# Dental Anthropology of the Madaklasht II: A Comparative Analysis of Morphological Variation — Are the Madaklasht an Intrusive Population in Northern Pakistan?

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**Key Words:** Migration; gene flow; phenetic distance; Central Asia; India

**Abstract**

*Standardized observations of morphological variations of the permanent tooth crown among 205 inhabitants of Madaklasht village, located in an isolated alpine valley of Chitral District, Khyber Pakhtunkhwa Province, Pakistan were compared to members of both prehistoric and living ethnic groups of southern Central Asia, the Indus Valley of Pakistan, and west-central and southeastern regions of peninsular India. Univariate and multivariate analyses of 17 tooth-trait combinations revealed that trait prevalence for both 'key' and 'distal' teeth within the same morphogenetic field must form the basis of comparison. Of the 17 tooth-trait combinations, retention of full hypocone development on the second maxillary molar proved to be most discerning among samples, while the presence of an accessory cusp, the entoconulid, on the second mandibular molar proved least discerning. Over all, maxillary traits were found to be more discerning than traits occurring on the mandibular teeth. No simple relationship was found between crown complexity and temporal context. This observation, along with the finding that morphological traits occurring upon anterior teeth (incisors, canines)only slightly outperform traits found on the posterior teeth (premolars, molars), indicate no marked biasn due to differential preservation of anterior and posterior teeth is introduced into biological distance analyses when prehistoric samples are considered alongside samples obtained from populations of living ethnic groups. Contrasts between samples grouped by geographic region indicate that no one set of tooth-trait combinations identifies similarities and differences within and between such aggregates. Instead, different mixtures of tooth-trait combinations provide the best discrimination with and between such geographic groupings. In South Asia, the proper population level for reconstruction of biological histories is at the level of local populations of tribes, self-identifying ethnic groups of Islamic Pakistan, and sub-castes in Hindu populations of India. Samples that encompass individuals from a multiplicity of such entities introduce damaging bias that renders such mixed samples of no utility for biological distance analysis. Theinhabitants of Madaklasht, like their Hindu Kush counterparts, the Khowars, are identified as distinct from populations of other regions of South Asia and from Late Bronze Age populations of southern Central Asia. Multivariate data reduction techniques disagree over the phenetic proximity of these two Hindu Kush highland populations to one another. One or both groups may represent long-standing isolated populations of the Hindu Kush highlands, or these groups may represent recently intrusive populations into northern Pakistan.*

## Introduction

Despite their strategic location, situated at the geographic juncture of Western, Central, and South Asia, little is known of the biological history of ethnic groups occupying the Hindu Kush and Karakoram highlands of northern Pakistan. Indeed, until recent years, what precious little that has been known has largely been the product of little more than oral traditions of vague, unsubstantiated claims of descent—often from such august personages as Alexander the Great (Kalasha, Pathan: Mansoor et al 2004; Quintana-Murci et al 2004) or Genghis Khan (Chengazi [*aka*, Hazara] Qamar et al 2002). The lack of scientifically grounded evidence of the biological affinities of such groups is unfortunate for several reasons.

First, recent studies of craniometric variation among ancient skeletons suggests biological connections between populations of western Central Asia and of Xinjiang on the one hand and between the latter and populations of the Indus Valley on the other that may extend all the way back to the Bronze Age (Hemphill in press a; Hemphill and Mallory 2004). Intriguingly, these indications of inter-regional interaction occur among populations located along what later in antiquity became known as the Great Silk Road (Erdosy 1995; Kuzmina 1998; Parpola 1995). Given their location interposed between the lowland populations of southern Central Asia to the northwest, the Taklamakan Basin of Xinjiang to the northeast, the Iranian Plateau to the southwest and the Indus Valley to the south, these highland populations—if they resided in their historical seats for a substantial extent into antiquity—likely played crucial roles in facilitating or mitigating contacts between the populations of these regions.

Second, although comparisons of samples of ancient populations from western Central Asia and the Indus Valley have failed to yield any evidence of contact between the peoples of these two regions prior to the dawn of the Christian Era (Hemphill 2009, in press a,b; Hemphill et al 1991; 1997; 1998; 2000, in press; Hemphill and Lukacs 1993; Lukacs and Hemphill 1991), a recent investigation of dental variation among the living Khowar of Chitral District found them to be uniquely aligned with the Bronze Age inhabitants of the Oxus Civilization rather than to any ofthe samples from South Asia—modern or prehistoric—considered (Blaylock and Hemphill 2007; Hemphill et alin press; Willits and Hemphill 2007).

Third, an array of recent genetic studies based upon mitochondrial DNA (mtDNA) (Mansoor et al 2004, Quintana-Murci et al 2004), Y-chromosome variations (Qamar et al 2002; Sengupta et al 2006), and genome-wide comparisons (Metspalu et al 2011) have indicated that the living members of ethnic groups found in the Hindu Kush and Karakoram highlands exhibit a wide array of genetic affinities. In some respects, these ethnic groups share close affinities to one another, but in other respects some of these ethnic groups are identified as possessing affinities to populations from Central Asia (Mansoor et al 2004; Metspalu et al 2011; Qamar et al 2002; Quintana-Murci et al 2004; but see Sengupta et al 2006), East Asia (Qamar et al 2002; Zerjal et al 2002; 2003) and beyond (Quintana-Murci et al 2001; 2004).

The inhabitants of Madaklasht live within a high alpine valley (Shishi Koh) located east-southeast of Chitral town, the capital of this most northerly district of Khyber Pakhtunkhwa Province, Pakistan. The Madaklasht claim to be descendants of Persians who immigrated to this isolated region some 350 years ago from northeastern Afghanistan and southern Tajikistan. Though surrounded by Khowari speakers, the Madaklasht speak Dari, a distinctive dialect of Farsi spoken in Afghanistan, practice Persian customs, and do not intermarry with neighbouring populations. As noted in the companion paper to the current contribution (Hemphill et al 2010), the inhabitants of Madaklasht take the name Badakhshi for their ethnic group and assert that their original homelands are to be found in the Badakhshan region of northeastern Afghanistan (Ghufran 1962), an area where Dari continues to be spoken.

Oral tradition among the inhabitants of Madaklasht holds that these people came to Chitral during the 17th century because they were recruited by the ruling family of Chitral for their skills as manufacturers of war materiel. Again, as noted in the companion paper (Hemphill et al 2010), these skilled armourers initially believed they would only remain in the region for a brief period of time, but according to the Madaklasht today, their Badakhshi ancestors decided to settle in the Shishi Valley permanently. Wahid Beg (1992:436) asserts the Madaklasht claim of historic era origins in northeastern Afghanistan and Tajikistan is supported by the fact that the Sumbola of Garam Chashma, located 50 km north-northwest of Chitral town, exhibit the same culture, speak the same Dari dialect of Farsi, and also share the oral tradition of emigration from a homeland in Badakhshan to Chitral District during the 17$^{th}$ century.

Assessment of dental variations offers particular insights into intra- and inter-regional population dynamics not available from comparisons of mtDNA, Y-chromosome single nucleotide polymorphisms, and traditional serological markers among living people. One of the most important advantages is that, because dental variations can be compared between members of living populations and those of ancient populations whose antiquity can be determined through radiocarbon or some other form of radiometric dating, assessment of dental variations can determine *when* in time interactions between populations took place. For example, mtDNA or Y-chromosome variations may inform the scientist that population A and population B exhibit evidence of gene flow between them, but because coalescence estimates based on these data are so broad (Matspalu et al 2011; Quintana-Merci et al 2001:540; Reich et al 2009; Zerjal et al 2002), these data may render it impossible to distinguish recent gene flow from that which occurred as much as a millennium ago.

Dental morphology provides a useful basis for a comparison of biological affinities among samples of human populations. Dental features appear to be determined by a large battery of genes and are under moderate to strong genetic control (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) and, as demonstrated in the previous study (Hemphill et al 2010; see also Hanihara 1992; 2008; Irish 1998; Scott 1973; 1980; Scott and Turner 1997; Smith and Shigey 1988), are not affected by sex dimorphism. Consequently, teeth from males, females, and individuals too fragmentary to determine sex, may be pooled to increase sample size. This latter quality is especially important when, as in the current study, some of the comparative samples are obtained from archaeological contexts (see below), for it is often the case that such dental remains are recovered in both fragmentary and heavily worn conditions. Because of these qualities teeth, as the only directly accessible hard tissues of the body, can be compared between living individuals and individuals of the past, thereby providing the temporal sensitivity lacking from DNA analyses based solely on living individuals.

The purpose of the current contribution is to place the pattern of morphological variation found in the permanent tooth crown among the Madaklasht into temporal and inter-regional perspectives. This is accomplished by contrasting the frequencies of a suite of dental morphology variables found among the Madaklasht to the frequencies found among a battery of prehistoric and living dental samples from southern Central Asia, the Indus Valley and peninsular India. In so doing, this contribution seeks to address five questions:

- Should trait consideration be limited to 'key' teeth, or must trait expression on both 'key' and 'distal' teeth within a specific morphogenetic field be assessed in order that truly meaningful information about the biological relatedness among populations be considered?
- Which tooth-trait combinations are most useful for distinguishing biological similarities and differences among populations of the Hindu Kush highlands and beyond in Central Asia, the Indus Valley of Pakistan, and in peninsular India?
- Are there tooth-trait combinations that consistently identify biological differences between samples of populations from different regions of South Asia and neighbouring populations in Central Asia?
- What is the proper population, or taxonomic, unit, for reconstruction of the biological history of the various tribes, self-identifying ethnic groups, and castes of South Asia?
- Are the Madaklasht truly an intrusive population in northern Pakistan?

## Materials and Methods

Dental casts were collected on an impromptu basis in Madaklasht village and at the Aga Khan Diamond Jubilee School. A total of 205 individuals (101 males, 104 females) are represented by plaster casts of their maxillary and mandibular teeth. The sample is dominated by older adolescents and young adults (males: avg. = 18.9, sd= 6.9; females: avg.= 14.5, sd= 2.2) due to a sampling strategy that sought individuals who have experienced eruption of all permanent teeth, except third molars, and who have suffered minimally from dental disease or mechanical disorders that negatively impact the permanent tooth crown (see Hemphill et al 2010).

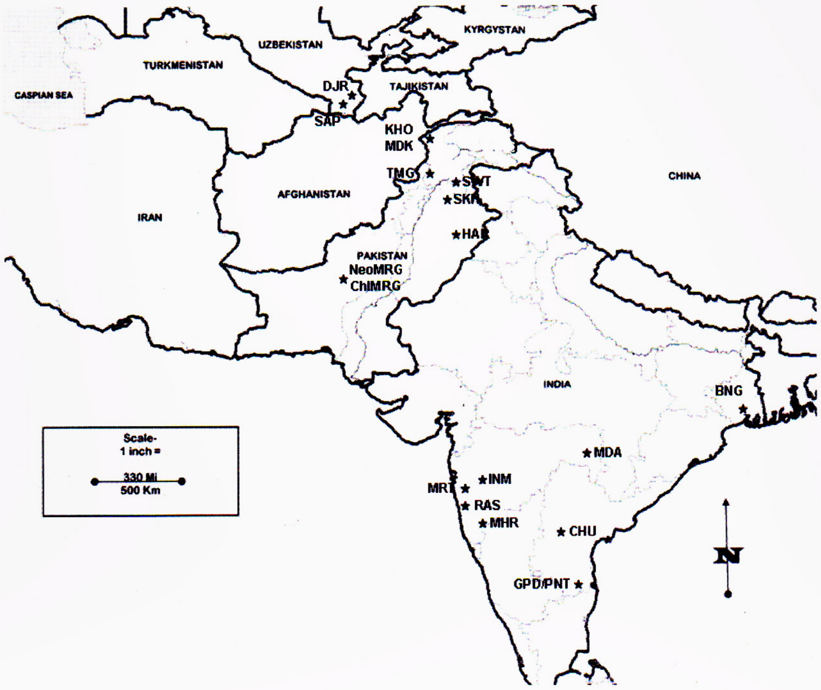
As noted in the previous study (Hemphill et al 2010), the dental casts of each individual were assessed for 26 dental traits scored as 71 tooth-trait combinations in accordance with the Arizona State University Dental Anthropology System (ASUDAS) (Scott and Turner 1997; Turner et al 1991). Observations 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; 1977; 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 1973; 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 1973; 1977).

The two-step trait editing procedure recommended by Irish (2010) and Harris and Sjovøld (2004) is followed here. The original battery of 71 tooth-trait combinations was analyzed in raw form (in which trait expression is scored by ordinal grade of expression) for assessment of inter-trait correlations with Kendall's tau-b correlation coefficient among all samples of living individuals. Assessment of inter-trait correlations was limited to living samples because of the greater sample sizes available and the lesser degree of missing data that plague archaeologically derived samples. All tooth-trait combinations found to be significantly correlated ($\tau_B > 0.5$) were removed from further consideration. The second step tested the non-correlated tooth-trait combinations for significant among-group differences. Traits considered to contain "contributing information" were those that exhibit "a statistically significant difference between at least one pair of the groups being evaluated" (Harris and Sjovøld 2004: 91).

While variation in trait morphology was scored along an ordinal scale among the Madaklasht, trait expression was dichotomized into presence/absence only for comparative purposes. For dichotomization any degree of expression was considered a positive manifestation. The only exceptions were labial curvature of the central maxillary incisor, in which at least grade 2 curvature had to be present to be considered a positive expression, and shovelling of the maxillary incisors and canines, which also had to be expressed at grade 2 to be considered a positive expression. Sex-pooled trait frequencies among the Madaklasht were obtained by taking the average of male and female frequencies. This approach ensured that pooled trait frequencies were not skewed in favour of the sex represented by the most observations for a specific trait.

Frequencies of sex-pooled dental traits among the Madaklasht (MDK) were compared to 1,908 individuals from 19 additional samples **(Fig. 1, Table 1)**. These additional samples include both prehistoric and living individuals. Prehistoric samples encompass individuals from the Indus Valley, southern Central Asia, and peninsular India. Prehistoric Indus Valley samples include Neolithic (*c.* 6500 – 6000 BC, Jarrige, 1984; Jarrige and Lechevallier 1979; 1980) (NeoMRG) (Lukacs 1986) and Chalcolithic (*c.* 4500 BC, Jarrige 1984; Jarrige and Lechevallier 1979; 1980) (ChlMRG) occupants of Mehrgarh (Lukacs and Hemphill 1991), Mature Phase (2600 – 1900 BCE, Kenoyer 1998: 17) Harappans from Harappa (HAR) (Hemphill et al 1991), Late Bronze Age Gandharan Grave Culture (1400 – 850 BC, Dani 1966; 1967) inhabitants of Timargarha (TMG) and the Iron Age occupants of Sarai Khola (SKH) (*c.* 200 BC, Bernhard 1969; Lukacs 1983). Prehistoric Central Asian samples derive from the Late Bronze Age Bactrian-Margianan Archaeological Complex (BMAC:*aka* "Oxus Civilization") urban centers of Sapalli tepe (SKH) (*c.* 2300 – 2100 BC, Hiebert 1994) and Djarkutan (DJR, KUZ, MOL) (*c.* 2100 – 1650 BCE, Hiebert 1994) (Hemphill et al 1998). The sole prehistoric sample from peninsular India is the Jorwe Period inhabitants of Inamgaon (1400 – 700 BCE, Sankalia 1984), located in west-central Indian state of Maharashtra (Lukacs 1987).




1. Geographic locations of dental samples. Sample abbreviations from Table 1.

Samples of living individuals include Khowars from Chitral town (Blaylock 2008; Hemphill et al in press), the inhabitants of Madaklasht (Hemphill 2009; Hemphill et al 2010) from the Hindu Kush highlands as well as an array of samples from peninsular India. Peninsular Indian samples are from Maharashtra in west-central India, Andhra Pradesh in southeastern India, and from Bengal in northeastern India. Maharashtran samples include high-status caste Marathas (MRT) (Lukacs et al 1998; Hemphill et al 2000), low-status caste Mahars (MHR) (Lukacs et al 1998; Hemphill et al 2000), tribal Madia Gonds (MDA) (Lukacs et al 1998; Hemphill et al 2000) and an urban mixed caste sample from Pune (RAS) (Hemphill 1991). Samples from Andhra Pradesh include high-status caste Pakanati Reddis (PNT), low-status caste Gompadhompti Madigas (GPD), and tribal Chenchus (CHU) (Hemphill 1991). The single sample from northeastern India is an urban mixed caste sample from Kolkata (BNG) (Hemphill 1991).

