	49	Hemphill *et al.* (1998)	2300-2100 BC	Hiebert (1994)
Sarai Khola	SKH	25	Lukacs (1983)	200-100 BC	Bernhard (1969)
Swatis	SWT	190	Hemphill (2009b)	Living	N/A
Tepe Hissar	TH	139	Dyson & Lawn (1989)	3385-1885 BC	Hemphill (in press)
Timargarha	TMG	21	Lukacs (1983)	1400-850 BC	Dani (1966, 1967)

TOTAL		2298			

Differences between samples were quantified with squared Euclidean distances and the patterning of inter-sample differences was simplified with neighbour-joining cluster analysis (Felsenstein, 1989; Saitou and Nei, 1987), multidimensional scaling with Guttman's (1968) coefficient of alienation, and principal coordinates analysis (Gower, 1966). Multidimensional scaling was accomplished into the first three dimensions and the goodness of fit was assessed through the degree of stress experienced in fitting the model. The symmetric matrix of Smith's MMD values was double-centreed prior to principal coordinates analysis (Rohlf, 2000). The first three principal coordinate axes were retained and group scores calculated along these axes. Results obtained by multidimensional scaling and principal coordinates analyses were ordinated into three-dimensional space and a minimum spanning tree (Hartigan, 1975) was imposed on the array of data points to ease interpretation of the patterning of intersample associations.

Total crown areas were calculated for each sample to test whether systemic bias affects comparisons of tooth size gradients between prehistoric and living samples. Total crown area was calculated by multiplying mesiodistal tooth lengths by buccolingual tooth breadths and summing the areas from the central incisors to the second molars of the mandible and maxilla. Total crown areas were ranked along an ordinal scale for the 18 samples included in both tooth size allocation and dental morphology analyses. In cases where more than one sample possessed identical total crown areas each sample was awarded the average rank score for the number of tied ranks involved. Total crown areas were regressed against ranked compound complexity scores (see below) and against ranked sample value on the first dimension obtained from multidimensional scaling as well as the first principal axis obtained by principal coordinates analysis with Spearman's rho (Sokal and Rolf, 1995; Zar, 1999).

If geometric scaling removes the effect of overall size, differential allocation of permanent tooth size throughout the dentition among the various groups being compared should be reflected by the absence of a significant correlation between total crown area and group scores obtained for the first dimension from multidimensional scaling or the first principal coordinate axis. Conversely, if compound complexity scores reflect coordinated enhancement of crown complexity or simplification, significant correlations should occur between compound complexity scores and group scores along the first dimension obtained from multidimensional scaling and the first coordinate axis obtained by principal coordinates analysis.

Dental Morphology:

Dental traits were scored in accordance with the standards of the Arizona State University Dental Anthropology System (Scott and Turner, 1997). Where possible, the dentition of each individual was assessed for 26 dental traits scored as 71 tooth-trait combinations. Observations were made on both right and left antimeres. Frequencies of dental traits were calculated for each grade of expression according to the individual count method of Scott (1973, 1980; see also Scott and Turner, 1997) in which the greatest degree of expression, regardless of side, was considered the score for that individual under the assumption that this procedure reflects the maximum genetic potential for each trait (Turner, 1985; Turner *et al.* 1991).

Trait selection is a critical issue in any biological distance analysis (Harris and Sjovøld, 2004; Irish, 2010; Sjovøld, 1977: 31). The most discriminating variables differ with the array of samples considered. Two important issues arise when such an analysis involves both living and archaeologically-derived prehistoric samples. First, sample sizes are usually relatively small and trait representation is often biased when archaeologically derived samples are considered. This is due to the limited preservation of ancient remains, the non-random greater post-mortem loss of anterior teeth from skeletonized remains, and heightened levels of tooth wear among ancient peoples. Second, because it is unlikely individual traits, let alone the expression of individual traits on various teeth, are controlled by separate genes or separate batteries of genes (see Keene, 1991; Mitsiadis and Smith, 2006; Nichol, 1989; Osborn, 1978; Townsend et al, 2009), it is important to determine whether specific tooth-trait combinations are inter-correlated thereby leading to artificial inflation of inter-group differences (Sjovøld, 1977).

The two-step trait editing procedure recommended by Irish (2010) and Harris and Sjovøld (2004) is followed here (see Hemphill, in press). Once inter-correlated and insufficiently variant tooth-trait combinations were removed, the remaining battery of ordinally-graded trait expressions was dichotomized into presence/absence only for comparative purposes, where any degree of expression was considered a positive manifestation. The only exception is shovelling of the maxillary anterior teeth, where grade 2 was considered the minimum level of positive expression. Because numerous studies have found minimal sex dimorphism in trait expression (T. Hanihara, 1992, 2008; Irish, 1998; Scott, 1973, 1980; Smith and Shigey, 1988), males and females were pooled for comparative purposes.

Frequencies of sex-pooled dental morphology trait frequencies from 2242 individuals from 22 samples that include both prehistoric and living individuals form the basis of comparison (Table 2, Fig. 2). Trait frequencies were compared with Smith's mean measure of divergence (MMD) statistic with Freeman and Tukey's (1950) angular adjustment and Green and Suchey's (1976) correction for low- and high-frequency traits. This distance measure normalizes trait frequency distributions and is especially useful when dealing with missing observations and/or the small sample sizes often encountered when incorporating archaeologically derived dental samples (Harris and Sjovøld, 2004; Sjøvold, 1977).

Table 2. Samples used in the Dental Morphology Comparison.

			Source of		Source of Archaeological
Sample	**Abb.**	**n_{max}[1]**	**Dental Data**	**Date**	**Context & Date**
Bengalis	BNG	73	Hemphill (1991)	Living	N/A

Chalcolithic Mehrgarh	ChlMRG	25	Lukacs & Hemphill (1991)	4500 BC	Jarrige (1984); Jarige & Lechevallier (1979, 1980)
Chenchus	CHU	194	Hemphill (1991)	Living	N/A
Djarkutan	DJR	39	Hemphill *et al.* (1998)	2100-1950 BC	Hiebert (1994)
Gompadhompti Madigas	GPD	178	Hemphill (1991)	Living	N/A
Harappa	HAR	33	Hemphill *et al.* (1991)	2600-1900 BC	Kenoyer (1998)
Inamgaon	INM	41	Lukacs (1987)	1600-700 BC	Sankalia (1984)
Khowar	KHO	136	Blaylock (2008); Hemphill *et al.* (in press)	Living	N/A
Kuzali	KUZ	24	Hemphill *et al.* (1998)	1950-1800 BC	Hiebert (1994)
Madaklasht	MDK	181	Hemphill (2008); Hemphill *et al.* (2010)	Living	N/A

Madia Gonds	MDA	169	Lukacs *et al.* (1998); Hemphill *et al.* (2000)	Living	N/A
Mahars	MHR	195	Lukacs *et al.* (1998); Hemphill *et al.* (2000)	Living	N/A
Marathas	MRT	198	Lukacs *et al.* (1998); Hemphill *et al.* (2000)	Living	N/A
Molali	MOL	41	Hemphill *et al.* (1998)	1800-1650 BC	Hiebert (1994)
Neolithic Mehrgarh	NeoMRG	49	Lukacs (1986)	6500-6000 BC	Jarrige (1984); Jarrige & Lechevallier (1979, 1980)
Pakanati Reddis	PNT	182	Hemphill (1991)	Living	N/A
Mixed Maharashtrans	RAS	68	Hemphill (1991)	Living	N/A
Sapalli Tepe	SAP	43	Hemphill *et al.* (1998)	2300-2100 BC	Hiebert (1994)

Sarai Khola	SKH	15	Lukacs (1983)	200-100 BC	Bernhard (1969)
Swatis	SWT	182	Hemphill (2009b)	Living	N/A
Tepe Hissar	TH	151	Hemphill *et al.* (in press)	3300-2500 BC	Dyson & Lawn (1989)
Timargarha	TMG	25	Lukacs (1983)	1400-850 BC	Dani (1966, 1967)
TOTAL		2242			
1. n_{max} represents the greatest number of individuals scored for a non-metric trait.					

The patterning of inter-sample differences reflected in the triangular matrix of pairwise Smith's MMD values was simplified with neighbour-joining cluster analysis, multidimensional scaling with Guttman's (1968) coefficient of alienation, and principal coordinates analysis. For both multidimensional scaling and principal coordinates analyses, results were ordinated into three-dimensional space and a minimum spanning tree was imposed on the array of data points to ease interpretation of the patterning of intersample associations.

A compound complexity score was calculated for each sample to test whether systemic bias affects comparisons of dental morphology trait frequencies between prehistoric and living samples. A complexity score was calculated by ranking the samples relative to one another along an ordinal scale for the 18 samples included in both dental morphology and tooth size allocation analyses. In cases where more than one sample possessed a specific tooth-trait combination in identical frequencies each sample was awarded the average rank score for the number of tied ranks involved. The compound complexity score was based on the summed rank scores for the retained 17 tooth-trait combinations. Compound complexity scores were regressed against ranked total crown area and against ranked sample value on the first dimension obtained from multidimensional scaling and the first coordinate axis obtained from principal coordinate analysis with Spearman's rho (Sokal and Rolf, 1995; Zar, 1999).

The matrix correspondence test (Mantel, 1967), a permutation procedure commonly employed to test the statistical significance of correlations between various matrices (Dietz, 1983; Douglas and Endler, 1982; Manly, 1986; Sokal, 1979), was used to further assess the comparability of results obtained through assessment of dental morphology and allocation of tooth size. Such tests have often been used to test hypotheses about spatial or temporal impacts upon genetic or phenetic distances (Hemphill, 1998, 1999; Hemphill and Mallory, 2004; Smouse et al, 1986). Significantly high correlations between measures of biological relatedness and either geographic distances or temporal differences have often been interpreted as evidence of differentiation through isolation-by-distance (Congdon et al, 2000; Irish, 2010; Maes and Volckaert, 2002; Manel et al, 2003) and/or through long-standing historical divergence (Telles and Diniz-Filho, 2005; Epperson, 2003; Lampert et al, 2003).

The three matrix permutation test (Smouse et al, 1986) was used to provide additional insight into the comparability of dental morphology trait frequency and tooth size allocation data for reconstruction of biological history. As outlined by Dow and Cheverud (1985), the two triangular dissimilarity matrices (squared Euclidean distances, matrix A; Smith's MMD distances, matrix B) were compared to a triangular matrix of pairwise geographic distances (matrix C). This matrix is tested against the original two matrices to determine whether the two biological distance matrices (squared Euclidean distance, Smith's MMD distances) are the product of geographic factors acting upon the same process of differentiation. A partial correlation between matrices A and B, conditional upon matrix C is computed by first regressing the elements of matrix A on the equivalent elements of matrix C to obtain a matrix of residuals *res* (A.C). A matrix of residuals of matrix B on matrix C, *res* (B.C) is similarly computed. Then least-squared regression obtains the partial correlation coefficient $r_{AB.C}$ by calculating the product-moment coefficient of the two residuals *res* (A.C) and *res* (B.C). The significance of the partial correlation between the two residuals matrices is assessed by performing a Mantel test between the residuals matrices after 10,000 permutations.

Results:

Archaeologically-Derived Samples, Living Samples and Systemic Bias:

The two-step trait editing procedure resulted in elimination of 54 tooth-trait combinations. The leading factors behind elimination in order of the number of variables removed were: 1) extremely low sample sizes ($n < 10$), which were especially under-represented for third molar variants due to the sampling protocol employed for living samples (see Hemphill, 2008, 2009a, Hemphill et al, 2010, in press); 2) lack of discrimination, usually due to either trait fixation or absence; and 3.) inter-trait correlation.

The remaining battery of 17 tooth-trait combinations, nine maxillary and eight mandibular, was retained for comparative purposes. The maxillary variables include shovelling of UI1 and UI2, tuberculum dentale development on these same teeth, hypocone reduction on UM1 and UM2, Carabelli's trait expression on UM1, and presence of the metaconule on UM1 and UM2. The mandibular tooth-trait combinations include the presence of the Y-groove on LM1 and LM2, and presence of the hypoconulid, entoconulid, and metaconulid on these same teeth.

Ranked total crown area was contrasted against each group's ranked compound complexity score to test whether systemic bias renders comparisons between samples of ancient and living ethnic groups moot. The correlation between ranked total crown area and ranked complexity score among the 18 samples in which data was available for both tooth size and crown complexity is 0.004, which is not significant ($p = 0.986$).

Total crown area was contrasted to the sample's ranked position on the first dimension produced by multidimensional scaling and the first principal coordinate axis produced by principal coordinates analysis with Spearman's rho. A non-significant relationship between total crown area and group scores obtained for the first dimension from multidimensional scaling and the first principal coordinate axis ensures that geometric scaling removes the effect of overall size but leaves disparities in the allocation of tooth size throughout the dentition to differentiate among groups. This relationship was found to be non-significant for both the first dimension obtained through multidimensional scaling (r_s= -0.233; p= 0.351) and for the first principal coordinate axis (r_s= 0.158; p= 0.530).

Ranked compound complexity scores were contrasted to the sample's ranked position on the first dimension produced by multidimensional scaling and the first principal coordinate axis produced by principal coordinates analysis with Spearman's rho. If compound complexity scores reflect coordinated enhancement or simplification of crown complexity, then significant correlations ought to occur between compound complexity scores and group scores along the first dimension obtained from multidimensional scaling and the first coordinate axis obtained by principal coordinates analysis. Correlations between ranked compound complexity score and ranked position on the first dimension obtained by multidimensional scaling (r_s= 0.709; p= 0.001) and on the first principal coordinate axis (r_s= -0.699; p= 0.001) are both highly significant.

Two things are clear from such results. First, geometric scaling of mesiodistal tooth lengths and buccolingual tooth breadths removes the impact of overall size leaving different proportions in tooth size to distinguish between samples with multidimensional scaling and principal coordinates analysis. Second, analysis of dental morphology variation with Smith's MMD statistic with these same two data reduction techniques differentiates among samples along coordinated vectors of crown enhancement and simplification. Thus, when such results are considered together, it is clear that no systemic bias is introduced into contrasts of dental morphology trait frequencies or allocation of tooth size when prehistoric and living samples are included in a single analysis.

Are Tooth Size Allocation and Crown Complexity the Product of the Same Differentiating Process?

The null hypothesis expects assessment of dental morphology trait frequencies and assessment of size allocation throughout the dentition to provide information about population histories through patterning of pairwise phenetic distances between samples. If the two triangular matrices of Smith's MMD values and squared Euclidean distances based upon geometrically scaled mesiodistal tooth lengths and tooth breadths are realizations of the same variation generating process, and if a significant influence upon that process is geographic propinquity, each distance matrix should be significantly correlated with geographic differences. If the observed correlation between the two is the consequence only of geography, their partial correlation after geography has been removed should be zero (Oden and Sokal, 1992: 280).

Thus, it appears three things are required to demonstrate that variation in tooth morphology can yield results consistent with those obtained from allocation of permanent tooth size for reconstructing biological histories. First, there must be a significant correlation in the triangular matrices of pairwise differences between samples yielded by these two assessments of biological distance. Second, each of these matrices must be significantly correlated with a matrix of geographic distances between sample pairs. Third, the partial correlation between the matrix of Smith's MMD values and the matrix of squared Euclidean distances must be effectively zero after the effect of geography has been removed.