Interobserver variation in morphological evaluations was assessed by repeated scoring of 35 tooth-trait combinations in a random sample of 50 plaster dental casts scored by Lukacs (1976). Observer differences were assessed according to the method of Nichol and Turner (1986) and this assessment found the level of interobserver error to be well within acceptable limits (see Hemphill 1991; Lukacs and Hemphill 1991: 81-83).

Dichotomized frequencies of those tooth-trait combinations retained for comparative analysis were compared by sample, geographic region (Hindu Kush highlands, Central Asia, Indus Valley, west-central peninsular India, southeast peninsular India) and temporal context (prehistoric, living). Differences in trait frequencies across all samples were tested for statistical significance with analysis of variance. Differences in trait frequencies between sample pairs and between samples aggregated into prehistoric and living temporal contexts were tested for statistical significance with chi-square, while Tukey's HSD was used to test for significant differences in dichotomized trait frequencies between samples aggregated into geographic regions.

Table 1. Dental Series used in the Current Study

| **Sample** | **Abb.** | **Date** | **$N_{max}$**[1] |
|---|---|---|---|
| Bengalis | BNG | Living | 73 |
| Chalcolithic Mehrgarh | ChlMRG | 4500 BC | 25 |
| Chenchus | CHU | Living | 194 |
| Djarkutan | DJR | 2100-1950 BC | 39 |
| Gompadhompti Madigas | GPD | Living | 178 |
| Harappa | HAR | 2300-1700 BC | 33 |
| Inamgaon | INM | 1600-700 BC | 41 |
| Khowar | KHO | Living | 136 |
| Kuzali | KUZ | 1950-1800 BC | 24 |
| Madaklasht | MDK | Living | 180 |
| Madia Gonds | MDA | Living | 169 |
| Mahars | MHR | Living | 195 |
| Marathas | MRT | Living | 198 |
| Molali | MOL | 1800-1650 BC | 41 |
| Neolithic Mehrgarh | NeoMRG | 6000 BC | 49 |
| Pakanati Reddis | PNT | Living | 182 |
| Mixed Maharashtrans | RAS | Living | 68 |
| Sapalli Tepe | SAP | 2300-2150 | 43 |
| Sarai Khola | SKH | 200-100 BC | 15 |
| Timargarha | TMG | 1400-850 BC | 25 |
| TOTAL | | | 1908 |

1. $N_{max}$ represents the greatest number of individuals scored for a non-metric trait.

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 especilly 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). Because some have questioned the utility of Smith's MMD statistic for estimation of population distances (Harris 2008; Konigsberg 2006; Konigsberg and Buikstra 2006), an array of recent studies have compared results of this statistic with Mahalanobis $D^2$ values based on tetrachoric correlations. The studies found no significant differences in either the patterning or magnitude of affinities between samples, provided sample sizes are reasonable and traits known to be correlated are either eliminated or minimized in the battery of traits forming the basis of comparison (Edgar 2004: 61; Irish 2010: 390-391; Sutter and Verano 2007: 201).

Since the pattern of variation among 20 samples is difficult to visualize from a 190-cell diagonal matrix, Smith's MMD values were used as input for three data reduction procedures. Following standard practice, all negative standardized MMD values were set at zero prior to submission to data reduction analyses. The patterning of inter-sample differences reflected in the triangular matrix of pairwise Smith's MMD values 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 matrix of Smith's MMD values was double-centered prior to principal coordinates analysis (Rohlf 2000). The first three principal coordinate axes were retained and group scores calculated along these axes. For both multidimensional scaling and principal coordinates analyses, results 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 inter-sample associations.

## Results

### *Univariate Variation*

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 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, median lingual ridge development (*tuberculum dentale*) on these same teeth, hypocone reduction on UM1 and UM2, Carabelli's trait expression on UM1, and presence of the metaconule (C5) 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 (C5), entoconulid (C6), and metaconulid (C7) on these same teeth. Frequencies of these traits by sample are provided in Table 2.

Table 2. Frequencies of Selected Dental Morphology Traits among all Samples with Sexes Pooled

| | | | Bengalis (BNG) | | | Chalcolithic Mehrgarh (ChlMRG) | | | Chenchus (CHU) | | | Djarkutan (DJR) | | | Gompadhompti Madigas (GPD) | | | Harappa (HAR) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dental Trait | Tooth | Abb. | p | n | Freq. | p | n | Freq. | p | n | Freq. | p | n | Freq. | p | n | Freq. | p | n | Freq. |
| Shovelling | UI1 | SHOVI1 | 27 | 73 | 0.370 | 13 | 25 | 0.520 | 64 | 194 | 0.330 | 3 | 16 | 0.188 | 63 | 175 | 0.360 | 2 | 15 | 0.600 |
| Shovelling | UI2 | SHOVI2 | 13 | 73 | 0.178 | 14 | 24 | 0.583 | 33 | 191 | 0.173 | 8 | 22 | 0.364 | 22 | 174 | 0.126 | 4 | 16 | 0.625 |
| Med. Ling. Ridge | UI1 | MLRI1 | 46 | 71 | 0.648 | 14 | 25 | 0.560 | 88 | 194 | 0.454 | 3 | 17 | 0.176 | 85 | 176 | 0.483 | 8 | 12 | 0.667 |
| Med. Ling. Ridge | UI2 | MLRI2 | 49 | 72 | 0.681 | 7 | 24 | 0.292 | 45 | 191 | 0.236 | 4 | 22 | 0.182 | 52 | 177 | 0.294 | 6 | 13 | 0.462 |
| Hypocone Size | UM1 | HYPOM1 | 69 | 72 | 0.958 | 22 | 22 | 1.000 | 192 | 193 | 0.995 | 30 | 30 | 1.000 | 177 | 178 | 0.994 | 16 | 16 | 1.000 |
| Hypocone Size | UM2 | HYPOM2 | 23 | 73 | 0.315 | 10 | 18 | 0.556 | 80 | 187 | 0.428 | 21 | 32 | 0.656 | 55 | 170 | 0.324 | 2 | 18 | 0.111 |
| Carabelli's Trait | UM1 | CARAM1 | 50 | 72 | 0.694 | 11 | 18 | 0.611 | 105 | 193 | 0.544 | 3 | 21 | 0.143 | 108 | 177 | 0.610 | 4 | 9 | 0.444 |
| Metaconule | UM1 | MTCLM1 | 13 | 73 | 0.178 | 5 | 19 | 0.263 | 50 | 191 | 0.262 | 1 | 29 | 0.034 | 49 | 178 | 0.275 | 6 | 13 | 0.462 |
| Metaconule | UM2 | MTCLM2 | 12 | 72 | 0.167 | 6 | 18 | 0.333 | 32 | 183 | 0.175 | 0 | 32 | 0.000 | 36 | 168 | 0.214 | 4 | 16 | 0.250 |
| Y-Groove Pattern | LM1 | YGRVM1 | 58 | 60 | 0.967 | 15 | 21 | 0.714 | 151 | 173 | 0.873 | 20 | 22 | 0.909 | 149 | 159 | 0.937 | 15 | 17 | 0.882 |
| Y-Groove Pattern | LM2 | YGRVM2 | 26 | 66 | 0.394 | 6 | 22 | 0.273 | 51 | 182 | 0.280 | 11 | 35 | 0.314 | 65 | 166 | 0.392 | 3 | 31 | 0.097 |
| Cusp Number | LM1 | CSPNM1 | 66 | 70 | 0.943 | 20 | 23 | 0.870 | 188 | 192 | 0.979 | 20 | 21 | 0.952 | 169 | 171 | 0.988 | 17 | 20 | 0.850 |
| Cusp Number | LM2 | CSPNM2 | 25 | 69 | 0.362 | 2 | 24 | 0.083 | 53 | 191 | 0.277 | 2 | 36 | 0.056 | 64 | 172 | 0.372 | 0 | 33 | 0.000 |
| Entoconulid | LM1 | C6M1 | 7 | 70 | 0.100 | 5 | 23 | 0.217 | 13 | 186 | 0.070 | 1 | 20 | 0.050 | 21 | 169 | 0.124 | 1 | 20 | 0.050 |
| Entoconulid | LM2 | C6M2 | 0 | 71 | 0.000 | 2 | 18 | 0.111 | 1 | 186 | 0.005 | 0 | 36 | 0.000 | 5 | 172 | 0.029 | 0 | 28 | 0.000 |
| Metaconulid | LM1 | C7M1 | 14 | 71 | 0.197 | 3 | 25 | 0.120 | 48 | 195 | 0.246 | 1 | 32 | 0.031 | 23 | 172 | 0.134 | 1 | 22 | 0.045 |
| Metaconulid | LM2 | C7M2 | 9 | 72 | 0.125 | 0 | 24 | 0.000 | 18 | 194 | 0.093 | 1 | 39 | 0.026 | 19 | 173 | 0.110 | 0 | 28 | 0.000 |

Table 2. Continued...

| Dental Trait | Tooth | Abb. | Inamgaon (INM) | | | Khowar (KHO) | | | Kuzali (KUZ) | | | Madaklaskt (MDK) | | | Madia Gonds (MDA) | | | Mahars (MHR) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | p | n | Freq. | p | n | Freq. | p | n | Freq. | p | n | Freq. | p | n | Freq. | p | n | Freq. |
| Shovelling | UI1 | SHOVI1 | 9 | 24 | 0.375 | 33 | 122 | 0.270 | 1 | 13 | 0.077 | 73 | 179 | 0.408 | 80 | 163 | 0.491 | 77 | 186 | 0.414 |
| Shovelling | UI2 | SHOVI2 | 4 | 19 | 0.211 | 24 | 121 | 0.198 | 5 | 14 | 0.357 | 38 | 173 | 0.220 | 23 | 161 | 0.143 | 22 | 181 | 0.122 |
| Med. Ling. Ridge | UI1 | MLRI1 | 14 | 25 | 0.560 | 77 | 127 | 0.606 | 2 | 13 | 0.154 | 125 | 178 | 0.702 | 60 | 153 | 0.392 | 106 | 177 | 0.599 |
| Med. Ling. Ridge | UI2 | MLRI2 | 1 | 20 | 0.050 | 23 | 123 | 0.187 | 6 | 14 | 0.429 | 63 | 177 | 0.356 | 21 | 149 | 0.141 | 41 | 174 | 0.236 |
| Hypocone Size | UM1 | HYPOM1 | 27 | 41 | 0.659 | 134 | 136 | 0.985 | 23 | 23 | 1.000 | 177 | 180 | 0.983 | 155 | 169 | 0.917 | 163 | 195 | 0.836 |
| Hypocone Size | UM2 | HYPOM2 | 0 | 20 | 0.000 | 15 | 61 | 0.246 | 11 | 22 | 0.500 | 15 | 150 | 0.100 | 10 | 153 | 0.065 | 10 | 164 | 0.061 |
| Carabelli's Trait | UM1 | CARAM1 | 13 | 40 | 0.325 | 87 | 130 | 0.669 | 2 | 20 | 0.100 | 133 | 180 | 0.739 | 86 | 165 | 0.521 | 140 | 187 | 0.749 |
| Metaconule | UM1 | MTCLM1 | 6 | 41 | 0.146 | 9 | 133 | 0.068 | 2 | 21 | 0.095 | 5 | 178 | 0.028 | 36 | 156 | 0.231 | 43 | 191 | 0.225 |
| Metaconule | UM2 | MTCLM2 | 3 | 20 | 0.150 | 4 | 51 | 0.078 | 1 | 24 | 0.042 | 17 | 147 | 0.116 | 34 | 138 | 0.246 | 33 | 153 | 0.216 |
| Y-Groove Pattern | LM1 | YGRVM1 | 32 | 35 | 0.914 | 101 | 110 | 0.918 | 10 | 14 | 0.714 | 115 | 142 | 0.810 | 112 | 115 | 0.974 | 115 | 127 | 0.906 |
| Y-Groove Pattern | LM2 | YGRVM2 | 7 | 24 | 0.292 | 16 | 86 | 0.186 | 5 | 15 | 0.333 | 38 | 144 | 0.264 | 31 | 133 | 0.233 | 30 | 161 | 0.186 |
| Cusp Number | LM1 | CSPNM1 | 32 | 39 | 0.821 | 111 | 128 | 0.867 | 10 | 15 | 0.667 | 158 | 176 | 0.898 | 149 | 161 | 0.925 | 170 | 192 | 0.885 |
| Cusp Number | LM2 | CSPNM2 | 4 | 24 | 0.167 | 10 | 80 | 0.125 | 1 | 14 | 0.071 | 36 | 160 | 0.225 | 32 | 158 | 0.203 | 30 | 178 | 0.169 |
| Entoconulid | LM1 | C6M1 | 4 | 37 | 0.108 | 4 | 129 | 0.031 | 0 | 14 | 0.000 | 9 | 177 | 0.051 | 12 | 158 | 0.076 | 13 | 191 | 0.068 |
| Entoconulid | LM2 | C6M2 | 0 | 24 | 0.000 | 0 | 85 | 0.000 | 0 | 15 | 0.000 | 2 | 165 | 0.012 | 5 | 152 | 0.033 | 3 | 174 | 0.017 |
| Metaconulid | LM1 | C7M1 | 2 | 36 | 0.056 | 12 | 129 | 0.093 | 0 | 18 | 0.000 | 10 | 176 | 0.057 | 27 | 165 | 0.164 | 25 | 191 | 0.131 |
| Metaconulid | LM2 | C7M2 | 1 | 25 | 0.040 | 1 | 90 | 0.011 | 0 | 18 | 0.000 | 1 | 163 | 0.006 | 7 | 158 | 0.044 | 3 | 177 | 0.017 |

Table 2 Continued...

| | | | Marathas (MRT) | | | Molali (MOL) | | | Neolithic Mehrgarh (NeoMRG) | | | Pakanati Reddis (PNT) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dental Trait | Tooth | Abb. | p | n | Freq. | p | n | Freq. | p | n | Freq. | p | n | Freq. |
| Shovelling | UI1 | SHOVI1 | 81 | 198 | 0.409 | 4 | 25 | 0.160 | 18 | 28 | 0.893 | 52 | 176 | 0.295 |
| Shovelling | UI2 | SHOVI2 | 24 | 194 | 0.124 | 14 | 27 | 0.519 | 17 | 37 | 0.838 | 27 | 177 | 0.153 |
| Med. Ling. Ridge | UI1 | MLRI1 | 95 | 194 | 0.490 | 9 | 23 | 0.391 | 15 | 26 | 0.577 | 110 | 177 | 0.621 |
| Med. Ling. Ridge | UI2 | MLRI2 | 42 | 190 | 0.221 | 8 | 25 | 0.320 | 2 | 29 | 0.069 | 61 | 177 | 0.345 |
| Hypocone Size | UM1 | HYPOM1 | 170 | 197 | 0.863 | 41 | 41 | 1.000 | 35 | 42 | 0.833 | 177 | 182 | 0.973 |
| Hypocone Size | UM2 | HYPOM2 | 4 | 179 | 0.022 | 23 | 37 | 0.622 | 2 | 41 | 0.049 | 40 | 170 | 0.235 |
| Carabelli's Trait | UM1 | CARAM1 | 122 | 198 | 0.616 | 13 | 36 | 0.361 | 7 | 27 | 0.259 | 136 | 182 | 0.319 |
| Metaconule | UM1 | MTCLM1 | 56 | 193 | 0.290 | 3 | 39 | 0.077 | 7 | 28 | 0.250 | 58 | 182 | 0.319 |
| Metaconule | UM2 | MTCLM2 | 32 | 169 | 0.189 | 3 | 37 | 0.081 | 10 | 25 | 0.400 | 34 | 168 | 0.202 |
| Y-Groove Pattern | LM1 | YGRVM1 | 117 | 128 | 0.914 | 25 | 34 | 0.735 | 23 | 25 | 0.920 | 142 | 148 | 0.959 |
| Y-Groove Pattern | LM2 | YGRVM2 | 51 | 181 | 0.282 | 5 | 33 | 0.152 | 12 | 37 | 0.324 | 67 | 165 | 0.406 |
| Cusp Number | LM1 | CSPNM1 | 166 | 195 | 0.851 | 29 | 33 | 0.879 | 39 | 43 | 0.907 | 173 | 181 | 0.956 |
| Cusp Number | LM2 | CSPNM2 | 28 | 192 | 0.146 | 2 | 35 | 0.057 | 3 | 49 | 0.061 | 43 | 180 | 0.239 |
| Entoconulid | LM1 | C6M1 | 17 | 194 | 0.088 | 3 | 33 | 0.091 | 3 | 37 | 0.081 | 22 | 182 | 0.121 |
| Entoconulid | LM2 | C6M2 | 5 | 191 | 0.026 | 0 | 35 | 0.000 | 0 | 44 | 0.000 | 5 | 179 | 0.028 |
| Metaconulid | LM1 | C7M1 | 15 | 198 | 0.076 | 2 | 39 | 0.051 | 4 | 40 | 0.100 | 31 | 181 | 0.171 |
| Metaconulid | LM2 | C7M2 | 1 | 197 | 0.005 | 1 | 36 | 0.028 | 0 | 43 | 0.000 | 11 | 182 | 0.060 |