The degree of correspondence between the triangular matrix of pairwise Smith's MMD values (Table 3) yielded by dental morphology trait frequencies and the triangular matrix of squared Euclidean distances yielded by geometrically scaled mesiodistal tooth lengths and buccolingual tooth breadths (Table 4) for the 18 samples with both sets of data was assessed with the Mantel test. This test yielded a t-value of 2.083, which indicates that the two matrices are not significantly different from one another (r= 0.205; p= 0.981). The degree of correspondence between the triangular matrix of Smith's MMD values and straight-line geographic distances between sample pairs (Table 5) yields a t-value of 3.532, which indicates that geographic distance is significantly correlated with the divergence values yielded by dental morphology trait frequencies (r= 0.336; p= 0.999), for the likelihood of finding such correspondence by chance through 10,000 iterations is infinitesimally small (p= 0.0026). A similar assessment of the degree of correspondence between the squared Euclidean distances and straight-line geographic distances between sample pairs yielded a t-value of 2.983, which also indicates that the two matrices are significantly correlated (r= 0.347; p= 0.999); the likelihood of occurring purely by chance is again very small (p= 0.0025). However, once the effect of geography is removed, the partial correlation of the residuals yielded by the triangular matrices of Smith's MMD values and squared Euclidean distances is not significant (t= 0.934; r= 0.010; p= 0.825). Such results indicate that dental morphology trait frequencies and allocation of permanent tooth size represent realizations of the same variation generating process. Further, both measures are significantly auto correlated with straight-line geographic distances.

Table 3. Squared Euclidean Distances (x100) between Sample Pairs

	ALT	BHI	ChlMRG	CHU	DJR	GRS	GKS	GPD	HAR	INM	KHO	KUZ	MDK	MOL	NeoMRG	PNT	RAJ	RAS	SKH	SAP	SWT	TH	TMG
ALT	0.000																						
BHI	3.890	0.000																					
ChlMRG	4.225	2.584	0.000																				
CHU	3.507	2.843	3.564	0.000																			
DJR	3.769	3.873	3.105	3.113	0.000																		
GRS	3.780	1.434	2.854	2.623	3.609	0.000																	
GKS	4.589	4.215	3.500	3.650	2.657	3.942	0.000																
GPD	3.953	2.099	2.489	2.738	3.795	2.012	3.909	0.000															
HAR	4.303	2.844	2.613	3.297	3.614	3.090	3.838	2.764	0.000														
INM	5.244	2.911	2.813	4.136	4.400	3.402	4.687	3.001	2.581	0.000													
KHO	3.216	3.337	2.972	2.799	1.972	2.938	2.534	3.273	3.574	4.481	0.000												
KUZ	4.548	4.512	3.688	3.706	3.460	4.411	2.978	3.951	3.504	4.412	3.305	0.000											
MDK	3.496	2.710	2.349	2.303	2.513	2.573	2.902	2.388	2.545	3.337	2.196	2.984	0.000										
MOL	4.331	4.312	3.229	3.902	2.859	4.258	2.732	4.105	3.642	4.667	2.652	2.371	2.678	0.000									
NeoMRG	3.873	2.111	1.668	2.845	2.828	2.403	3.027	2.325	2.298	2.747	2.752	3.249	1.937	3.083	0.000								
PNT	4.006	2.111	2.441	2.434	3.336	1.952	3.637	1.005	2.476	2.676	3.043	3.704	2.056	3.862	2.205	0.000							
RAJ	3.628	1.926	2.887	2.231	3.384	1.405	3.937	1.717	2.918	3.343	2.956	4.250	2.264	4.094	2.530	1.333	0.000						
RAS	3.716	1.795	2.067	2.609	3.358	1.861	3.280	1.271	2.535	2.981	2.704	3.433	1.991	3.317	1.748	1.388	1.851	0.000					
SKH	4.550	3.090	3.098	3.290	3.061	2.982	2.791	3.556	2.859	3.887	2.723	3.617	2.533	3.189	2.231	3.321	3.210	3.013	0.000				
SAP	3.935	3.950	3.185	3.400	2.321	3.808	1.883	3.910	3.595	4.692	1.935	2.541	2.683	1.982	2.763	3.675	3.789	3.083	2.520	0.000			
SWT	3.140	2.287	2.398	2.114	2.634	2.016	3.343	1.992	2.847	3.530	2.234	3.573	1.453	3.212	2.063	1.668	1.635	1.695	3.096	3.141	0.000		
TH	3.810	3.265	2.604	3.165	2.662	3.522	3.073	3.063	3.299	4.059	2.834	3.633	2.074	3.123	2.240	2.982	3.220	2.516	3.160	2.749	2.390	0.000	
TMG	4.944	3.379	3.134	3.300	3.626	3.580	3.402	3.346	2.309	3.521	3.422	3.028	2.892	3.344	2.621	3.120	3.436	2.864	2.313	2.888	3.428	3.184	0.000

Table 4. Mean Measure of Divergence Analysis (MMD values below diagonal, standard deviations below diagonal)

	BNG	ChlMRG	CHU	DJR	GPD	HAR	INM	KHO	KUZ	MDK	MDA	MHR	MRT	MOL	NeoMRG	PNT	RAS	SAP	SKH	SWT	TH	TMG
BNG	---	2.045	0.666	1.852	0.683	2.515	1.765	0.834	2.568	0.691	0.71	0.681	0.67	1.534	1.505	0.68	1.02	1.773	3.467	0.7	0.976	3.145
ChlMRG	9.758	---	1.744	2.904	1.761	3.572	2.828	1.913	3.618	1.769	1.788	1.759	1.747	2.597	2.576	1.758	2.093	2.818	4.517	1.779	2.025	4.146
CHU	5.542	4.854	---	1.556	0.380	2.225	1.469	0.536	2.268	0.387	0.407	0.378	0.366	1.234	1.206	0.376	0.717	1.480	3.171	0.398	0.691	2.868
DJR	21.059	10.198	7.855	---	1.574	3.405	2.624	1.704	3.450	1.579	1.599	1.571	1.560	2.427	2.393	1.570	1.902	2.678	4.352	1.586	1.888	4.026
GPD	2.929	7.134	0.540	13.000	---	2.242	1.487	0.553	2.285	0.405	0.425	0.396	0.384	1.251	1.223	0.394	0.735	1.497	3.188	0.415	0.707	2.884
HAR	6.523	5.020	4.881	13.930	5.838	---	3.268	2.372	4.061	2.247	2.267	2.239	2.229	3.074	3.064	2.239	2.562	3.326	5.012	2.255	2.548	4.648
INM	14.294	11.615	7.628	12.657	7.441	3.906	---	1.644	3.350	1.495	1.513	1.485	1.473	2.332	2.289	1.483	1.810	2.562	4.229	1.506	1.774	3.950
KHO	7.813	7.776	3.550	11.120	4.690	2.655	4.152	---	2.422	0.562	0.580	0.553	0.540	1.394	1.368	0.550	0.883	1.628	3.319	0.576	0.836	3.015
KUZ	18.282	10.082	9.961	-4.419	14.322	7.591	11.858	12.309	---	2.292	2.311	2.283	2.271	3.139	3.090	2.282	2.617	3.370	5.042	2.299	2.572	4.704
MDK	5.214	9.291	7.561	20.776	6.104	5.144	6.566	1.327	18.960	---	0.432	0.404	0.392	1.258	1.230	0.402	0.742	1.503	3.194	0.424	0.712	2.889
MDA	10.859	10.418	4.236	15.208	3.773	4.879	0.851	4.253	16.620	6.488	---	0.423	0.412	1.278	1.251	0.421	0.763	1.523	3.215	0.443	0.731	2.908
MHR	7.811	10.352	6.121	22.756	5.050	2.546	2.776	2.093	22.086	2.298	1.908	---	0.383	1.249	1.222	0.392	0.404	1.495	3.187	0.414	0.705	2.882
MRT	9.322	10.660	5.997	18.497	4.530	1.501	0.513	3.208	16.643	4.093	0.531	0.161	---	1.237	1.211	0.381	0.723	1.484	3.176	0.402	0.694	2.870
MOL	13.329	2.087	4.769	-2.635	9.832	4.870	11.441	5.471	-3.287	12.053	13.479	15.117	13.979	---	2.071	1.248	1.582	2.353	4.031	1.266	1.559	3.725
NeoMRG	19.140	6.124	11.259	16.742	11.774	6.355	-0.420	10.944	17.776	12.032	3.626	8.359	5.663	15.250	---	1.220	1.557	2.313	4.013	1.240	1.521	3.672
PNT	2.104	7.583	2.779	18.947	0.773	2.666	8.186	3.489	18.933	4.088	5.095	2.773	3.335	12.576	12.718	---	0.732	1.494	3.185	0.412	0.705	2.881
RAS	-0.521	4.835	3.974	20.778	1.865	3.339	9.570	6.707	19.114	4.275	6.488	4.768	5.406	13.528	9.481	1.160	---	1.822	3.521	0.752	1.023	3.188
SAP	17.556	6.455	6.912	-4.368	12.234	8.987	14.634	8.703	-5.332	17.729	16.326	19.566	17.078	-5.141	20.681	16.255	18.726	---	4.278	1.510	1.824	3.987
SKH	21.177	14.816	7.236	5.763	9.692	2.572	-0.308	7.991	-1.490	15.799	5.836	9.628	4.112	6.165	9.840	11.768	18.223	3.851	---	3.202	3.486	5.602
SWT	2.520	7.428	4.858	17.146	4.152	2.484	7.360	0.552	16.479	-0.171	6.551	2.536	4.466	9.004	12.286	1.879	2.737	14.046	14.990	---	0.719	2.899
TH	23.835	15.351	11.203	-3.900	15.918	13.730	16.501	14.608	-3.511	24.961	18.874	25.910	21.110	0.647	21.718	21.329	24.447	-2.101	5.170	20.578	---	3.221
TMG	13.547	8.126	3.811	8.330	5.809	-0.136	-1.345	0.092	4.076	3.943	0.579	0.996	-0.873	4.272	4.463	6.192	10.547	7.101	-7.645	5.552	11.297	---