Table 2 Continued...

| Dental Trait | Tooth | Abb. | Mixed Maharashtrans (RAS) | | | Sapalli Tepe (SAP) | | | Sarai Khola (SKH) | | | Timargarha (TMG) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | p | n | Freq. | p | n | Freq. | p | n | Freq. | p | n | Freq. |
| Shovelling | UI1 | SHOVI1 | 37 | 67 | 0.552 | 2 | 19 | 0.105 | 0 | 9 | 0.000 | 1 | 7 | 0.143 |
| Shovelling | UI2 | SHOVI2 | 15 | 67 | 0.224 | 5 | 17 | 0.294 | 0 | 9 | 0.000 | 2 | 7 | 0.286 |
| Med. Ling. Ridge | UI1 | MLRI1 | 47 | 68 | 0.691 | 4 | 17 | 0.235 | 2 | 9 | 0.222 | 3 | 8 | 0.375 |
| Med. Ling. Ridge | UI2 | MLRI2 | 35 | 67 | 0.552 | 5 | 17 | 0.294 | 0 | 9 | 0.000 | 0 | 7 | 0.000 |
| Hypocone Size | UM1 | HYPOM1 | 68 | 68 | 1.000 | 36 | 36 | 1.000 | 11 | 14 | 0.786 | 17 | 22 | 0.773 |
| Hypocone Size | UM2 | HYPOM2 | 17 | 68 | 0.250 | 23 | 32 | 0.719 | 2 | 13 | 0.154 | 0 | 13 | 0.000 |
| Carabelli's Trait | UM1 | CARAM1 | 42 | 68 | 0.618 | 8 | 25 | 0.320 | 2 | 9 | 0.222 | 9 | 18 | 0.500 |
| Metaconule | UM1 | MTCLM1 | 21 | 68 | 0.309 | 3 | 37 | 0.081 | 3 | 9 | 0.333 | 4 | 19 | 0.211 |
| Metaconule | UM2 | MTCLM2 | 16 | 68 | 0.235 | 2 | 34 | 0.059 | 2 | 14 | 0.143 | 0 | 13 | 0.000 |
| Y-Groove Pattern | LM1 | YGRVM1 | 37 | 39 | 0.949 | 19 | 24 | 0.792 | 5 | 7 | 0.714 | 12 | 17 | 0.706 |
| Y-Groove Pattern | LM2 | YGRVM2 | 23 | 62 | 0.371 | 7 | 38 | 0.184 | 5 | 14 | 0.357 | 3 | 18 | 0.167 |
| Cusp Number | LM1 | CSPNM1 | 60 | 65 | 0.923 | 22 | 28 | 0.786 | 9 | 15 | 0.600 | 19 | 25 | 0.760 |
| Cusp Number | LM2 | CSPNM2 | 19 | 67 | 0.284 | 2 | 41 | 0.049 | 1 | 15 | 0.067 | 3 | 17 | 0.176 |
| Entoconulid | LM1 | C6M1 | 6 | 65 | 0.092 | 3 | 25 | 0.120 | 1 | 14 | 0.071 | 0 | 22 | 0.000 |
| Entoconulid | LM2 | C6M2 | 1 | 68 | 0.015 | 0 | 40 | 0.000 | 0 | 15 | 0.000 | 1 | 18 | 0.056 |
| Metaconulid | LM1 | C7M1 | 13 | 66 | 0.197 | 1 | 38 | 0.026 | 1 | 15 | 0.067 | 2 | 24 | 0.083 |
| Metaconulid | LM2 | C7M2 | 8 | 68 | 0.118 | 0 | 43 | 0.000 | 0 | 15 | 0.000 | 2 | 20 | 0.100 |

## Maxillary Anterior Teeth

### INCISOR SHOVELLING

Analysis of variance **(Table 3)** across all samples reveals that there is significant heterogeneity in the frequency of shovelling of the central incisor (SHOVUI1). Shovelling of the central incisor occurs with the highest frequency among the Neolithic inhabitants of Mehrgarh (NeoMRG), where 64.3% of individuals express this trait **(Fig. 2a)**. Lowest frequencies occur among the inhabitants of the Late Bronze/Early Iron Age site of Sarai Khola, where no individuals express the trait. Chi-square analysis indicates that shovelling frequencies are significantly higher among the 10 living samples (avg.= 0.390) than among the 10 prehistoric samples (avg.= 0.234), but the range in frequency is greater among prehistoric samples (range= 0.643) than among living samples (range= 0.282).

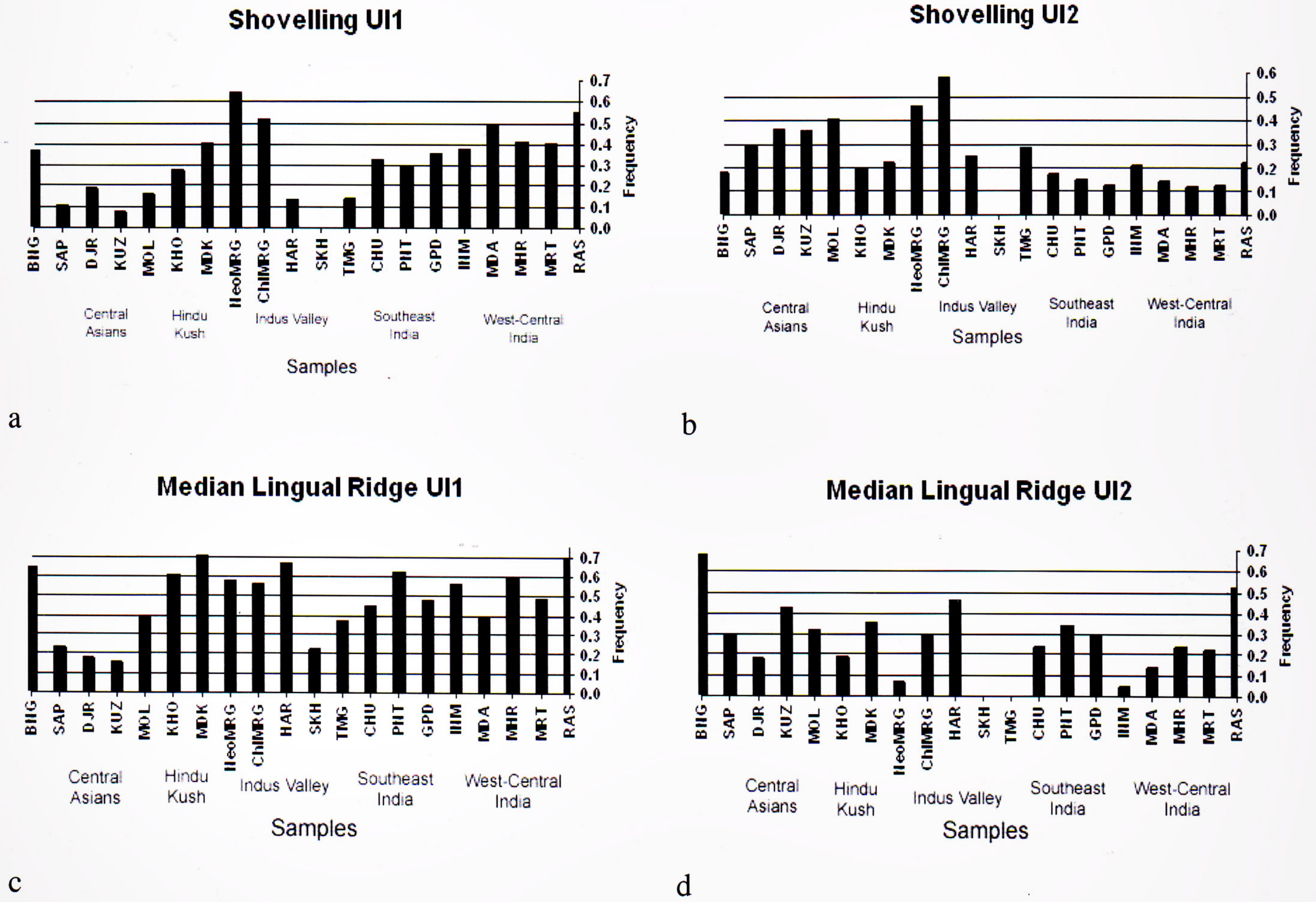



Fig 2 Frequencies of dental morphology traits among maxillary anterior teeth. Living samples in alphabetical order by geographic region from left to right. Archaeologically derived sampled in temporal order by geographic region. Sample abbreviations and geographic region assignment from Table 1.a.) Shovelling UI1, b.) Shovelling UI2, c.) Median Lingual Ridge (*Tuberculum Dentale*) UI1, d.) Median Lingual Ridge (*Tuberculum Dentale*) UI2.

When considered by geographic region, highest average frequencies of shovelling on the central incisor occur among inhabitants of west-central India (avg.= 0.448), followed by living inhabitants of southeast India (avg.= 0.328) and prehistoric inhabitants of the Indus Valley (avg.= 0.288), while lowest average frequencies are found among prehistoric Central Asians (avg.= 0.132). The greatest variation by far in shovelling presence on the central incisor occurs among prehistoric inhabitants of the Indus Valley (sd= 0.277), for inhabitants of all other regions exhibit dramatically less intraregional variation (west-central Indians: sd= 0.072; prehistoric Central Asians: sd= 0.050; southeast Indians: sd= 0.032). Indeed, the amount of intraregional variation found among the prehistoric Indus Valley samples is over eight times that seen among living inhabitants of southeastern India (8.587), more than five times that seen among prehistoric Central Asians (5.506) and nearly four times greater than that seen among prehistoric and living inhabitants of west-central India (3.856). An inspection of Figure 2a reveals that the high level of intraregional variation among prehistoric Indus Valley samples separates the two earliest samples (NeoMRG, ChlMRG) from all subsequent samples.

Tukey's HSD **(Table 3)** indicates the generally low frequencies of shovelling on the central incisor among prehistoric Central Asians separate them significantly from samples of all other geographic regions. By contrast, the generally high relative frequencies found among living ethnic groups of west-central India separate them significantly from members of all other geographic regions, except those from the Indus Valley. The lack of a significant interregional difference between prehistoric inhabitants of the Indus Valley and inhabitants of west-central India is driven by the high frequencies of shovelling among the two early samples from Mehrgarh among the former and the relatively high frequencies among the sample of tribal Madia Gonds and the mixed caste urban sample from Pune among the latter.

The Madaklasht, with a frequency of 40.8%, rank seventh highest among the 20 samples with respect to shovelling on the central incisor, far higher than their Hindu Kush counterparts, the Khowars, where this trait occurs among only 27% of individuals. The Madaklasht are most similar in trait prevalence to high-status Marathas (40.9%) and low-status Mahars (41.4%) of west-central India. The Madaklasht differ strongly in the frequency of shovelling of the central incisor from all prehistoric Central Asians (< 20%), and early prehistoric inhabitants of the Indus Valley (> 50%). Chi-square analysis **(Table 4)** reveals the Madaklasht have significantly more shovelling than Khowars, all but Djarkutan period Central Asians, high-status Pakanati Reddis of southeast India and the Iron Age inhabitants of Sarai Khola, coupled with significantly less shovelling than Late Chalcolithic inhabitants of Harappa, the Neolithic inhabitants of Mehrgarh, and living members of the mixed caste urban sample from Pune.

Analysis of variance **(Table 3)** across all samples reveals that there is significant heterogeneity in the frequency of shovelling of the lateral incisor (SHOVUI2). Shovelling of the lateral incisor is found with the highest frequency among the Chalcolithic inhabitants of Mehrgarh (58.3%). Lowest frequencies occur among the inhabitants of the Early Iron Age site of Sarai Khola, where no individuals express the trait **(Table 2)**. In a reversal of results obtained for shovelling on the central incisor, chi-square analysis indicates shovelling frequencies are significantly higher among the 10 prehistoric samples (avg.= 0.321) than among the 10 living samples (avg.= 0.166). Once again, the range in frequency is greater among the prehistoric samples (range= 0.583) than among their living counterparts (range= 0.102). In fact, the range in variation among prehistoric samples is nearly six times (5.716) that seen among the living samples.

When considered by geographic region, highest average frequencies are found among the prehistoric inhabitants of Central Asia (avg.= 0.356), followed by the prehistoric inhabitants of the Indus Valley (avg.= 0.316). Frequencies of shovelling of the lateral incisor among living populations of west-central (avg.= 0.165) and southeastern India (avg.= 0.151) are much lower. As in the central incisor, the greatest variation by far in expression of shovelling on the lateral incisor occurs among prehistoric inhabitants of the Indus Valley (sd= 0.222), for the inhabitants of all other regions exhibit far less intraregional variation (west-central Indians: sd= 0.049; prehistoric Central Asians: sd= 0.047; southeast Indians: sd= 0.023). The amount of intraregional variation found among the prehistoric Indus Valley samples is nearly ten times greater than that seen among living inhabitants of southeast India (9.652) and over four and a half times that seen among living inhabitants of west-central India (4.531) and the prehistoric inhabitants of Central Asians (4.723). Examination of Figure 2b shows that the high intraregional variability in shovelling prevalence among prehistoric inhabitants of the Indus Valley is due to the high frequencies found among the two early samples from Mehrgarh, coupled with the complete absence of shovelling on the lateral incisors of individuals recovered from the Early Iron Age inhabitants of Sarai Khola.

Tukey's HSD analysis **(Table 3)** reveals that variation in lateral incisor shovelling prevalence draws a distinction between prehistoric Central Asians with high overall frequencies, from southeast and west-central peninsular Indians with low overall frequencies. Both prehistoric Indus Valley inhabitants and living Hindu Kush highlanders stand in between the three other regional aggregates with high to moderate prevalence **(Fig. 2b)**. Driven by high prevalence among the two samples from Mehrgarh, and to a lesser extent the Late Chalcolithic sample from Harappa, Indus Valley samples possess significantly higher shovelling prevalence relative to all other samples, except Central Asians. By contrast, Hindu Kush samples are marked by significantly less shovelling prevalence relative to prehistoric inhabitants of the Indus Valley and Central Asia, coupled with insignificantly higher prevalence relative to southeast and west-central peninsular Indians.

With a frequency of 22% the Madaklasht rank 10th among the 20 samples with respect to shovelling on the lateral incisor—a prevalence somewhat higher than that found among the Khowar (19.8%). The Madaklasht are most similar in prevalence to the mixed caste urban sample from Pune (RAS: 22.4%), the Late Jorwe period sample from Inamgaon (21.1%) and the Late Chalcolithic sample from Harappa (HAR: 25%). Chi-square analysis (Table 4) reveals that the Madaklasht are marked by significantly higher frequencies of shovelling on the lateral incisor than low-status Gompadhompti Madigas from southeast India, as well as low-status Mahars and high-status Marathas from west-central India, but significantly lower frequencies than the two early prehistoric samples from Mehrgarh, or the latest of the prehistoric samples from Central Asia, the Molali period occupants of Djarkutan.

When shovelling among the maxillary teeth is considered as a whole, the majority of samples (n= 11) feature dentitions in which shovelling is more often expressed on the central incisor than on the lateral incisor. The difference in expression of this trait across these two teeth is most marked among living inhabitants of west-central India where, with the sole exception of the mixed caste urban sample from Pune (RAS: $f[I^1/I^2]$= 2.467), shovelling occurs with a frequency in excess of three times more often on the central incisor than on its lateral counterpart (MDA: $f[I^1/I^2]$= 3.436; MHR $f[I^1/I^2]$= 3.406; MRT: $f[I^1/I^2]$= 3.307). The ratio of shovelling of the central incisor to the lateral incisor is also high among variation in median lingual ridge development on this tooth occurs among prehistoric inhabitants of the Indus Valley (sd= 0.179), while the inhabitants of all other regions exhibit far less intraregional variation (west-central Indians: sd= 0.113; prehistoric Central Asians: sd= 0.107; southeast Indians: sd= 0.090). However, unlike shovelling, the amount of intraregional variation found among the prehistoric Indus Valley samples is not markedly different from that seen among the inhabitants of other regions, for intraregional variation among prehistoric Indus Valley inhabitants is only slightly over one and half to nearly two times greater (Indus Valley vs. West-Central Indians= 1.586; Indus Valley vs. prehistoric Central Asians= 1.672; Indus Valley vs. Southeast Indians= 1.996).