Table 5. Straight-line Geographic Distances between Sample Pairs among the 18 Samples included in both Tooth Size Allocation and Dental Morphology Analyses[2]

	ChlMRG	CHU	DJR	GPD	HAR	INM	KHO	KUZ	MDK	MOL	NeoMRG	PNT	RAS	SAP	SKH	SWT	TH
CHU	1712																
DJR	860	2460															
GPD	1985	282	2741														
HAR	470	1585	870	1870													
INM	1235	545	2094	814	1188												
KHO	750	1985	400	2267	570	1748											
KUZ	860	2460	0	2741	870	2094	400										
MDK	690	1960	435	2242	535	1723	40	435									
MOL	860	2460	0	2741	870	2094	400	0	435								
NeoMRG	0	1712	890	1985	470	1235	750	890	690	890							
PNT	1985	282	2741	0	1870	814	2267	2741	2242	2741	1985						
RAS	2005	550	2115	804	1208	15	1763	2115	1738	2115	2005	804					
SAP	795	2424	45	2706	830	2064	405	75	412	75	795	2706	2079				
SKH	645	1762	595	2044	345	1533	250	595	220	595	645	2044	1548	580			
SWT	690	1797	590	2050	412	1600	240	590	180	590	690	2050	1615	580	35		
TH	1265	3100	1080	3382	1665	2665	1540	1080	1440	1080	1265	3382	2109	1012	1523	1545	
TMG	425	1818	500	2100	405	1593	185	500	130	500	425	2100	1607	515	110	115	1448

2. Sample abbreviations are from Table 1, distances are in kilometers.

Reconstruction of Population History—Odontometric Analysis:

NEIGHBOUR-JOINING CLUSTER ANALYSIS (FIG. 3)

Neighbour-joining cluster analysis indicates that the sample from Tepe Hissar (TH) shares closest phenetic affinities to prehistoric Central Asians from southern Uzbekistan (DJR, KUZ, MOL, SAP) and from the Tedjen Oasis of southeastern Turkmenistan (GKS), although these affinities are not close. Remaining samples tend to aggregate by region, with several exceptions. The prehistoric samples from the Indus Valley exhibit closest affinities to one another, except for the sample from Harappa, which has closest affinities to the sample from Inamgaon (INM) located in west-central peninsular India. Affinities are particularly close between the two post-Mature Phase samples from Timargarha (TMG) and Sarai Khola (SKH). The two temporally distinct samples from Mehrgarh do not show close affinities to one another and are identified as peripheral members of the aggregate that includes the other prehistoric samples Indus Valley. The remaining samples from west-central peninsular India are marked by closest affinities to one another, except for the mixed caste urban sample from Pune (RAS), which is identified as possessing closer affinities to Dravidian-speaking caste Hindus from southeastern India. The three ethnic group samples from the Hindu Kush highlands (KHO, SWT, MDK) possess no affinities to one another. The Swatis (SWT) are part of a three sample aggregate that also includes the sample of Dravidian-speaking tribals from southeast India (CHU) as well as the Namazga V period sample from the Kopet Dagh foothill plain of southern Turkmenistan (ALT). As such, this aggregate includes samples separated by the greatest geographic and linguistic distances. The sample from Madaklasht (MDK) is found in the centre of the array and appears to share no affinities to any of the other samples. In marked contrast, Khowars (KHO) are identified as possessing closest affinities to the BMAC samples from southern Uzbekistan, as well as to the Namazga III period sample from the Tedjen Oasis of southeastern Turkmenistan (GKS).

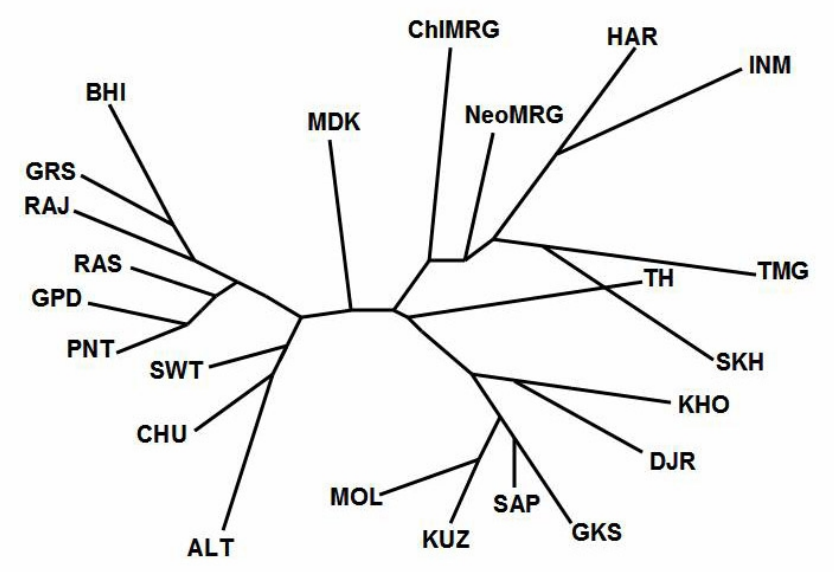

Figure 3. Neighbour-joining cluster analysis of squared Euclidean differences in geometrically scaled mesiodistal tooth lengths and buccolingual tooth breadths for all teeth, except third molars. Sample abbreviations are from Table 1.