Tukey's HSD **(Table 3)** confirms that prehistoric Central Asians are distinguished from all other regional aggregates by possessing significantly lower frequencies of median lingual ridge development on the central incisor. With the highest aggregate frequencies of all regions considered, Hindu Kush highlanders possess significantly higher prevalence of the median lingual ridge than living inhabitants of southeastern and west-central peninsular India. Due to overall low sample size ($n_{max}$= 80, see Table 2), prehistoric Indus Valley inhabitants are not identified as possessing significantly lower prevalence of the median lingual ridge relative to Hindu Kush highlanders despite a lower average prevalence than prehistoric Central Asians.

With a frequency of just over 70%, the Madaklasht exhibit this trait more often than Khowars (60.6%), and possess a frequency for this trait that is most similar to the urban mixed caste sample from Pune (69.1%), the Late Chalcolithic inhabitants of Harappa (66.7%), and the urban mixed caste sample from Kolkata (64.8%). Chi-square analysis (Table 4) indicates the Madaklasht possess significantly higher prevalence of median lingual ridge development on the central incisor than all Central Asians, the latest of the prehistoric Indus Valley samples (SKH), tribal Chenchus and low-status Gompadhompti Madigas from southeast India, as well as tribal Madia Gonds and high-status Marathas from west-central India.

Development of the medial lingual ridge (*tuberculum dentale*) on the lateral incisor (MLRUI2) occurs with highest frequency in the urban mixed caste sample from Kolkata **(Fig. 2d)**, where nearly 70% of individuals (BNG: f=0.681) possess this trait **(Table 2)**. Lowest frequencies occur among the post-Chalcolithic era prehistoric samples from Timargarha and Sarai Khola, where no individuals were observed expressing this trait. Analysis of variance across all groups aggregated into regional samples indicates that heterogeneity in lingual ridge development is not statistically significant (F= 0.068, Table 3). Consequently chi-square analysis **(Table 3)** fails to yield a significant difference in medial lingual ridge development between prehistoric and living samples. Nevertheless, as for medial lingual ridge development on the central incisor, overall frequencies of median lingual ridge development on the lateral incisor tend to be higher among the 10 living samples (avg.= 0.322) than among the 10 prehistoric samples (avg.= 0.210). Unlike median lingual ridge development on the central incisor, the range in frequency for development of this trait on the lateral incisor is greater among the living samples (range= 0.540) than among the prehistoric samples (range= 0.462).

Gompadhompti Madigas (GPD $f[I^1/I^2]$= 2.847), is somewhat less among members of the mixed caste urban sample from Kolkata (BNG: $f[I^1/I^2]$= 2.077), the two remaining samples from southeast India (PNT: $f[I^1/I^2]$= 1.937); CHU: $f[I^1/I^2]$= 1.909), as well as the prehistoric sample from Inamgaon (INM: $f[I^1/I^2]$= 1.781) and lesser still among the Neolithic inhabitants of Mehrgarh (NeoMRG: $f[I^1/I^2]$= 1.399) and the living Khowar of the Hindu Kush highlands (KHO: $f[I^1/I^2]$= 1.364). Shovelling occurs with identical frequencies on the central and lateral incisor in three samples and all three are prehistoric samples from the Indus Valley (ChlMRG, TMG, SKH). Four samples stand apart from all others by featuring maxillary incisors in which the frequency of shovelling on the lateral incisors exceeds that found on the central incisor. All but one of these samples are prehistoric samples from Central Asia. The sole exception is the prehistoric Indus Valley sample from Harappa. This latter sample is marked by the least degree of overrepresentation of shovelling on the lateral incisor relative to the central (HAR: $f[I^2/I^1]$= 1.875). By contrast, the Central Asian samples feature dentitions in which shovelling frequencies on the lateral incisor are at least twice (DJR: $f[I^2/I^1]$= 1.939; MOL: $f[I^2/I^1]$= 2.546; SAP: $f[I^2/I^1]$= 2.794) and as much as more than four times (KUZ: $f[I^2/I^1]$= 4.643) more common on the lateral incisor relative to its central counterpart.

The Madaklasht feature a dentition in which shovelling occurs more often on the central incisor (40.8%) than on the lateral incisor (22%) by a factor of nearly two to one (1.855:1). As such, the Madaklasht are most similar in relative shovelling frequencies across these two teeth to high-status Pakanati Reddis (1.937) and tribal Chenchus (1.909) from southeast India as well as to the prehistoric inhabitants of Inamgaon (1.781). They bear little resemblance to their fellow inhabitants of the Hindu Kush highlands, the Khowar (1.364) in this tooth-trait pattern of expression. Given the similarity in shovelling prevalence on the lateral incisor (MDK= 22%; KHO= 19.8%), the difference in relative shovelling prevalence between these two Hindu Kush ethnic groups is almost completely driven by the shovelling prevalence on the central incisor (MDK= 40.8%; KHO= 27.0%).

### Median Lingual Ridge Development

Analysis of variance **(Table 3)** across all samples reveals there is significant heterogeneity in the frequency of median lingual ridge development (*tuberculum dentale*) on the central incisor (MLRUI1). Development of the medial lingual ridge on the central incisor occurs with the highest frequency among the inhabitants of Madaklasht, where just over 70% of individuals possess this trait **(Fig. 2c)**. Lowest frequencies occur among the Kuzali period occupants (KUZ) of the Central Asian site of Djarkutan, where just over 15% of individuals express this trait **(Table 2)**. As with shovelling of the central incisor, chi-square analysis **(Table 3)** indicates that overall frequencies of median lingual ridge development on this tooth are significantly higher among the 10 living samples (avg.= 0.569) than among the 10 prehistoric samples (avg.= 0.392), while the range in frequency is greater among the prehistoric samples (range= 0.513) than among the living samples (range= 0.310).

When considered by geographic region, highest average frequencies of median lingual ridge development on the central incisor occur among Hindu Kush highlanders (avg.= 0.654), followed by inhabitants of west-central India (avg.= 0.546), living inhabitants of southeast India (avg.= 0.519) and prehistoric inhabitants of the Indus Valley (avg.= 0.480). Lowest average frequencies occur among prehistoric Central Asians (avg.= 0.239). Once again, as for shovelling on this same tooth, the greatest variation in median lingual ridge development on this tooth occurs among prehistoric inhabitants of the Indus Valley (sd= 0.179), while the inhabitants of all other regions exhibit far less intraregional variation (west-central Indians: sd= 0.113; prehistoric Central Asians: sd= 0.107; southeast Indians: sd= 0.090). However, unlike shovelling, the amount of intraregional variation found among the prehistoric Indus Valley samples is not markedly different from that seen among the inhabitants of other regions, for intraregional variation among prehistoric Indus Valley inhabitants is only slightly over one and half to nearly two times greater (Indus Valley vs. West-Central Indians= 1.586; Indus Valley vs. prehistoric Central Asians= 1.672; Indus Valley vs. Southeast Indians= 1.996).

Tukey's HSD **(Table 3)** confirms that prehistoric Central Asians are distinguished from all other regional aggregates by possessing significantly lower frequencies of median lingual ridge development on the central incisor. With the highest aggregate frequencies of all regions considered, Hindu Kush highlanders possess significantly higher prevalence of the median lingual ridge than living inhabitants of southeastern and west-central peninsular India. Due to overall low sample size ($n_{max}$= 80, see Table 2), prehistoric Indus Valley inhabitants are not identified as possessing significantly lower prevalence of the median lingual ridge relative to Hindu Kush highlanders despite a lower average prevalence than prehistoric Central Asians.

With a frequency of just over 70%, the Madaklasht exhibit this trait more often than Khowars (60.6%), and possess a frequency for this trait that is most similar to the urban mixed caste sample from Pune (69.1%), the Late Chalcolithic inhabitants of Harappa (66.7%), and the urban mixed caste sample from Kolkata (64.8%). Chi-square analysis (Table 4) indicates the Madaklasht possess significantly higher prevalence of median lingual ridge development on the central incisor than all Central Asians, the latest of the prehistoric Indus Valley samples (SKH), tribal Chenchus and low-status Gompadhompti Madigas from southeast India, as well as tribal Madia Gonds and high-status Marathas from west-central India.

Development of the medial lingual ridge (*tuberculum dentale*) on the lateral incisor (MLRUI2) occurs with highest frequency in the urban mixed caste sample from Kolkata **(Fig. 2d)**, where nearly 70% of individuals (BNG: f=0.681) possess this trait **(Table 2)**. Lowest frequencies occur among the post-Chalcolithic era prehistoric samples from Timargarha and Sarai Khola, where no individuals were observed expressing this trait. Analysis of variance across all groups aggregated into regional samples indicates that heterogeneity in lingual ridge development is not statistically significant (F= 0.068, Table 3). Consequently chi-square analysis **(Table 3)** fails to yield a significant difference in medial lingual ridge development between prehistoric and living samples. Nevertheless, as for medial lingual ridge development on the central incisor, overall frequencies of median lingual ridge development on the lateral incisor tend to be higher among the 10 living samples (avg.= 0.322) than among the 10 prehistoric samples (avg.= 0.210). Unlike median lingual ridge development on the central incisor, the range in frequency for development of this trait on the lateral incisor is greater among the living samples (range= 0.540) than among the prehistoric samples (range= 0.462).

Table 3. Analysis of Variance of Trait Frequency Differences Across all Samples, Chi-Square Analysis of Trait Frequency Differences between Living and Prehistoric Aggregated Groups, and Tukey's HSD Analysis of Regionally Aggregated Groups (*Significant Differences at $_{0.05}$ italicized*)

| | All Groups | | Living vs. Prehistoric | | Central Asians vs. Hindu Kush | | Central Asians vs. Indus Valley | | Central Asians vs. SE Indians | | Central Asians vs. W-C Indians | | Hindu Kush vs. Indus Valley | | Hindu Kush vs. SE Indians | | Hindu Kush Vs. W-C Indians | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Trait** | F | p | $X^2$ | p | AMD[1] | p | AMD | p | AMD | p | AMD | p | AMD | p | AMD | p | AMD | p |
| **C6LM1** | 2.517 | *0.040* | 0.072 | 0.788 | 0.034 | 0.839 | 0.010 | 0.999 | 0.028 | 0.891 | 0.005 | 1.000 | 0.044 | 0.583 | 0.062 | *0.014* | 0.038 | 0.260 |
| **C6LM2** | 0.811 | 0.518 | 0.529 | 0.467 | 0.000 | 1.000 | 0.016 | 0.875 | 0.013 | 0.885 | 0.015 | 0.790 | 0.016 | 0.810 | 0.012 | 0.752 | 0.015 | 0.584 |
| **C7LM1** | 9.732 | *0.000* | 13.980 | *0.000* | 0.041 | 0.767 | 0.056 | 0.658 | 0.155 | *0.000* | 0.094 | *0.027* | 0.015 | 0.992 | 0.114 | *0.000* | 0.053 | 0.137 |
| **C7LM2** | 10.251 | *0.000* | 5.916 | *0.015* | 0.007 | 0.998 | 0.001 | 1.000 | 0.073 | *0.002* | 0.017 | 0.896 | 0.007 | 0.997 | 0.080 | *0.000* | 0.024 | 0.498 |
| **CARAUM1** | 21.380 | *0.000* | 85.742 | *0.000* | 0.455 | *0.000* | 0.153 | 0.201 | 0.377 | *0.000* | 0.358 | *0.000* | 0.302 | *0.000* | 0.077 | 0.150 | 0.097 | *0.026* |
| **CSPNLM1** | 12.858 | *0.000* | 21.918 | *0.000* | 0.050 | 0.573 | 0.010 | 0.999 | 0.139 | *0.000* | 0.050 | 0.502 | 0.059 | 0.291 | 0.089 | *0.000* | 0.000 | 1.000 |
| **CSPNLM2** | 16.460 | *0.000* | 37.557 | *0.000* | 0.136 | *0.014* | 0.010 | 1.000 | 0.239 | *0.000* | 0.127 | *0.009* | 0.126 | *0.022* | 0.103 | *0.007* | 0.009 | 0.998 |
| **HYPOUM1** | 26.296 | *0.000* | 7.907 | *0.005* | 0.008 | 0.998 | 0.122 | *0.001* | 0.005 | 1.000 | 0.122 | *0.000* | 0.113 | *0.000* | 0.003 | 1.000 | 0.114 | *0.000* |
| **HYPOUM2** | 73.633 | *0.000* | 45.047 | *0.000* | 0.492 | *0.000* | 0.479 | *0.000* | 0.302 | *0.000* | 0.564 | *0.000* | 0.013 | 0.998 | 0.190 | *0.000* | 0.072 | 0.127 |
| **MLRUI1** | 10.940 | *0.000* | 10.012 | *0.002* | 0.405 | *0.000* | 0.268 | *0.008* | 0.260 | *0.000* | 0.265 | *0.000* | 0.137 | 0.173 | 0.145 | *0.000* | 0.140 | *0.000* |
| **MLRUI2** | 2.193 | 0.068 | 2.239 | 0.135 | 0.008 | 1.000 | 0.112 | 0.491 | 0.005 | 1.000 | 0.062 | 0.773 | 0.104 | 0.321 | 0.003 | 1.000 | 0.053 | 0.424 |
| **MTCLUM1** | 24.322 | *0.000* | 5.581 | *0.018* | 0.026 | 0.971 | 0.213 | *0.001* | 0.214 | *0.000* | 0.178 | *0.000* | 0.239 | *0.000* | 0.240 | *0.000* | 0.205 | *0.000* |
| **MTCLUM2** | 7.924 | *0.000* | 4.453 | *0.035* | 0.059 | 0.658 | 0.209 | *0.001* | 0.149 | *0.001* | 0.168 | *0.000* | 0.150 | *0.021* | 0.090 | *0.037* | 0.109 | *0.005* |
| **SHOVUI1** | 9.463 | *0.000* | 5.667 | *0.017* | 0.215 | 0.005 | 0.268 | *0.004* | 0.191 | *0.012* | 0.308 | *0.000* | 0.053 | 0.901 | 0.024 | 0.959 | 0.093 | *0.044* |
| **SHOVUI2** | 15.088 | *0.000* | 48.208 | *0.000* | 0.152 | *0.014* | 0.035 | 0.974 | 0.211 | *0.000* | 0.221 | *0.000* | 0.187 | *0.000* | 0.060 | 0.193 | 0.069 | 0.074 |
| **YGRVLM1** | 8.262 | *0.000* | 17.787 | *0.000* | 0.070 | 0.312 | 0.017 | 0.995 | 0.134 | *0.001* | 0.143 | *0.000* | 0.053 | 0.631 | 0.064 | 0.054 | 0.073 | *0.019* |
| **YGRVLM2** | 5.487 | *0.000* | 2.831 | 0.092 | 0.003 | 1.000 | 0.006 | 1.000 | 0.125 | *0.044* | 0.022 | 0.989 | 0.003 | 1.000 | 0.122 | *0.005* | 0.018 | 0.985 |

1. AMD is the pairwise absolute mean difference.

Table 3. Continued...*(Number of Traits Significantly Different above Diagonal, Identification of Traits Significantly Different below)*

| | | West-Central India | | | | | |
|---|---|---|---|---|---|---|---|
| | | INM | MDA | MHR | MRT | RAS | BNG |
| Hindu Kush Highlanders | MDK | 4 | 8 | 7 | 8 | 8 | 7 |
| | KHO | 3 | 7 | 5 | 6 | 8 | 6 |
| Prehistoric Indus Valley | NeoMRG | 0 | 3 | 5 | 4 | 7 | 8 |
| | ChlMRG | 4 | 3 | 4 | 3 | 4 | 4 |
| | HAR | 3 | 3 | 2 | 3 | 3 | 2 |
| | TMG | 0 | 2 | 2 | 2 | 3 | 5 |
| | SKH | 0 | 3 | 3 | 3 | 5 | 4 |
| Prehistoric Central Asia | SAP | 3 | 8 | 8 | 7 | 10 | 10 |
| | DJR | 3 | 7 | 7 | 6 | 8 | 6 |
| | KUZ | 4 | 7 | 6 | 5 | 5 | 4 |
| | MOL | 4 | 7 | 8 | 7 | 11 | 9 |
| Southeast India | CHU | 5 | 6 | 9 | 6 | 4 | 4 |
| | GPD | 6 | 8 | 8 | 6 | 4 | 2 |
| | PNT | 6 | 7 | 8 | 11 | 3 | 3 |

Table 3. Continued... (*Number of Traits Significantly Different above Diagonal, Identification of Traits Significantly Different below*)

| | | Hindu Kush Highlanders | | Prehistoric Indus Valley | | | | | Prehistoric Central Asia | | | | Southeast India | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | MDK | KHO | NeoMRG | ChlMRG | HAR | TMG | SKH | SAP | DJR | KUZ | MOL | CHU | GPD | PNT |
| West-Central Indians | INM | 5, 8, 11, 12 | 5, 8, 9 | None | 5, 8, 9, 15 | 8, 11, 12 | None | None | 8, 9, 10 | 8, 9, 10 | 8, 9, 10, 11 | 8, 9, 15, 16 | 3, 5, 6, 8, 9 | 5, 6, 7, 8, 9, 11 | 5, 6, 8, 9, 11, 12 |
| | MDA | 3, 5, 8, 10, 11, 12, 13, 16 | 5, 8, 9, 10, 12, 13, 14 | 5, 7, 15 | 9, 15, 16 | 7, 11, 14 | 6, 16 | 6, 14, 16 | 3, 6, 7, 9, 12, 13, 14, 16 | 5, 7, 9, 12, 13, 14, 15 | 5, 6, 9, 11, 13, 14, 16 | 7, 9, 12, 13, 14, 15, 16 | 6, 8, 9, 11, 14, 16 | 4, 6, 7, 8, 9, 11, 14, 17 | 5, 8, 9, 10, 11, 14, 17 |
| | MHR | 3, 8, 11, 12, 13, 15, 16 | 8, 9, 12, 13, 14 | 5, 11, 13, 14, 15 | 1, 9, 15, 16 | 7, 14 | 5, 16 | 5, 6, 14 | 5, 7, 8, 9, 10, 12, 13, 14 | 5, 8, 9, 10, 12, 13, 15 | 5, 6, 9, 10, 14, 15 | 5, 8, 9, 10, 12, 14, 15, 16 | 3, 4, 5, 6, 7, 8, 9, 10, 17 | 4, 5, 6, 7, 8, 9, 10, 17 | 4, 6, 8, 9, 11, 14, 17 |
| | MRT | 5, 8, 9, 10, 11, 12, 15, 16 | 1, 8, 9, 10, 12, 14 | 5, 13, 14, 15 | 9, 15, 16 | 7, 14, 17 | 4, 16 | 5, 6, 14 | 5, 8, 9, 10, 12, 14, 15 | 5, 9, 10, 12, 13, 15 | 5, 9, 10, 14, 15 | 5, 8, 9, 12, 14, 15, 16 | 3, 4, 6, 7, 8, 9 | 4, 6, 7, 8, 9, 17 | 3, 4, 5, 6, 7, 8, 9, 10, 11, 14, 17 |
| | RAS | 3, 4, 9, 11, 12, 13, 14, 16 | 3, 4, 7, 11, 12, 13, 14, 17 | 4, 5, 7, 8, 9, 11, 15 | 7, 8, 15, 16 | 7, 14, 17 | 8, 13, 16 | 6, 8, 10, 11, 14 | 3, 4, 5, 7, 9, 10, 12, 13, 14, 17 | 5, 7, 9, 10, 11, 12, 13, 14 | 5, 6, 8, 10, 14 | 3, 5, 6, 9, 10, 12, 13, 14, 15, 16, 17 | 9, 10, 11, 14 | 6, 10, 11, 14 | 5, 11, 14 |
| | BNG | 3, 4, 7, 9, 11, 12, 16 | 3, 4, 7, 11, 12, 17 | 4, 5, 7, 9, 11, 13, 14, 15 | 7, 10, 15, 16 | 7, 17 | 6, 8, 9, 11, 16 | 5, 6, 10, 11 | 3, 4, 5, 7, 9, 10, 11, 14, 16, 17 | 5, 7, 9, 10, 11, 13 | 5, 6, 10, 16 | 3, 5, 7, 9, 10, 11, 14, 15, 16 | 5, 10, 11, 16 | 10, 11 | 7, 11, 12 |

Table 3 Continued...*(Number of Traits Significantly Different above Diagonal, Identification of Traits Significantly Different below)*

| | | West-Central India | | | | | |
|---|---|---|---|---|---|---|---|
| | | INM | MDA | MHR | MRT | RAS | BNG |
| West-Central Indians | INM | ----- | 2 | 2 | 2 | 4 | 4 |
| | MDA | 5, 8 | ----- | 5 | 4 | 5 | 7 |
| | MHR | 5, 8 | 5, 8, 10, 11, 16 | ----- | 3 | 8 | 6 |
| | MRT | 5, 8 | 3, 4, 6, 16 | 5, 10, 17 | ----- | 9 | 8 |
| | RAS | 5, 8, 9, 11 | 8, 9, 10, 11, 17 | 4, 5, 7, 8, 9, 11, 15, 17 | 3, 4, 7, 8, 9, 10, 11, 14, 15 | ----- | 1 |
| | BNG | 5, 8, 9, 11 | 4, 5, 7, 9, 10, 11, 17 | 4, 7, 8, 9, 11, 17 | 3, 4, 6, 7, 8, 9, 10, 11 | 14 | ----- |

In a marked departure from the central incisor, highest average frequencies of medial lingual ridge development on the lateral incisor occur among prehistoric Central Asians (avg.= 0.306), followed by living inhabitants of southeast (avg.= 0.291) and west-central India (avg.= 0.234), while lowest average frequencies occur among the prehistoric inhabitants of the Indus Valley (avg.= 0.164). The pattern of intraregional variation in median lingual ridge development on the lateral incisor across samples also differs from that seen for this trait on the central incisor. On the lateral incisor, the greatest intraregional variation in medial lingual ridge development occurs among the prehistoric inhabitants of the Indus Valley (sd= 0.205), followed by west-central Indians (sd= 0.177) and prehistoric Central Asians (sd= 0.101), while intraregional variation is least among living southeast Indians (sd= 0.055). The amount of internal variation by region for median lingual ridge development on the lateral incisor is somewhat greater that that seen for the central incisor. The amount of intraregional variation found among the prehistoric Indus Valley samples ranges from just over 15% to 67% (Indus Valley vs. west-central Indians= 1.154; Indus Valley vs. prehistoric Central Asians= 1.672) to nearly four times (Indus Valley vs. living southeast Indians= 3.753). Given the absence of significant heterogeneity across all samples, or between prehistoric and living samples, it is no surprise that Tukey's HSD **(Table 3)** fails to identify any significant differences in median lingual ridge development between regional aggregate pairs.

The Madaklasht **(Fig. 2d)**, with a frequency of 35.6%, exhibit this trait on the lateral incisor far more often than Khowars (18.7%) and are most similar to three of the prehistoric samples from Central Asia (KUZ= 42.9%; MOL= 32%; 29.4%) and to the two Hindu caste samples from southeast India (PNT= 34.5%; GPD= 29.4%). The Madaklasht differ significantly from the urban mixed caste samples from Kolkata (68.1%) and Pune (52.2%), all west-central Indians (f< 24%), both tribal samples from the Indian peninsula (CHU= 23.6%; MDA= 14.1%), and all other prehistoric samples from the Indus Valley

Table 3 Continued...(*Number of Traits Significantly Different above Diagonal, Identification of Traits Significantly Different below)*

| | | West-Central India | | | | | |
|---|---|---|---|---|---|---|---|
| | | INM | MDA | MHR | MRT | RAS | BNG |
| West-Central Indians | INM | ----- | 2 | 2 | 2 | 4 | 4 |
| | MDA | 5, 8 | ----- | 5 | 4 | 5 | 7 |
| | MHR | 5, 8 | 5, 8, 10, 11, 16 | ----- | 3 | 8 | 6 |
| | MRT | 5, 8 | 3, 4, 6, 16 | 5, 10, 17 | ----- | 9 | 8 |
| | RAS | 5, 8, 9, 11 | 8, 9, 10, 11, 17 | 4, 5, 7, 8, 9, 11, 15, 17 | 3, 4, 7, 8, 9, 10, 11, 14, 15 | ----- | 1 |
| | BNG | 5, 8, 9, 11 | 4, 5, 7, 9, 10, 11, 17 | 4, 7, 8, 9, 11, 17 | 3, 4, 6, 7, 8, 9, 10, 11 | 14 | ----- |

In a marked departure from the central incisor, highest average frequencies of medial lingual ridge development on the lateral incisor occur among prehistoric Central Asians (avg.= 0.306), followed by living inhabitants of southeast (avg.= 0.291) and west-central India (avg.= 0.234), while lowest average frequencies occur among the prehistoric inhabitants of the Indus Valley (avg.= 0.164). The pattern of intraregional variation in median lingual ridge development on the lateral incisor across samples also differs from that seen for this trait on the central incisor. On the lateral incisor, the greatest intraregional variation in medial lingual ridge development occurs among the prehistoric inhabitants of the Indus Valley (sd= 0.205), followed by west-central Indians (sd= 0.177) and prehistoric Central Asians (sd= 0.101), while intraregional variation is least among living southeast Indians (sd= 0.055). The amount of internal variation by region for median lingual ridge development on the lateral incisor is somewhat greater that that seen for the central incisor. The amount of intraregional variation found among the prehistoric Indus Valley samples ranges from just over 15% to 67% (Indus Valley vs. west-central Indians= 1.154; Indus Valley vs. prehistoric Central Asians= 1.672) to nearly four times (Indus Valley vs. living southeast Indians= 3.753). Given the absence of significant heterogeneity across all samples, or between prehistoric and living samples, it is no surprise that Tukey's HSD **(Table 3)** fails to identify any significant differences in median lingual ridge development between regional aggregate pairs.

The Madaklasht **(Fig. 2d)**, with a frequency of 35.6%, exhibit this trait on the lateral incisor far more often than Khowars (18.7%) and are most similar to three of the prehistoric samples from Central Asia (KUZ= 42.9%; MOL= 32%; 29.4%) and to the two Hindu caste samples from southeast India (PNT= 34.5%; GPD= 29.4%). The Madaklasht differ significantly from the urban mixed caste samples from Kolkata (68.1%) and Pune (52.2%), all west-central Indians (f< 24%), both tribal samples from the Indian peninsula (CHU= 23.6%; MDA= 14.1%), and all other prehistoric samples from the Indus Valley

(HAR= 46.2%, all others= f< 7%), except the early Chalcolithic inhabitants of Mehrgarh (ChlMRG= 29.2%,) in the frequency of median lingual ridge development on the lateral incisor **(Table 4).**

When median lingual ridge development among the maxillary teeth is considered as a whole, a great majority of samples (n= 16) feature dentitions in which median lingual ridge development is more often expressed on the central incisor than on the lateral incisor. In fact, no lingual ridge development was found on the lateral incisor in two samples (SKH, TMG). The difference in expression of this trait across these two teeth is most marked among the Late Jorwe occupants of the prehistoric site of Inamgaon, located in west-central India, where ridge development is greater than 11 times more common ($f[I^1/I^2]$= 11.2) on the central incisor (56%) than on the lateral incisor (5%). Differences in frequency across the two incisors are also marked among the Neolithic inhabitants of Mehrgarh, where ridge development is greater than eight times more prevalent ($f[I^1/I^2]$= 8.365) on the central incisor (57.7%) than on the lateral incisor (6.9%). Among the remaining samples where median lingual ridge development is more common on the central incisor than on the lateral incisor, and where there is at least *some* presence of the median lingual ridge on this latter tooth, frequencies on the central incisor are less than four times and most often (8 of 12 samples) less than two times higher. In four remaining samples, frequencies of median lingual ridge development are greater on the lateral incisor than on the central incisor. In three samples the differences in frequency across the two teeth are relatively minor (DJR: $I^1$= 17.6%, $I^2$= 18.2%, $f[I^2/I^1]$= 1.030; BNG: $I^1$= 64.8%, $I^2$= 68.1%, $f[I^2/I^1]$= 1.050; SAP: $I^1$= 23.5%; I2= 29.4%, $f[I^2/I^1]$= 1.250), but in the fourth the difference is much more marked (KUZ: $I^1$= 15.4%, $I^2$= 42.9%, $f[I^2/I^1]$= 2.080).

Several patterns emerge when the configuration of median lingual ridge development across the two maxillary incisors is considered by geographic region. Samples from west-central India, led by the prehistoric sample from Inamgaon ($f[I^1/I^2]$= 11.2), are all marked by dentitions in which expression occurs more than twice as often on the central incisors than on the lateral incisors (MDA: $f[I^1/I^2]$= 2.782; MHR: $f[I^1/I^2]$= 2.542; MRT: $f[I^1/I^2]$= 2.215). The only exception is the urban mixed caste sample from Pune (RAS: $f[I^1/I^2]$= 1.323). Samples of living ethnic groups from southeast India are also marked by dentitions in which development of the median lingual ridge occurs more often on the central incisor than on the lateral incisor. However, among southeast Indians the difference is less than that seen among west-central Indians, for the differences in frequency between these two teeth ranges from just less than two times greater on the central incisor to just over one and a half times greater (CHU: $f[I^1/I^2]$= 1.925; PNT: $f[I^1/I^2]$= 1.803; GPD: $f[I^1/I^2]$= 1.644). Prehistoric samples from Central Asia stand apart from all peninsular Indians (except for the urban mixed caste sample from Kolkata) in possessing dentitions in which there is only a slight difference in median lingual ridge frequency between the two maxillary incisors or in which the frequency is higher on the lateral incisor than on the lingual incisor.

Prehistoric samples from the Indus Valley are all across the board with regard to the relative frequency of median lingual ridge development on the maxillary incisors. The Neolithic inhabitants of Mehrgarh feature one of the greatest overrepresentations of ridge development on the central incisor relative to the lateral, the Early Chalcolithic inhabitants of this same site and the Late Chalcolithic inhabitants of Harappa are marked by a moderate overrepresentation on the central incisor, while the two post-Chalcolithic prehistoric samples have no expression of median lingual ridge development on the lateral incisor at all. Thus tooth-trait expression of the median lingual ridge among these samples is marked by regional distinctiveness and a fair amount of intraregional cohesion for all regions, except for the prehistoric inhabitants of the Indus Valley. Prehistoric inhabitants of the Indus Valley express the

Table 4. Pairwise Chi-square Analysis of Trait Frequencies (*Number of Traits Significantly Different above Diagonal, Identification of Traits Significantly Different below*)