MULTIDIMENSIONAL SCALING (FIG. 4)

Multidimensional scaling of the diagonal matrix of squared Euclidean distances into three dimensions with Guttman's coefficient of alienation accounts for 95.8% of the total variance (stress= 0.092) after 64 iterations. Located in the lower left of the array, multidimensional scaling identifies the inhabitants of Tepe Hissar (TH) as possessing rather distant affinities to the BMAC samples from southern Uzbekistan (DJR, KUZ, MOL, SAP) and the Namazga III period sample from the Tedjen Oasis of southeastern Turkmenistan (GKS). Remaining samples generally fall into regional aggregates, but with exceptions. Prehistoric Indus Valley samples occupy the lower centre with fairly close affinities between the two post-Mature phase samples (TMG, SKH) and the later sample from Mehrgarh (ChlMRG). Affinities are somewhat more distant for the earlier sample from Mehrgarh (NeoMRG), and especially the Mature Phase sample from Harappa (HAR). The prehistoric sample from west-central peninsular India (INM) is identified as distantly associated with these prehistoric Indus Valley samples. The three living samples from west-central India (BHI, GRS, RAJ) are most similar to one another and have secondary affinities to the two Dravidian-speaking caste samples from southeast India (GPD, PNT) . The mixed caste urban sample from Pune (RAS) is markedly divergent from the other living samples from peninsular India with rather distant affinities to the prehistoric Indus Valley sample from Timargarha (TMG) one and the living Swatis (SWT) of the Hindu Kush highlands. The three Hindu Kush ethnic groups are identified as possessing closer affinities to one another than suggested by neighbour-joining cluster analysis. Affinities are particularly close between the Madaklasht (MDK) and Swatis (SWT), with Khowars (KHO) more distantly removed toward the phenetic space occupied by the prehistoric Central Asian samples from southern Uzbekistan. Two samples are as phenetically isolated from all others: tribal Chenchus (CHU) from southeastern India, and the Namazga V period inhabitants of Altyn depe (ALT).

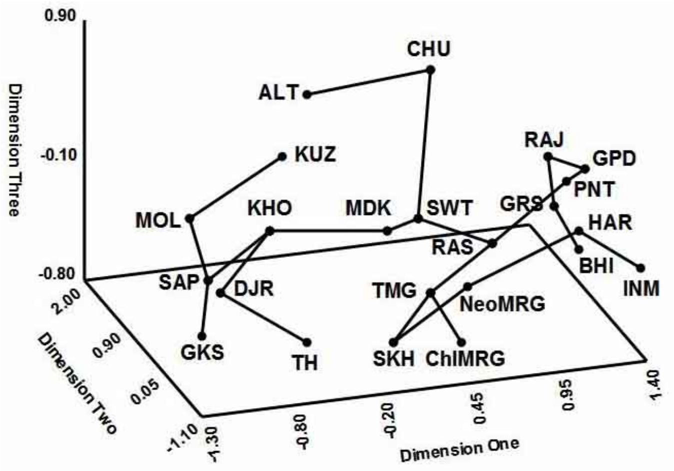

Figure 4. Multidimensional scaling of squared Euclidean differences in geometrically scaled mesiodistal tooth lengths and buccolingual tooth breadths for all teeth, except third molars with Guttman's coefficient of alienation. Sample abbreviations are from Table 1.

PRINCIPAL COORDINATES ANALYSIS (FIG. 5)

The first three principal coordinate axes account for 66% of the total variance. Individuals from Tepe Hissar (TH) occupy a highly isolated position in the upper right of the array that links to the other samples by only a very distant and tenuous connection to the latest of the prehistoric BMAC samples from southern Uzbekistan (MOL). Remaining samples are largely arranged by regional aggregates, but again there are exceptions. Peninsular Indians occupy the lower left side and for inhabitants of both Gujarat and Andhra Pradesh, affinities are closer between the two Hindu caste samples (GRS and RAJ, GPD and PNT) than to their respective tribal samples (BHI, CHU). This is especially the case for the Chenchus (CHU), who occupy a highly isolated phenetic position. The mixed caste urban sample from Pune is rather divergent from the other three living samples from west-central India (BHI, GRS, RAJ) and links peninsular Indian samples to samples from other regions via a distant connection to the Swatis (SWT) of the Hindu Kush highlands. The three samples from the Hindu Kush exhibit closest affinities to one another, but it is clear that affinities are closer, but not especially close, between Swatis and the inhabitants of Madaklasht (MDK) than either group shares with Khowars (KHO). Instead Khowars occupy a position peripheral to the prehistoric samples from southern Uzbekistan and to the Namazga III period sample from the Tedjen Oasis (GKS). The remaining prehistoric sample from Central Asia, Altyn depe, occupies a highly isolated position in the right foreground. Prehistoric samples from the Indus Valley are widely dispersed throughout the centre and upper right. Affinities are fairly close between the two post-Mature Phase samples (TMG. SKH), as are affinities between the two samples from Mehrgarh (NeoMRG, ChlMRG), while the Mature Phase sample from Harappa (HAR) links these pairs of prehistoric Indus Valley samples to one another. Once again, the prehistoric sample from west-central peninsular India (INM) is associated with these prehistoric samples from the Indus Valley.

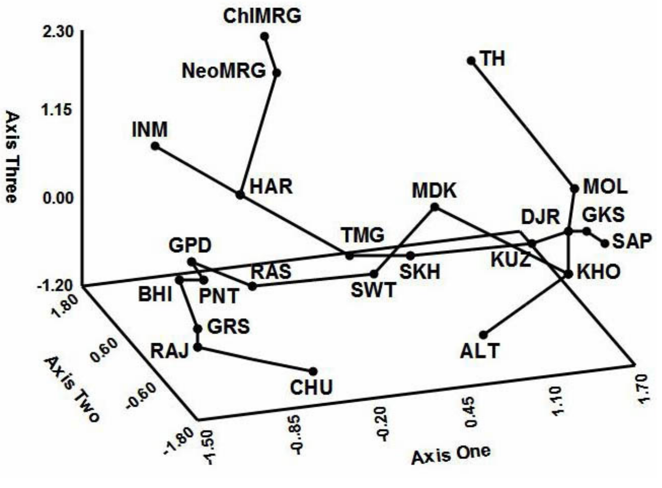

Figure 5. Principal coordinates analysis of squared Euclidean differences in geometrically scaled mesiodistal tooth lengths and buccolingual tooth breadths for all teeth, except third molars. Sample abbreviations are from Table 1.

Reconstruction of Population History—Dental Morphology

NEIGHBOUR-JOINING CLUSTER ANALYSIS (FIG. 6)

Located in the lower left corner of the array, Tepe Hissar (TH) is identified as possessing closest affinities to the BMAC samples from southern Uzbekistan. Affinities are closest with the Djarkutan period sample (DJR) and most distant with the latest Molali period (MOL) sample. The Molali period sample links to prehistoric Indus Valley samples via the latest of these samples, Sarai Khola (SKH). Affinities are increasingly remote for the Late Bronze/Early Iron Age sample from Timargarha (TMG) and the Mature Phase sample from Harappa (HAR). The two pre-Mature Phase Indus Valley samples from Mehrgarh exhibit no affinities to one another or to any of the other samples from the Indus Valley. The earlier sample from the aceramic Neolithic levels (NeoMRG) links to samples from west-central peninsular India. This affinity is closest with the Jorwe period sample from Inamgaon (INM) and is more remote for the living samples, but of these latter samples, affinities are closer with the tribal Madia Gond sample (MDA) from eastern Maharashtra than to the two Hindu caste samples (MRT, MHR). In marked contrast, the early Chalcolithic sample from Mehrgarh (ChlMRG) has closest affinities to living samples of Dravidian-speaking ethnic groups of southeast India, especially tribal Chenchus (CHU). The three samples from the Hindu Kush highlands (KHO, MDK, SWT) exhibit closest affinities to one another and have affinities intermediate between living samples from west-central and southeastern peninsular India, as well as to the prehistoric Indus Valley samples from Harappa and Timargarha. The two urban mixed caste samples from Kolkata (BNG) and Pune (RAS) exhibit surprisingly close affinities to one another, followed by more distant affinities to the two Dravidian-speaking Hindu caste samples from southeast India (PNT, GPD).