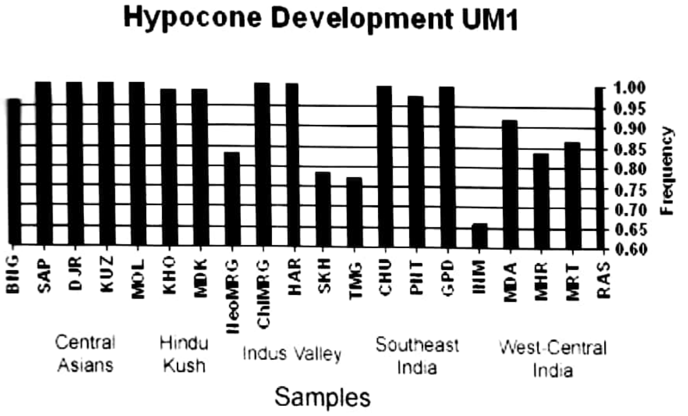
| | | Hindu Kush Highlanders | | Prehistoric Indus Valley | | | | | Prehistoric Central Asia | | | | Southeast India | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | MDK | KHO | NeoMRG | ChlMRG | HAR | TMG | SKH | SAP | DJR | KUZ | MOL | CHU | GPD | PNT |
| Hindu Kush Highlanders | MDK | ----- | 4 | 8 | 5 | 4 | 4 | 6 | 5 | 4 | 5 | 6 | 8 | 13 | 10 |
| | KHO | 9, 11, 14, 16 | ----- | 7 | 8 | 1 | 2 | 4 | 3 | 3 | 3 | 4 | 8 | 9 | 8 |
| Prehistoric Indus Valley | NeoMRG | 5, 7, 8, 11, 12, 13, 14,15 | 5, 8, 9, 12, 13, 14, 15 | ----- | 2 | 3 | 1 | 3 | 5 | 5 | 5 | 5 | 9 | 10 | 8 |
| | ChlMRG | 1, 9, 12, 13, 15 | 1, 2, 9, 12, 13, 14, 15, 16 | 5, 9 | ----- | 3 | 1 | 3 | 3 | 4 | 4 | 2 | 5 | 5 | 4 |
| | HAR | 7, 12, 14, 17 | 12 | 11, 14, 17 | 9, 14, 15 | ----- | 0 | 0 | 2 | 5 | 3 | 2 | 4 | 3 | 2 |
| | TMG | 4, 5, 8, 12 | 8, 16 | 13 | 9 | None | ----- | 0 | 2 | 3 | 2 | 2 | 3 | 4 | 5 |
| | SKH | 5, 6, 8, 10, 12, 14 | 5, 6, 8, 12 | 6, 14, 15 | 9, 14, 15 | None | None | ----- | 2 | 3 | 0 | 3 | 2 | 4 | 5 |
| Prehistoric Central Asia | SAP | 5, 7, 9, 10, 14 | 5, 9, 10 | 8, 9, 10, 13, 14 | 10, 13, 14 | 9, 12 | 8, 9 | 8, 9 | ----- | 0 | 0 | 0 | 7 | 11 | 9 |
| | DJR | 5, 7, 9, 10 | 5, 9, 10 | 9, 10, 12, 13, 14 | 5, 10, 13, 14 | 9, 10, 12, 13, 17 | 5, 8, 9 | 5, 8, 9 | None | ----- | 0 | 0 | 7 | 7 | 7 |
| | KUZ | 5, 6, 9, 10, 14 | 5, 9, 10 | 9, 10, 11, 13, 14 | 5, 10, 13, 14 | 9, 10, 12 | 5, 9 | None | None | None | ----- | 1 | 4 | 6 | 6 |
| | MOL | 5, 7, 9, 10, 14, 15 | 5, 9, 15, 16 | 8, 9, 10, 13, 14 | 13, 14 | 9, 12 | 8, 9 | 8, 9, 15 | None | None | 5 | ----- | 8 | 9 | 11 |
| Southeast India | CHU | 3, 4, 5, 6, 8, 10, 11, 12 | 3, 4, 5, 6, 7, 9, 10, 12 | 3, 5, 7, 8, 9, 11, 13, 14, 15 | 1, 2, 6, 7, 15 | 6, 7, 9, 17 | 6, 8, 9 | 6, 8 | 3, 5, 6, 7, 9, 12, 14 | 3, 5, 7, 9, 10, 12, 13 | 3, 5, 6, 10 | 3, 5, 6, 7, 9, 12, 15, 16 | ----- | 4 | 6 |
| | GPD | 1, 3, 4, 5, 6, 7, 9, 10, 12, 13, 15, 16, 17 | 1, 4, 6, 7, 10, 11, 12, 13, 17 | 4, 5, 6, 7, 8, 9, 11, 13, 14, 15 | 6, 7, 9, 15, 16 | 6, 7, 17 | 6, 8, 9, 16 | 5, 6, 7, 8 | 4, 5, 6, 7, 9, 10, 12, 13, 14, 16, 17 | 5, 7, 9, 10, 12, 13, 15 | 5, 6, 7, 10, 15, 16 | 5, 6, 7, 9, 12, 14, 15, 16, 17 | 3, 9, 16, 17 | ----- | 3 |
| | PNT | 1, 3, 4, 6, 9, 12, 13, 14, 16, 17 | 1, 3, 6, 7, 11, 12, 13, 17 | 5, 7, 8, 9, 11, 13, 14, 15 | 9, 14, 15, 16 | 7, 17 | 5, 6, 8, 16, 17 | 5, 6, 8, 10, 16 | 3, 5, 6, 7, 9, 10, 12, 13, 16 | 5, 7, 9, 10, 12, 13, 15 | 5, 6, 9, 10, 12, 16 | 5, 7, 9, 10, 12, 15, 16, 17 | 5, 9, 10, 11, 16, 17 | 5, 7, 10 | ----- |

Table 4.*Continued…*

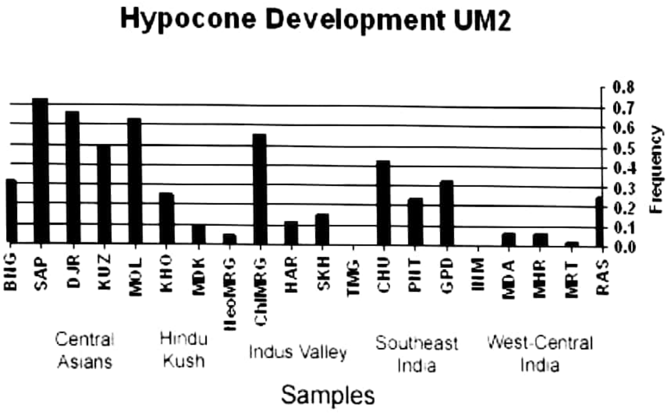
| | Indus Valley vs. SE Indians | | Indus Valley vs. W-C Indians | | SE Indians vs. W-C Indians | |
|---|---|---|---|---|---|---|
| **Trait** | AMD | p | AMD | P | AMD | P |
| **C6LM1** | 0.018 | 0.967 | 0.006 | 1.000 | 0.024 | 0.573 |
| **C6LM2** | 0.004 | 0.999 | 0.001 | 1.000 | 0.003 | 0.998 |
| **C7LM1** | 0.099 | *0.019* | 0.038 | 0.762 | 0.061 | *0.011* |
| **C7LM2** | 0.072 | *0.002* | 0.017 | 0.914 | 0.055 | *0.000* |
| **CARAUM1** | 0.225 | *0.001* | 0.205 | *0.002* | 0.020 | 0.953 |
| **CSPNLM1** | 0.149 | *0.000* | 0.060 | 0.209 | 0.089 | *0.000* |
| **CSPNLM2** | 0.229 | *0.000* | 0.117 | *0.013* | 0.112 | *0.000* |
| **HYPOUM1** | 0.117 | *0.000* | 0.001 | 1.000 | 0.117 | *0.000* |
| **HYPOUM2** | 0.177 | *0.000* | 0.085 | 0.221 | 0.262 | *0.000* |
| **MLRUI1** | 0.008 | 1.000 | 0.003 | 1.000 | 0.005 | 1.000 |
| **MLRUI2** | 0.107 | 0.240 | 0.050 | 0.867 | 0.057 | 0.189 |
| **MTCLUM1** | 0.001 | 1.000 | 0.034 | 0.942 | 0.035 | 0.543 |
| **MTCLUM2** | 0.059 | 0.671 | 0.040 | 0.892 | 0.019 | 0.930 |
| **SHOVUI1** | 0.076 | 0.654 | 0.040 | 0.950 | 0.117 | *0.000* |
| **SHOVUI2** | 0.247 | *0.000* | 0.256 | *0.000* | 0.010 | 0.992 |
| **YGRVLM1** | 0.116 | *0.009* | 0.126 | *0.004* | 0.009 | 0.990 |
| **YGRVLM2** | 0.119 | 0.063 | 0.015 | 0.997 | 0.104 | *0.001* |

greatest internal variation and a temporal trend of increasing parity in median lingual ridge frequencies across the two maxillary incisors from the Neolithic through the Late Chalcolithic, followed by complete absence of this trait on the lateral incisor in the post-Chalcolithic era.

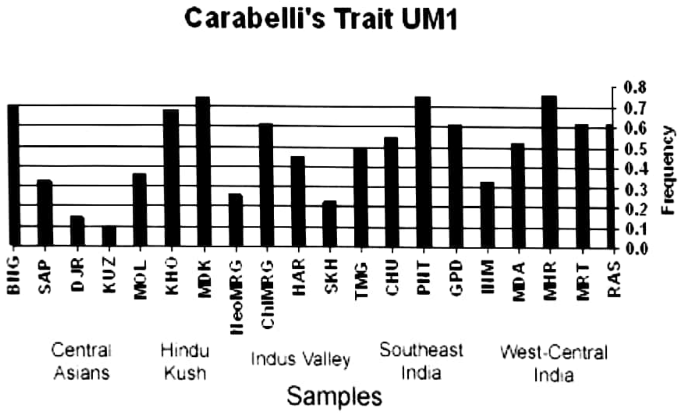
Members of living ethnic groups from the Hindu Kush highlands are also marked by differences in the relative frequencies of median lingual ridge development on the central and lateral incisors. The Madaklasht are marked by the highest frequencies of median lingual ridge development (70.2%) among all of the samples considered, while Khowar frequencies (60.6%) fall within the upper third. For the lateral incisor, frequencies are lower in both ethnic groups but the fall-off is much more marked among the Khowar (18.7%) than among the Madaklasht (35.6%). Thus, unlike shovelling, where relative differences in prevalence are driven exclusively by the central incisor, relative differences in trait prevalence across the two incisors for median lingual ridge development relative are driven to a greater degree by the lateral incisor.




a




b

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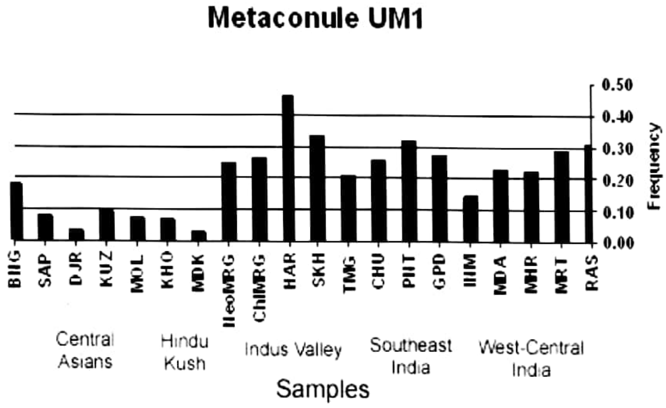
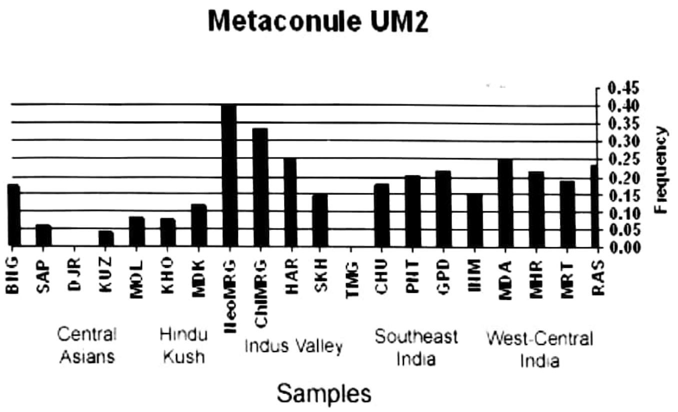



d




e

Fig 3 Frequencies of dental morphology traits among maxillary posterior teeth. Living samples in alphabetical order by geographic region from left to right. Archaeologically derived sampled in temporal order by geographic region. Sample abbreviations and geographic region assignment from Table 1. a.) Hypoconulid Development UM1, b.) Hypoconulid Development UM2, c.) Carabelli's Trait UM1, d.) Metaconule UM1, e.) Metaconule UM2.

## Maxillary Posterior Teeth

### Hypocone Development

Full development of the hypocone on the first maxillary molar (HYPOUM1) is ubiquitous in seven of the comparative samples (ChlMRG, DJR, HAR, KUZ, MOL, RAS, SAP) **(Fig. 3a)**. Lowest frequencies of full hypocone development are found among the prehistoric inhabitants of Inamgaon (65.9%).

Analysis of variance **(Table 3)** across all samples reveals there is significant heterogeneity in the frequency of hypocone reduction on the first molar. Chi-square analysis **(Table 3)** reveals that, contrary to expectations of an evolutionary reduction in both tooth size and crown complexity with an increasing experience of agricultural production and consumption of increased levels of agricultural produce and increased premasticatory preparation of food (see Calcagno 1986; Lukacs 1985; Lukacs and Hemphill 1991; but see Hemphill in press b), full development of the hypocone is significantly more common among the 10 living samples (avg.= 0.951) than among the 10 prehistoric samples (avg.= 0.905). Indeed, the range in the frequency of full hypocone development is greater among the prehistoric samples (range= 0.341) than among the living samples (range= 0.164).

When considered by geographic region, highest average frequencies occur among the prehistoric inhabitants of Central Asia, where none of the four temporally distinct samples exhibit a single case of hypocone reduction. Next highest frequencies occur among the samples of living ethnic groups of southeast India (avg.= 0.987), followed by the prehistoric inhabitants of the Indus Valley (avg.= 0.878). Lowest frequencies of full hypocone development occur among the inhabitants of west-central India (avg.= 0.855). Not surprisingly, given the generally high presence of full hypocone development on the first maxillary molar, intraregional variation in expression of this trait runs opposite to average frequencies. Hence, highest intraregional variation occurs among west-central Indian samples (sd= 0.126), followed by prehistoric inhabitants of the Indus Valley (sd= 0.113) and living ethnic groups of southeast India (sd= 0.013). With universal expression of full hypocone development, the prehistoric inhabitants of Central Asia, of course, exhibit no intraregional variation in the expression of this trait (sd= 0.000).

Tukey's HSD **(Table 3)** identifies a fundamental dichotomy among sample aggregates between those aggregates marked by very high frequencies of full hypocone development (prehistoric Central Asians, living Hindu Kush highlanders and southeast Indians) and those in which some of the samples have experienced reduction of the hypocone (prehistoric Indus Valley, west-central Indians). Intriguingly, among prehistoric Indus Valley samples, no reduction of the hypocone is observed among the Chalcolithic period samples from Mehrgarh and Harappa, while reduction occurs with substantial prevalence among the earliest (NeoMRG) and two latest samples (TMG, SKH). Among west-central Indians, reduction of the hypocone occurs with moderate prevalence among tribal Madia Gonds, low-status Mahars, and high-status Marathas. There is no reduction of the hypocone among members of the mixed urban caste sample from Pune, while reduction occurs with the highest prevalence among the prehistoric inhabitants of Inamgaon.

The Madaklasht, with a frequency of just over 98% (f= 0.983), rank 11th highest among the 20 samples and exhibit this trait with nearly identical frequency as their fellow Hindu Kush highland dwellers, the Khowars (f= 0.985). The Madaklasht are most similar in the frequency of full hypocone development to the Khowars and to the three samples from southeast India (CHU, GPD, PNT). Chi-square analysis **(Table 4)** indicates the Madaklasht differ significantly in the frequency of full hypocone development on the first maxillary molar from all prehistoric and living samples from west-central India, except the urban mixed caste sample from Pune, as well as from all prehistoric samples from the Indus Valley, except the Chalcolithic samples from Mehrgarh and Harappa.

Analysis of variance **(Table 3)** across all samples reveals there is significant heterogeneity in the frequency of hypocone reduction on the second molar (HYPOUM2). Full development of the hypocone on the second maxillary molar occurs less often (avg.= 0.271) and is more variably expressed across samples (sd= 0.217) than on the first maxillary molar (avg.= 0.928; sd= 0.094). The highest frequency of fully developed hypocones is found in the earliest prehistoric sample from Central Asia, Sapalli Tepe, where 71.9% of individuals possess this trait **(Table 2)**. Lowest frequencies occur among the prehistoric samples from Inamgaon and Timargarha, where no individuals were found to possess second maxillary molars with fully developed hypocones **(Fig. 3b)**.

Directly opposite to full development of the hypocone on the first maxillary molar, chi-square analysis (Table 3) indicates that overall frequencies of this trait on the second maxillary molar are significantly higher among the 10 prehistoric samples (avg.= 0.337) than among the 10 living samples (avg.= 0.205), but like the expression of this trait on the first maxillary molar the range in frequency on the second maxillary molar is greater among the prehistoric samples (range= 0.719) than among the living samples (range= 0.405). As found for the first maxillary molar, when retention of full hypocone development is considered by geographic region, highest average frequencies on the second maxillary molar occur among prehistoric Central Asians (avg.= 0.624), followed by living inhabitants of southeast India (avg.= 0.329). In a departure from the results obtained for the first maxillary molar, average frequencies of fully developed hypocones on the second maxillary molar are higher among the prehistoric inhabitants of the Indus Valley (avg.= 0.174) than among the samples from west-central India (avg.= 0.080).

Tukey's HSD **(Table 3)** confirms that differences between regional aggregates highlight a division between regions in which full hypocone development occurs at relatively high frequencies (prehistoric Central Asians, southeast Indians) and those in which retention of fully developed hypocones is relatively rare (Hindu Kush, Indus Valley, west-Central Indians). Intriguingly, within each of these latter regional aggregates a single sample stands in opposition to the overall trend. Among Hindu Kush highlanders it is the Khowar, among Indus Valley samples it is the Early Chalcolithic inhabitants of Mehrgarh, while among west-central Indians it is the mixed caste urban sample from Pune who possess relatively high prevalence of full hypocone development.

The pattern of intraregional variation in full development of the hypocone on the maxillary second molar across samples differs from that seen for this trait on the first maxillary molar. For the first maxillary molar, the level of variation varied inversely to overall trait frequency, such that the region with the highest average frequencies exhibit the least intraregional variation, while the region with the second highest frequencies exhibit the second least amount of variation, and so on. This pattern holds true for full development of the hypocone for prehistoric Central Asians (f= 0.624; sd= 0.092) and for the living inhabitants of southeast India (avg.= 0.329; sd= 0.096), but not for prehistoric Indus Valley dwellers (avg.= 0.174, sd= 0.221) or inhabitants of west-central India (avg.= 0.080; sd= 0.099). The amount of intraregional variation found among the prehistoric Indus Valley samples ranges from just over 55.6% to zero, among inhabitants of west-central India frequencies range from 25% to zero, among prehistoric Central Asians 71.9% to 50%, and among living ethnic groups from southeast India from 42.8% to 23.5%.

In a marked departure from what was found for the first maxillary molar, the **Madaklasht** with a frequency of 10% rank 14th among the 20 samples considered and as such exhibit full development of the hypocone on the second maxillary molar far less often than Khowars (24.6%). Full hypocone prevalence among the Madaklasht is most similar to the prehistoric Indus Valley samples from Harappa (11.1%) and Sarai Khola (15.4%), as well as to two of the living ethnic groups from west-central India (MDA= 6.5%; MHR= 6.1%). Chi-square analysis **(Table 4)** indicates the Madaklasht are marked by significantly lower frequencies of full hypocone prevalence when compared to prehistoric Central Asians (71.9% to 50%), the Chalcolithic inhabitants of Mehrgarh (55.6%), living ethnic groups from southeast India (42.8 to 23.5%), and the two urban mixed caste samples from Kolkata (31.5%) and Pune (25%). By contrast, the Madaklasht possess a significantly higher prevalence of full hypocone development on the second maxillary molar when compared to high-status Marathas from west-central India.

All samples, including the Madaklasht, exhibit full development of the hypocone on the first maxillary molar more often than on the second maxillary molar. In fact, as noted above, no fully developed hypocones were found on the second molars among the prehistoric inhabitants of Inamgaon or Timargarha. The difference in frequency of fully developed hypocones across the two maxillary molars differs markedly between samples. The greatest overrepresentation of fully developed hypocones on the first maxillary molar relative to the second, where at least *some* individuals possess fully developed hypocones on the second molar, occurs among high-status caste Marathas from west-central India. Among Marathas, fully developed hypocones are more than 38 times more common ($f[M^1/M^2]$= 38.617) on the first molar (86.3%) than on the second molar (2.2%). Differences in frequency across the maxillary molars are also marked among the Neolithic inhabitants of Mehrgarh, where full development is more than 17 times more common ($f[M^1/M^2]$= 17.083) on the first molar (57.7%) than on the second (4.9%), as well as among two of the other living caste samples from west-central India (MDA: $M^1$= 91.7%, $M^2$= 6.5%, $f[M^1/M^2]$= 14.033; MHR: $M^1$= 83.6%, $M^2$= 6.1%, $f[M^1/M^2]$= 13.709).

Several configurations emerge when the pattern of full development of the hypocone across the two maxillary molars is considered by geographic region. All west-central Indian samples are marked by dentitions in which full hypocone development occurs more than 10 times as often on first maxillary molars than on second maxillary molars. The only exception is the urban mixed caste sample from Pune (RAS: $f[M^1/M^2]$= 4.000). Samples of living ethnic groups from southeast India possess dentitions in which full development of the hypocone occurs with moderately greater frequency on first molars than on second molars (PNT: $f[IM/M^2]$= 4.133; GPD: $f[IM/M^2]$= 3.074; CHU: $f[IM/M^2]$= 2.325). Samples of prehistoric inhabitants of Central Asia are marked by some of the lowest levels of overrepresentation of fully developed hypocones on the first maxillary molar relative to the second (KUZ: $f[IM/M^2]$= 2.000; MOL: $f[IM/M^2]$= 1.609; DJR: $f[IM/M^2]$= 1.524; SAP: $f[IM/M^2]$= 1.391), a phenomenon driven by the relatively higher frequencies of full hypocone development on the second molars of these individuals compared to individuals of the other geographic regions. As was observed for median lingual ridge development, prehistoric samples from the Indus Valley are all across the board with respect to the relative frequency of full hypocone development on the maxillary first and second molars.

As noted above, the Neolithic inhabitants of Mehrgarh feature one of the greatest overrepresentations of full hypocone development on the first molar to the second, the late Chalcolithic inhabitants of Harappa are marked by high to moderate overrepresentation ($f[IM/M^2]$= 9.000), the Iron Age sample from Sarai Khola features moderate overrepresentation ($f[IM/M^2]$= 5.107), the Early

Chalcolithic sample from Mehrgarh has only a low overrepresentation (f[IM/M$^2$]= 1.800), while the Late Bronze/Early Iron Age sample from Timargarha features no individuals at all with fully developed hypocones on the second maxillary molar. Thus, as with marginal lingual ridge development, tooth-trait expression of fully development of the hypocone among these samples is marked by regional distinctiveness and a fair amount of intraregional cohesion for all regions, except for the prehistoric inhabitants of the Indus Valley. Prehistoric inhabitants of the Indus Valley express the greatest internal variation, but unlike the median lingual ridge, there is no clearly discernible temporal trend in hypocone expression among maxillary first and second molars from the Neolithic through the Late Bronze/Early Iron Age.

The relative expression of full hypocone development on first versus second molars among the Madaklasht (f[IM/M$^2$]= 9.833) is most like that seen among the Late Chalcolithic inhabitants of Harappa, and is markedly different from that observed among the inhabitants of west-central and southeastern India, from all prehistoric inhabitants of the Indus Valley (except Harappans), and from all prehistoric inhabitants of Central Asia. By contrast, the relative expression of full hypocone development on first versus second molars among Khowars occurs with frequencies most like that seen among living inhabitants of southeast India (f[IM/M$^2$]= 4.007). Given the near identicality in the frequency of full development of the hypocone on the first molar among the two Hindu Kush samples (MDK= 98.3%; KHO= 98.5%), it is clear the difference in relative frequencies of full hypocone development across the two maxillary molars is driven solely by the much higher frequency of full hypocone development on second molars among Khowars (24.6%) than among the Madaklasht (10.0%).

CARABELLI'S TRAIT

Analysis of variance **(Table 3)** across all samples reveals there is significant heterogeneity in the frequency of Carabelli's trait prevalence on the mesiolingual surface the protocone of the first maxillary molar (CARAUM1). Carabelli's trait **(Fig. 3c)** occurs with highest frequencies among the low-status Mahars (74.9%) of west-central India and among the high-status Pakanati Reddis (74.7%) of southeastern India. Lowest frequencies (10.0%) occur among the Kuzali period inhabitants of Djarkutan located in Central Asia **(Table 2)**. Chi-square analysis **(Table 3)** reveals that frequencies are signficantly higher among the 10 living samples (avg.= 0.651) than among the 10 prehistoric samples(avg.= 0.329), but the range in frequency is greater among the prehistoric samples (range= 0.159) than among the living samples (range= 0.082).

When considered by geographic region, highest average frequencies occur among members of living ethnic groups from southeast India (avg.= 0.634), followed by inhabitants of west-central India (avg.= 0.566) and prehistoric inhabitants of the Indus Valley (avg.= 0.407). Lowest average frequencies occur among prehistoric Central Asians (avg.= 0.231). The greatest variation in Carabelli's trait frequencies on the first maxillary molar occurs among the prehistoric inhabitants of the Indus Valley (sd= 0.164), followed by west-central Indians (sd= 0.157) and prehistoric Central Asians (sd= 0.129), while variation is least among members of the living ethnic groups of southeast India (sd= 0.104).

Tukey's HSD **(Table 3)** indicates the generally low frequencies of Carabelli's trait among prehistoric Central Asians separate them significantly from samples of all other geographic regions, except the Indus Valley. With very high prevalence, Hindu Kush samples are significantly different from samples of all other regions, except southeast India. Both Indus Valley and west-central regional aggregates are marked by substantial intraregional variation **(Fig. 3c)**. For the Indus Valley, samples from Neolithic Mehrgarh and Sarai Khola stand apart with rather low frequencies of Carabelli's trait. Among west-central Indians, it is the prehistoric sample from Inamgaon that stands apart with low prevalence. It is this variability that results in the absence of significant differences with prehistoric Central Asians among the former and with southeast Indians among the latter.

The Madaklasht, with a frequency of 73.9% rank third among the 20 samples considered. As such, the Madaklasht exhibit Carabelli's trait somewhat more often than Khowars (66.9%), and are most similar to low-status Mahars (74.9%) of west-central India and to high-status Pakanati Reddis of southeastern India (74.7%). Chi-square analysis (Table 4) indicates the Madaklasht differ significantly with much higher frequency of Carabelli's trait relative to all prehistoric Central Asians (f< 37%), from all Indus Valley samples (except the Chalcolithic samples from Mehrgarh and Harappa), tribal Chenchus and low-status Gompadhompti Madigas from southeast India, and from all west-central Indian samples, except low-status Mahars and the mixed caste urban sample from Pune.

### PRESENCE OF THE METACONULE

Analysis of variance **(Table 3)** across all samples reveals there is significant heterogeneity in metaconule prevalence on the first molar (MTCLEUM1). Development of the metaconule along the distal margin of the first maxillary molar occurs with the highest frequency among the Late Chalcolithic inhabitants of Harappa, where nearly half (46.2%) of all individuals with first maxillary molars possess this trait **(Fig. 3d)**. Lowest frequencies occur among the Madaklasht, for less than 3% (2.8%) of all individuals who could be scored for this trait exhibit any development of the metaconule. Chi-square analysis **(Table 3)** indicates, like full development of the hypocone, that the presence of the metaconule occurs significantly more often among the 10 living samples (avg.= 0.219) than among the 10 prehistoric samples (avg.= 0.195) and the range in the frequency of the metaconule is greater among the prehistoric samples (range= 0.427) than among the living samples (range= 0.291).

When considered by geographic region, highest average frequencies occur among the prehistoric inhabitants of the Indus Valley (avg.= 0.304), followed by the living ethnic groups of southeast India (avg.= 0.285) and inhabitants of west-central India (avg.= 0.240). In marked contrast to the inhabitants of these three regions, metaconules occur at a far lower average frequency among prehistoric Central Asians (avg.= 0.072). Intraregional variation in the expression of this trait divides the four regions into two that exhibit relatively little internal variation (southeast Indians: sd= 0.057; prehistoric Central Asians: sd= 0.061) and two that are marked by three to five times greater internal variation (prehistoric Indus Valley: sd= 0.251; west-central Indians: avg.= 0.162). Tukey's HSD **(Table 3)** draws a statistically significant separation between regional groups marked by low prevalence of the metaconule (prehistoric Central Asians, Hindu Kush highlanders) and those in which the metaconule occurs with relatively high frequency (southeast and west-central peninsular Indians, prehistoric inhabitants of the Indus Valley).

The Madaklasht, with the lowest frequency of metaconule development on the first maxillary molar of all the samples considered, are most like their Hindu Kush counterparts, the Khowars (6.8%) and to prehistoric Central Asians in metaconule prevalence. By contrast, chi-square analysis **(Table 4)** indicates the Madaklasht differ significantly in metaconule frequency from all prehistoric inhabitants of the Indus Valley, especially the Late Chalcolithic sample from Harappa (46.2%) and the Early Iron Age sample from Sarai Khola (33.3%). The Madaklasht also differ significantly in metaconule frequency from all of the living ethnic groups from southeast India and west-central India included in this analysis.

Development of the metaconule on the second maxillary molar (MTCLEUM2) is less common overall (16.5%) than on the first molar (20.7%). Further, development of this trait on the second maxillary molar is marked by less variation among samples (sd= 0.096) than seen in the first molar (sd= 0.117). Nevertheless, analysis of variance **(Table 3)** across all samples reveals there is significant heterogeneity in metaconule prevalence on the second molar. This trait is found at highest frequencies among the Neolithic (40%) and Chalcolithic (33.3%) inhabitants of Mehrgarh **(Table 2)**, while lowest frequencies occur among the Djarkutan period inhabitants of Djarkutan and the Late Bronze/Early Iron Age inhabitants of Timargarha, where none of the individuals with second maxillary molars were found to possess this trait **(Fig. 3e)**. As with the first molar, chi-square analysis **(Table 3)** indicates that overall frequencies of this trait on the second maxillary molar are significantly higher among the 10 living samples (avg.= 0.184) than among the 10 prehistoric samples (avg.= 0.146). However, variation among the 10 prehistoric samples (sd= 0.140) is far higher than among the 10 living samples (sd= 0.053) and encompasses a far wider range in sample frequencies (range= 0.400; living: range= 0.168).

As found for the first maxillary molar, when considered by geographic region, highest average frequencies for the metaconule on the second maxillary molar occur among prehistoric inhabitants of the Indus Valley (avg.= 0.225). However, unlike the first molar, second highest frequencies in metaconule development on the second molar occur among the inhabitants of west-central India (avg.= 0.207), followed by the living ethnic groups of southeast India (avg.= 0.197). Once again, as in the first maxillary molar, lowest frequencies of the metaconule on the second molar are found among prehistoric Central Asians (avg.= 0.045).

The pattern of intraregional variation in metaconule frequencies on the second maxillary molar across samples is marked by much higher variation among the prehistoric inhabitants of the Indus Valley (sd= 0.158) relative to the other three regions (west-central Indians: sd= 0.039; prehistoric Central Asians: sd= 0.034; southeast Indians: sd= 0.020). In fact, intraregional variation among the prehistoric Indus Valley samples is nearly eight times greater than that seen among southeast Indians (7.834) and around four times greater than that seen among west-central Indians (4.094) and prehistoric Central Asians (3.773). Despite this difference, Tukey's HSD **(Table 3)** identifies a fundamental division among samples between those of geographic regions in which metaconule development on the second molar is of low prevalence (prehistoric Central Asians, Hindu Kush highlanders), and those where prevalence is relatively high (southeast and west-central peninsular Indians, all Indus Valley samples, except SKH).

In a marked departure from what was found for the first maxillary molar, the Madaklasht with a frequency of 11.6% for the metaconule on the second maxillary molar possess this trait more often than Khowars (7.8%). With respect to metaconule prevalence, the Madaklasht are most similar to the latest of the prehistoric samples from Central Asia (MOL: 8.1%) and the Indus Valley (SKH: 14.3%). Chi-square analysis **(Table 4)** indicates the Madaklasht differ significantly from pre-Late Chalcolithic prehistoric samples from the Indus Valley (f≥ 30%), from caste samples from southeast India (f> 20%), as well as from all samples of living individuals from west-central India (MDA, MHR, RAS), except high-status Marathas, in metaconule frequency on the second maxillary molar.