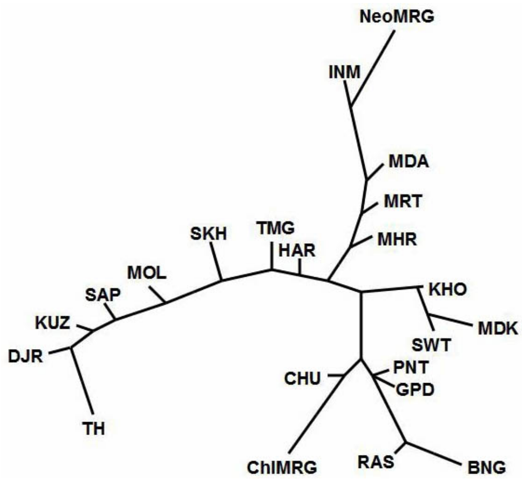

Figure 6. Neighbour-joining cluster analysis of Smith's MMD values based on differences in dental morphology trait frequencies for 17 tooth-trait combinations. Sample abbreviations are from Table 2.

MULTIDIMENSIONAL SCALING (FIG. 7)

After 36 iterations, multidimensional scaling of the triangular matrix of Smith's pairwise MMD values into three dimensions with Guttman's coefficient of alienation accounts for 95% of the total variance (stress= 0.100). Multidimensional scaling places the sample from Tepe Hissar (TH) on the extreme left side of the array. Tepe Hissar is identified as possessing closest affinities to the BMAC samples from southern Uzbekistan, and affinities are especially close with the Djarkutan period sample (DJR). These samples, which are found on the left, are strongly separated from South Asian samples, regardless of whether these latter samples derive from the Hindu Kush highlands, the Indus Valley of Pakistan, or peninsular India. The only partial exception to this pattern is the latest of the prehistoric samples from the Indus Valley, Sarai Khola (SKH), which occupies an intermediate position in the centre. The two samples from Mehrgarh are identified as possessing no affinities to one another. As with neighbour-joining cluster analysis, the earlier sample (NeoMRG) is identified as possessing closest affinities to inhabitants of west-central peninsular India. However, multidimensional scaling suggests that affinities are closer to living Madia Gond tribals (MDA) than to the prehistoric sample from Inamgaon (INM). Nevertheless, multidimensional scaling is consistent with neighbour-joining cluster analysis in identifying that the most distant affinities between west-central Indians and the Neolithic inhabitants of Mehrgarh occur with the two Hindu caste samples (MHR, MRT). Multidimensional scaling identifies the Chalcolithic period inhabitants of Mehrgarh (ChlMRG) as possessing closest affinities to living Dravidian-speaking samples, especially tribal Chenchus (CHU)—a result consistent with the findings of neighbour-joining cluster analysis. The three samples from the Hindu Kush highlands are found in the lower right. Khowars (KHO) are marked by affinities to Mature Phase Harappans (HAR) from the Indus Valley on the one hand and to Swatis (SWT) on the other. Swatis (SWT), and especially the residents of Madaklasht (MDK), do not share close affinities to any of the other samples, even to Khowars. The two mixed caste urban samples (BNG, RAS) occupy unexpected positions adjacent to one another among the living Dravidian-speaking samples from southeastern India.

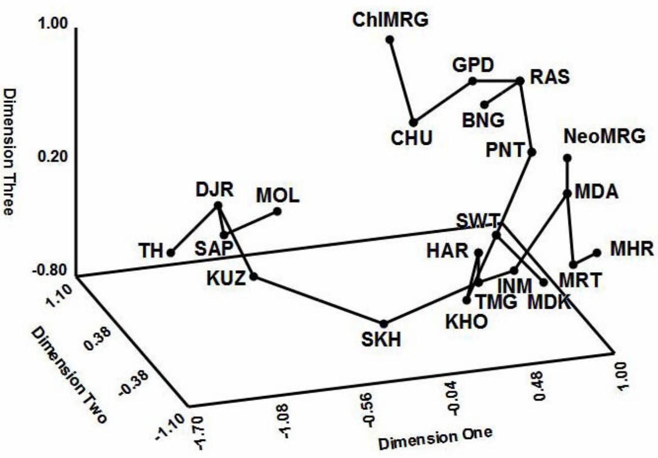

Figure 7. Multidimensional scaling of Smith's MMD values based on differences in dental morphology trait frequencies for 17 tooth-trait combinations with Guttman's coefficient of alienation. Sample abbreviations are from Table 2.

PRINCIPAL COORDINATES ANALYSIS (FIG. 8)

The first three principal coordinate axes account for 88.3% of the total variance. Principal coordinates analysis yields results highly consistent with those obtained by neighbour-joining cluster analysis and multidimensional scaling. The sample from Tepe Hissar (TH) is identified as occupying a position on the extreme edge of the array, this time on the right, with closest affinities to the BMAC samples. However, unlike the previous analyses, principal coordinates analysis suggests that closest affinities are with the earliest BMAC sample from Sapalli tepe (SAP). Overall, phenetic separation between Tepe Hissar and the Central Asian samples from southern Uzbekistan is not as marked as that depicted by neighbour-joining cluster analysis or by multidimensional scaling. The latest Indus Valley prehistoric sample, Sarai Khola (SKH) occupies an intermediate position along the first axis in the centre of the array, but unlike multidimensional scaling, the Chalcolithic period sample from Mehrgarh (ChlMRG) also occupies an intermediate position along this first axis. While the sample from Sarai Khola has affinities to two earlier prehistoric samples from the Indus Valley (TMG, HAR), the samples from Mehrgarh are identified as possessing no phenetic affinities to one another or to any of the other Indus Valley samples. The Neolithic sample (NeoMRG) is identified as possessing closest, albeit distant, affinities to living and prehistoric inhabitants of west-central peninsular India, particularly the tribal sample of Madia Gonds (MDA) from eastern Maharashtra. The later Chalcolithic inhabitants of Mehrgarh are identified as possessing closest affinities to Dravidian-speaking inhabitants of southeastern India; in this case, affinities are closest with the tribal sample of Chenchus (CHU). Located in the lower left, the three living samples of Hindu Kush highlanders occupy a phenetic position intermediate between living and prehistoric inhabitants of west-central India on the one hand, and living ethnic groups of southeastern India on the other. In contrast to results obtained by neighbour-joining cluster analysis and multidimensional scaling, principal coordinates analysis indicates that it is the Khowars, rather than the Madaklasht, that stand apart from other Hindu Kush highlanders. The two mixed caste urban samples (BNG, RAS) are identified as possessing closest affinities to living ethnic groups from southeast India, but unlike results obtained from the other analyses, principal coordinates analysis does not identify these two samples as possessing closest affinities to one another. Instead these two samples occupy positions equidistant, but in opposite phenetic directions, from the low-status Dravidian-speaking Hindu caste sample of Gompadhompti Madigas (GPD).

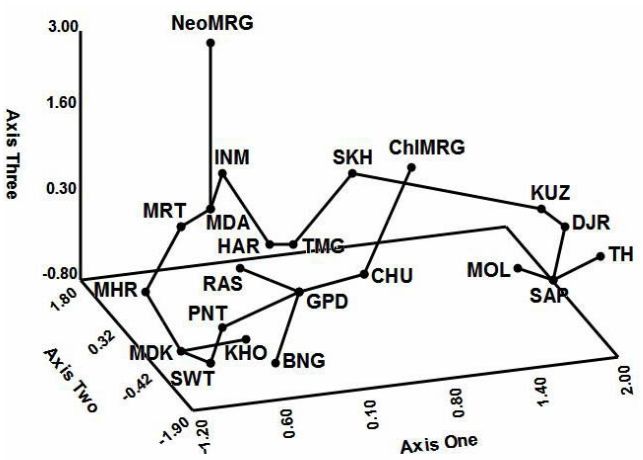

Figure 8. Principal coordinates analysis of Smith's MMD values based on differences in dental morphology trait frequencies for 17 tooth-trait combinations. Sample abbreviations are from Table 2.

Discussion

Are systemic biases introduced when prehistoric archaeologically derived samples are considered in the same analysis as samples of contemporary living individuals?

Total crown area, as a measure of overall tooth size, was ranked by sample and regressed upon each sample's ranked complexity score, as a measure of overall crown morphological elaboration to determine whether systemic bias is introduced when archaeologically derived samples are considered in the same analysis as samples of contemporary living individuals. No correlation (r_s= 0.004; p= 0.986) was found between these two variables. Thus, there appears to be no relationship between crown size and crown complexity among the samples considered here. Ranked crown area was also regressed upon the sample ranked scores along the first dimension yielded by multidimensional scaling and by the first principal coordinate axis yielded by principal coordinate analysis. Neither of these correlations were significant, demonstrating that the effect of gross size has been effectively removed thereby permitting assessment of differential tooth size allocation (or "gradients") across and within the various morphogenetic fields of the permanent dentition (Harris and Harris, 2007). Similar regressions of ranked complexity scores by sample along the first dimension yielded by multidimensional scaling and by the first principal coordinate axis yielded by principal coordinate analysis consistently yielded significant correlations. Such results indicate these data reduction techniques detect differences among the samples in coordinated crown elaboration and simplification. When considered in conjunction with differential tooth size allocation, such results indicate the dentitions of the various samples vary metrically and morphologically independently of antiquity.

Does Variation in Dental Morphology Yield Results Consistent with Those Obtained from Allocation of Permanent Tooth Size?

The research design employed here included different living samples of Khowars as well as different ethnic groups from western India and prehistoric groups from Central Asia to exacerbate potential differences in results obtained from dental morphology and allocation of permanent tooth size. A matrix correlation test between the triangular matrix of squared Euclidean distances obtained from geometrically scaled mesiodistal tooth lengths and buccolingual tooth breadths and the triangular matrix of Smith's MMD values obtained from dental morphology trait frequencies found these matrices to be significantly correlated. Further, both matrices were found to be significantly correlated to a triangular matrix of pairwise geographic distances between sample pairs. An examination of the partial correlation of residuals of these two matrices once the effect of geography was removed found these residuals to be non-significant. Following Oden and Sokal (1992: 289), if a non-significant result is obtained by the three matrix permutation test upon two matrices (squared Euclidean distances, Smith's MMD distances) that have been demonstrated to be spatially autocorrelated one can accept the null hypothesis that the two matrices are the product of geographic factors acting upon the same process of differentiation.

Considered as a whole, analyses based on these two types of data yield some results that are consistent and others that are not. Both identify a core of regional continuity for most regions, both indicate there are continuity problems for prehistoric samples from the Indus Valley, especially those that antedate the third millennium BC. The analyses also identify outliers that do not appear to be related to other samples included in this analysis, suggest that samples that combine members of different ethnic groups (castes) are problematic for comparative purposes, and appear unaffected by the inclusion of both prehistoric and living samples.

When consideration is limited to the 18 living and prehistoric samples for which dental morphology and odontometric data are considered, the two analyses differ in the following three ways: 1) the degree of phenetic separation of living Khowars from the other samples of living Hindu Kush highlanders and their phenetic proximity to prehistoric Central Asians from southern Uzbekistan; 2) the degree of phenetic separation between the two temporally distinct samples from Mehrgarh; and 3) the relative phenetic isolation of the tribal Chenchus from other southeast Indian samples and from all other samples.

The results obtained from tooth size allocation show no phenetic affinities between the BMAC samples from southern Uzbekistan to the Namazga V period inhabitants of Altyn depe, but indicate rather close affinities with the earlier Namazga III period inhabitants of the Tedjen Oasis. Such results are intriguing given the millennium that separates Geoksyur from the BMAC samples. Similar findings were obtained in an earlier study of craniometric variation (Hemphill, 1999) where, given the considerably earlier date for Geoksyur and the subsequent abandonment of the desiccated Tedjen Oasis, it was speculated that the descendants of the Geoksyur population may have migrated east, perhaps toward the Zeravshan River Valley and may have contributed to the ancestral population that later inhabited the urban centres of Sapalli tepe and Djarkutan.

If the Aryan Invasion Model is true, that populations attributable to the urban centres of Sapalli tepe and Djarkutan, perhaps under the influence of elite dominance from horse mounted steppe populations (Erdosy, 1995; Hiebert, 1994, 1998; Hiebert & Lamberg-Karlovsky, 1992; Kuzmina, 1998; Parpola, 1995), crossed the Hindu Kush and emigrated to the Indus Valley during the mid-2nd millennium BC, post-Mature phase inhabitants of the Indus Valley should reflect the biological impact of this invading population. Further, if the distribution of Y-chromosome haplotype R1a reflects the genetic “smoking gun” of these invaders, Indo-Aryan-speaking populations inhabiting much of the northern half of the Indian subcontinent should also reflect the biological signature of these intrusive Central Asians (Bamshad et al, 2001; Mukherjee et al, 2001; S. Roychoudhury et al, 2000; Thanseem et al, 2006; Wells et al, 2001).

None of the results obtained through dental morphology or tooth size allocation analyses support such a scenario. While results obtained from dental morphology provide *some* evidence of less phenetic separation between the latest of the prehistoric Indus Valley samples and the BMAC samples of southern Uzbekistan, this is not evident from either neighbour-joining analysis or principal coordinates analysis. Similarly, only the plot produced by principal coordinates analysis shows this phenetic proximity between the BMAC samples and Sarai Khola. Together, these results suggest the material evidence recovered from Quetta (Jarrige and Hassan, 1989), Mehrgarh VIII (Santoni, 1984), and Swat (Antonini, 1973) are unlikely to reflect an actual movement of Central Asians into the northwestern region of South Asia. These results also corroborate a number of recent genetic studies that likewise fail to find any substantial influx of Central Asian genes into South Asian populations (Sahoo et al, 2006; Sharma et al, 2006).

Whatever biological connections may exist between the populations of Central and South Asia appears limited to ethnic groups living in the Hindu Kush highlands of northern Pakistan. Analyses based on comparisons of dental morphology trait frequencies tend to identify these three samples as possessing fairly close affinities to one another. This is especially the case for neighbour-joining cluster analysis and principal coordinates analysis, but is less so for results obtained by multidimensional scaling. Further, dental morphology analyses yield volatile results with regard to the affinities of these ethnic groups to both living and prehistoric samples from other regions of South and Central Asia. Both neighbour-joining cluster analysis and multidimensional scaling suggest equidistant separations of these Hindu Kush highlanders from southeastern and west-central peninsular Indians, as well as from Mature Phase Harappans and the Late Bronze/Early Iron Age sample from Timargarha, coupled with no affinities to the two temporally distinct samples from Mehrgarh, prehistoric Central Asians, or the Bronze Age inhabitants of Tepe Hissar. By contrast, principal coordinates analysis suggests these Hindu Kush highlanders have closest affinities to peninsular Indians, coupled with no affinities to the prehistoric inhabitants of the Indus Valley, and are especially separated phenetically from prehistoric Central Asians and the prehistoric inhabitants of Tepe Hissar. Odontometric analyses suggest that affinities between these highlanders are not close. Swatis and the inhabitants of Madaklasht are identified as isolates to all other samples, while the Khowar consistently occupy a phenetic position peripheral to prehistoric Central Asians from southern Uzbekistan and the Tedjen Oasis of southeastern Turkmenistan.

Such disparate results may be the consequence of several factors. The first is that these populations, living in remote and extremely challenging environments, may have experienced a series of population bottlenecks and genetic drift. Indeed, such findings were found by Papiha (1996) among groups living in the mountainous sub-Himalayan region of Kinnaur District, Himachal Pradesh. A second possibility is that these groups are marked by such volatility in phenetic affinities because they share little biological affinities to one another or to any of the other samples included in this analysis.

The phenetic affinities of prehistoric samples from the Indus Valley clearly differ between dental morphology and odontometric data sets. Analyses based upon dental morphology trait frequencies identify fairly close phenetic affinities among post-4th millennium BC samples, coupled with a strong phenetic divergence between the two temporally distinct samples from Mehrgarh and these later prehistoric samples. The phenetic divergence of these early samples is so profound that the earlier sample from Mehrgarh stands as an isolate peripheral to living and prehistoric samples from west-central India, while the later sample stands as an isolate peripheral to living samples from southeast India. By contrast, analyses based upon the allocation of tooth size do not confirm the profound phenetic separation between the two samples from Mehrgarh. Although affinities do not appear particularly close, neither sample stands apart as possessing closer affinities to non-Indus Valley samples. Instead, it is the Mature Phase sample from Harappa that has affinities with the west-central peninsular prehistoric sample from Inamgaon. The fairly close phenetic affinities between the two post-Mature phase samples, Timargarha and Sarai Khola, identified by dental morphology analyses is confirmed by odontometrics.

Such striking differences in the phenetic affinities possessed by prehistoric Indus Valley samples that antedate the 3rd millennium BC cannot be attributed to the antiquity of these samples *per se*, for no correlation was found between tooth size and crown complexity, even though prehistoric samples from South Asia, like those from other world regions, exhibit a tendency toward reduction across the post-Pleistocene era (Lukacs, 1985a). The affinities identified from the dental morphology analysis between the Neolithic inhabitants of Mehrgarh with west-Central Indians in general, and with the Jorwe period inhabitants of Inamgaon, may reflect long-standing population continuity across the subcontinent that dates back to the initial dispersal of humanity to South Asia (Kivisild et al, 2003; McElreavy & Quintana-Murci 2005; Sahoo et al., 2006). Indeed, none of the analyses showed the affinity to be strong. In this regard, it is intriguing that tooth size allocation analysis yields a similar result, except the affinities are limited to the Jorwe period sample and are closer to the Mature Phase inhabitants of Harappa than to the Neolithic inhabitants of Mehrgarh. Yet, once again, these affinities are not particularly close. Further, it may be that the affinities identified by dental morphology between Neolithic Mehrgarh and Inamgaon and between Harappa and Inamgaon by tooth size allocation may signal patterns of interaction that ceased with the deurbanization of the Indus Civilization near the beginning of the 2nd millennium BC. Neither dental morphology nor allocation of tooth size analyses indicates any phenetic proximity between post-Mature Phase Indus Valley samples and peninsular Indians. This lack of relatedness to peninsular Indians extends to living inhabitants of the Hindu Kush highlands as well as to prehistoric Central Asians, while the separation between Indus Valley and peninsular Indians inhabitants has been confirmed for Y-chromosome variations by Sengupta and coworkers (2006; see also McElreavey and Quintana-Murci, 2005) and for mtDNA by Quintana-Murci and coworkers (2004; see also Metspalu et al, 2004).

Dental morphology analyses consistently identify a regional distinction between ethnic groups from Maharashtra in west-central India relative to ethnic groups from Andhra Pradesh in southeastern India, which corroborates numerous genetic studies consistent with long-standing population continuity and genetic differentiation through isolation-by-distance (Bamshad et al, 1996; Das et al, 1996; Ghosh et al, 1977; Majumdar 1998; Majumdar and Mukherjee, 1993; et al, 1999; Metspalu et al, 2004; Sahoo et al, 2006; Sengupta et al., 2006; Walter et al, 1977). However, these results confirm that tribal samples are consistently most distinctive relative to their Hindu caste counterparts, and that the prehistoric sample from Inamgaon is identified as being associated with both living ethnic groups from west-central India as well as prehistoric samples from the Indus Valley. This is consistent with numerous genetic studies which indicate a greater population structuring beyond simple isolation-by-distance; a structure that distinguishes between tribal and caste Hindu populations (Balakrishnan, 1978; Battacharayya et al, 1999; Cordaux et al, 2004; Kivisild et al., 2003; Livshits and Nei, 1990; Majumdar, 1998; A.K. Roychoudhury, 1983).

Odontometric analyses likewise consistently identify a regional distinction between living peninsular Indians, but the distinction is not as well marked as that yielded by dental morphology. Results of odontometric analyses also tend to identify the tribal samples of each region as divergent. However, odontometric analyses identify the Chenchus of southeastern India as highly divergent from their Hindu caste counterparts, while Bhils of Gujarat are much less so, which corroborates the assertion of strong genetic differences among tribal populations (Krithika et al, 2009) as well as their differing degrees of genetic separation from caste Hindus due to the absorption of former tribal populations into the caste system through the process of Hinduisation (Chaubey et al, 2007).

Conclusions

The current research was designed to test whether combining odontometric and dental morphology data from archaeologically-derived individuals with data from living individuals introduces bias that renders population history reconstruction moot and whether these two dental systems of biological variation are the product of the same differentiation process that may be used to reconstruction population histories.

Are systemic biases introduced when prehistoric archaeologically derived samples are considered in the same analysis as samples of contemporary living individuals?

As noted that the beginning of this paper, biological anthropologists have long been wary of mixing prehistoric and contemporary samples into any biological distance analysis because it is well-known that overall tooth size and crown complexity have been reduced in the post-Pleistocene era. Consequently many researchers have contended that the reduction in tooth size and crown complexity occurred in lock-step fashion due to positive selection from technological improvements in pre-masticatory food preparation techniques and a dietary shift from hunting and gathering to agriculturally-based food production. The association between tooth size and crown complexity was tested, and the correlation was found to be low and statistically insignificant. Similar results were found for the association between total crown area and compound complexity score. Thus, it appears clear, no systemic bias is introduced into either dental morphology analysis or analysis of permanent tooth size allocation when both prehistoric and living samples are included.

Does variation in dental morphology trait frequencies yield results consistent with results obtained from assessment of tooth size allocation?

A three matrix permutation test upon two biological distance matrices (squared Euclidean distances, Smith's MMD distances) and a matrix of geographic distances indicates that both measures of biological distance are spatially autocorrelated. Consequently, one can accept the null hypothesis that these two matrices of biological distance are the product of geographic factors acting upon the same process of differentiation. Nevertheless, results obtained from analysis of dental morphology trait frequencies is not identical to those obtained by analysis of the allocation of permanent tooth size throughout the dentition with regard to the patterning of pairwise affinities among samples. The key issue is whether the differences between the two analyses are so profound that they are discordant and therefore cannot be used in tandem to address questions about population origins and subsequent interactions. The data presented here indicates that they are concordant, at least on a regional level. Therefore, both dental trait frequencies and allocation of permanent tooth size are similar, but distinct, reflections of the same differentiating process. Because of this, researchers are best served by considering both when attempting to reconstruct the biological histories of populations of specific world regions.

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