Table 5. Mean Measure of Divergence Analysis (MMD values above diagonal, standard deviations above diagonal)

| | BNG | ChIMRG | CHU | DJR | GPD | HAR | INM | KHO | KUZ | MDK | MDA | MHR | MRT | MOL | NeoMRG | PNT | RAS | SAP | SKH | 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 | 3.145 |
| ChIMRG | 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 | 4.146 |
| CHU | 5.542 | 4.854 | --- | 1.556 | 0.38 | 2.225 | 1.469 | 0.536 | 2.268 | 0.387 | 0.407 | 0.378 | 0.366 | 1.234 | 1.206 | 0.376 | 0.717 | 1.48 | 3.171 | 2.868 |
| DJR | 21.059 | 10.198 | 7.855 | --- | 1.574 | 3.405 | 2.624 | 1.704 | 3.45 | 1.579 | 1.599 | 1.571 | 1.56 | 2.427 | 2.393 | 1.57 | 1.902 | 2.678 | 4.352 | 4.026 |
| GPD | 2.929 | 7.134 | 0.54 | 13 | --- | 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 | 2.884 |
| HAR | 6.523 | 5.02 | 4.881 | 13.93 | 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 | 4.648 |
| INM | 14.294 | 11.615 | 7.628 | 12.657 | 7.441 | 3.906 | --- | 1.644 | 3.35 | 1.495 | 1.513 | 1.485 | 1.473 | 2.332 | 2.289 | 1.483 | 1.81 | 2.562 | 4.229 | 3.95 |
| KHO | 7.813 | 7.776 | 3.55 | 11.12 | 4.69 | 2.655 | 4.152 | --- | 2.422 | 0.562 | 0.58 | 0.553 | 0.54 | 1.394 | 1.368 | 0.55 | 0.883 | 1.628 | 3.319 | 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 | 3.09 | 2.282 | 2.617 | 3.37 | 5.042 | 4.704 |
| MDK | 5.214 | 9.291 | 7.561 | 20.776 | 6.104 | 5.144 | 6.566 | 1.327 | 18.96 | --- | 0.432 | 0.404 | 0.392 | 1.258 | 1.23 | 0.402 | 0.742 | 1.503 | 3.194 | 2.889 |
| MDA | 10.859 | 10.418 | 4.236 | 15.208 | 3.773 | 4.879 | 0.851 | 4.253 | 16.62 | 6.488 | --- | 0.423 | 0.412 | 1.278 | 1.251 | 0.421 | 0.763 | 1.523 | 3.215 | 2.908 |
| MHR | 7.811 | 10.352 | 6.121 | 22.756 | 5.05 | 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 | 2.882 |
| MRT | 9.322 | 10.66 | 5.997 | 18.497 | 4.53 | 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 | 2.87 |
| MOL | 13.329 | 2.087 | 4.769 | -2.635 | 9.832 | 4.87 | 11.441 | 5.471 | -3.287 | 12.053 | 13.479 | | 13.979 | --- | 2.071 | 1.248 | 1.582 | 2.353 | 4.031 | 3.725 |
| NeoMRG | 19.14 | 6.124 | 11.259 | 16.742 | 11.774 | 6.355 | -0.42 | 10.944 | 17.776 | 12.032 | 3.626 | 8.359 | 5.663 | 15.25 | --- | 1.22 | 1.557 | 2.313 | 4.013 | 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 | 2.881 |
| RAS | -0.521 | 4.835 | 3.974 | 20.778 | 1.865 | 3.339 | 9.57 | 6.707 | 19.114 | 4.275 | 6.488 | 4.768 | 5.406 | 13.528 | 9.481 | 1.16 | --- | 1.822 | 3.521 | 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 | 3.987 |
| SKH | 21.177 | 14.816 | 7.236 | 5.763 | 9.692 | 2.572 | -0.308 | 7.991 | -1.49 | 15.799 | 5.836 | 9.628 | 4.112 | 6.165 | 9.84 | 11.768 | 18.223 | 3.851 | --- | 5.602 |
| TMG | 13.547 | 8.126 | 3.811 | 8.331 | 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 | --- |

When metaconule frequencies among maxillary first and second molars are considered as a whole, a small majority of samples in which this trait is expressed on both teeth (11 of 18) feature dentitions in which frequencies are higher on the first maxillary molar than on the second. The greatest overrepresentation of this trait on the first maxillary molar relative to the second occurs among the Iron Age Indus Valley inhabitants of Sarai Khola and among the Kuzali period Central Asian occupants of Djarkutan, where metaconule development is more than twice as common (SKH: $f[M^1/M^2]= 2.333$; KUZ: $f[M^1/M^2]= 2.286$) on the first molar (SKH: 33.3%; KUZ: 9.,5%) than on the second (SKH: 14.3%; KUZ: 4.2%). Overrepresentation of the metaconule on the first maxillary molar relative to the second is also rather marked among the Late Chalcolithic Indus Valley inhabitants of Harappa, where the metaconule occurs nearly twice as often ($f[M^1/M^2]= 1.846$) on the first molar (46.2%) than on the second (25%). Among five samples where metaconule frequencies are higher on the first molar than on the second, these differences range between 57.5% (PNT: $f[M^1/M^2]= 1.575$) and 28.5% (GPD: $f[M^1/M^2]= 1.285$) and include the three groups from southeast India. Two samples are marked by a minor overrepresentation of the metaconule on the first molar relative to the second (BNG: $f[M^1/M^2]= 1.068$; MHR: $f[M^1/M^2]= 1.044$].

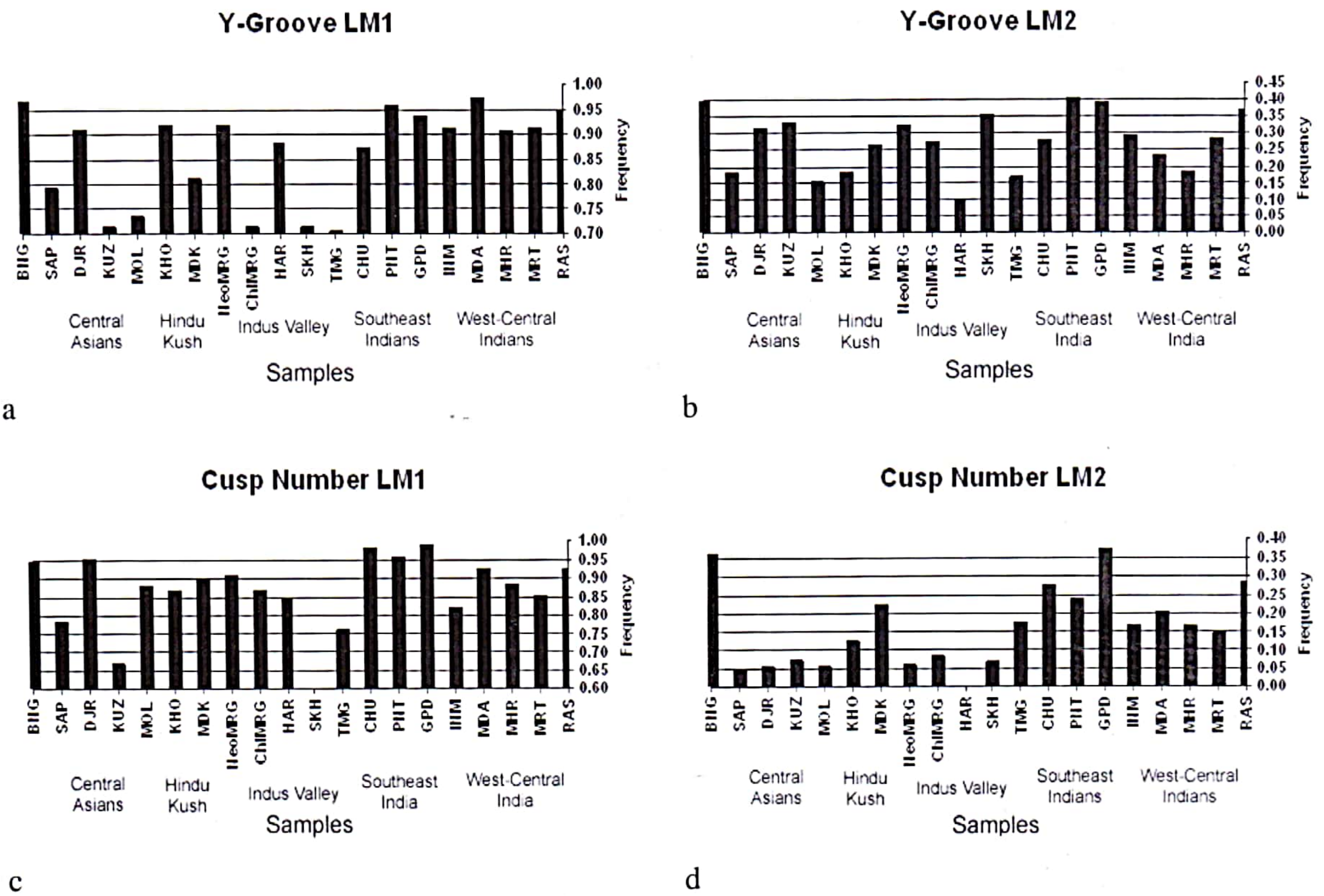



Fig 4 Frequencies of conservative morphology trait retention among mandibular posterior teeth. Living samples in alphabetical order by geographic region from left to right. Archaeologically derived sampled in temporal order by geographic region. Sample abbreviations and geographic region assignment from Table 1.a.) Y-Groove LM1, b.) Y-Groove LM2, c.) Cusp Number LM1, d.) Cusp Number LM2.

Seven samples are marked by dentitions in which metaconules are more common on the second maxillary molar than on the first and the Madaklasht represent the most dramatic expression of this (MDK: $M^2$= 11.6%, $M^1$= 2.8%; f[$M^2/M^1$]= 4.117). The remaining six samples that exhibit this reversal of relative metaconule prevalence across the two maxillary molars may be divided into two groups of three in which the first group is marked by a minor overrepresentation (<10%) of the metaconule on the second molar relative to the first (INM: f[$M^2/M^1$]= 1.025; MOL: f[$M^2/M^1$]= 1.054; MDA: f[$M^2/M^1$]= 1.068) and a second in which this difference in frequency is more marked (KHO: f[$M^2/M^1$]= 1.159; ChlMRG: f[$M^2/M^1$]= 1.267; NeoMRG: f[$M^2/M^1$]= 1.600). Clearly, the Madaklasht stand apart from all other samples in the distribution of metaconule frequencies across the first and second maxillary molars.

### Mandibular Posterior Teeth

#### Y-Groove Retention

Analysis of variance **(Table 3)** across all samples reveals significant heterogeneity in the prevalence of the Y-groove on the first mandibular molar (YGRVLM1). Retention of the conservative Y-groove pattern (Gregory 1916; Gregory and Hellman 1926; Hellman 1928; Jørgensen 1955) occurs with the highest frequency among the tribal Madia Gonds of west-central India (97.4%), followed by the urban mixed caste sample from Kolkata (BNG: 96.7%), high-status Pakistani Reddis (95.9%) from southeast India and the urban mixed caste sample from Pune (94.9%) **(Fig. 4a)**. Lowest frequencies occur among the Late Bronze/Early Iron Age Indus Valley occupants of Timargarha (70.6%), followed by the Kuzali phase Central Asian occupants of Djarkutan, the Early Chalcolithic inhabitants of Mehrgarh, and the Early Iron Age Indus Valley occupants of Sarai Khola, all of which possess this trait with identical frequencies of 71.4% **(Table 2)**.

Chi-square analysis **(Table 3)** indicates that, running contrary to expectations of evolutionary tooth crown simplification over time, retention of the Y-groove occurs at significantly higher frequencies among the 10 living samples (avg.= 0.921) than among the 10 prehistoric samples (avg.= 0.800). Also running contrary to these expectations is the fact that the range in Y-groove frequencies is greater among the prehistoric samples (range= 0.214) than among the living samples (range= 0.164).

When considered by geographic region, highest average frequencies occur among inhabitants of west-central India (avg.= 0.931), followed by living ethnic groups of southeast India (avg.= 0.923). By contrast, frequencies of Y-groove retention are markedly lower among the two sample aggregates of prehistoric teeth, where average frequencies are almost identical between the prehistoric inhabitants of Central Asia (avg.= 0.788) and the Indus Valley (avg.= 0.787). Intraregional variation in the expression of this trait divides the four regions into two regional samples of living individuals (except for INM) who are marked by higher average frequencies accompanied by lower levels of intraregional variation (west-central Indians: sd 0.029; southeast Indians: sd= 0.045) and the two regional samples dominated by prehistoric samples marked by lower average frequencies accompanied by higher levels of intraregional variation (Central Asians: sd= 0.087; Indus Valley: sd= 0.105).

Tukey's HSD **(Table 4)** indicates that significant differences in Y-groove prevalence among regional groups are largely the product of the separation between peninsular Indian samples, which have high retention of the conservative Y-groove, relative to the lesser retention rates found among *some* of the prehistoric samples from Central Asia and the Indus Valley. Among the former retention prevalence is low among all but the Djarkutan period sample, while among the latter retention prevalence is low among the Early Chalcolithic inhabitants of Mehrgarh and the two post-Chalcolithic samples from Timargarha and Sarai Khola. Tukey's HSD identifies Hindu Kush highlanders as possessing significantly lower Y-groove frequencies relative to west-central Indians, but not to southeast Indians.

The Madaklasht are marked by relatively low levels of Y-groove retention (81%), ranking 14th among the 20 samples considered. As such, they differ significantly from their Hindu Kush counterparts, the Khowar, who are marked by higher levels of Y-groove retention (91.8%). The Madaklasht are most similar in the frequency of Y-groove retention on the first mandibular molar to the earliest prehistoric sample from Central Asia (SAP: 79.2%) and to the tribal sample from southeast India (CHU: 87.3%). By contrast, the Madaklasht are marked by significantly lower frequencies of Y-groove retention from the two caste Hindu samples from southeast India (PNT, GPD), from the mixed caste urban sample from Kolkata (BNG), and from all of the samples from west-central India **(Table 4).**

Analysis of variance **(Table 3)** across all samples reveals there is significant heterogeneity of Y-groove retention prevalence on the occlusal surface of the second mandibular molar (YGRVLM2). Overall, retention of the conservative Y-groove occurs far less often (avg.= 27.4%) and varies more across samples (sd= 0.088) on the second mandibular molar than on the first (avg.= 86%; sd= 0.072). The Y-groove occurs with greatest frequencies among the two caste Hindu samples from southeast India (PNT= 40.6%, GPD= 39.2%) and the urban mixed caste sample from Kolkata (39.4%), while the lowest frequency occurs among the Late Chalcolithic Indus Valley inhabitants of Harappa (9.7%) **(Fig. 4b).** As for the first molar, overall frequencies Y-groove retention on the second molar tend to be higher among the 10 living samples (avg.= 0.299) than among the 10 prehistoric samples (avg.= 0.249), but chi-square reveals that his difference is not statistically significant **(Table 3).** In a departure from the occurrence of this trait on the first molar, variation among the 10 prehistoric samples (sd= 0.091) is only slightly higher than among the 10 living samples (sd= 0.086) for the second molar. Consequently, unlike the first molar, where a far wider range in sample frequencies was observed, this is not the case for Y-groove retention on the second (prehistoric: range= 0.260; living: range= 0.220).

When considered by geographic region, highest average frequencies of Y-groove retention are found among the living ethnic groups of southeast India (avg.= 0.359) followed by the inhabitants of west-central India (avg.= 0.273), while the two regional samples composed of prehistoric samples are marked by nearly equal low relative frequencies (Central Asians: avg.= 0.246; Indus Valley: avg.= 0.244). Once again, the pattern of intraregional variation in Y-groove frequencies on the second mandibular molar across samples is marked by higher variation among the prehistoric inhabitants of the Indus Valley (sd= 0.109) relative to the other three regions (prehistoric Central Asians: sd= 0.091; west-central Indians: sd= 0.069; southeast Indians: sd= 0.069), but this difference is not as great as for retention of the Y-groove on the first molar. Tukey's HSD **(Table 3)** reveals that interregional differences in Y-groove retention on the second molar are limited to a significant separation of southeast Indians from all other regional aggregates. Inspection of Figure 4c illustrates that this separation is driven by the two Hindu caste samples (GPD, PNT) and not by the sample of tribal Chenchus.

The Madaklasht retain the Y-groove on the second molar with a frequency of 26.4%, a rate substantially higher than that seen among the Khowar (18.6%). As such, the Madaklasht are most similar in the frequency of Y-groove retention of the second molar to the early Chalcolithic inhabitants of

Mehrgarh (27.3%), tribal Chenchus from southeast India (28%), and high-status Marathas from west-central India (28.2%). Chi-square analysis (Table 4) indicates the Madaklasht differ significantly from the two caste Hindu samples from southeast India (PNT: 40.6%; GPD: 39.2%), and from the Late Chalcolthic Indus Valley inhabitants of Harappa (9.7%) in the frequency of Y-groove retention on the second mandibular molar.

All samples are marked by higher frequencies of retention of the conservative Y-groove on the mandibular first molar than on the second molar. However, the degree to which Y-grooves are overrepresented on first molars relative to seconds differs markedly across samples. The greatest overrepresentation of retained Y-grooves on first molars relative to second molars occurs among the Late Chalcolithic Indus Valley inhabitants of Harappa, where Y-grooves are found on over nine times as many first molars as seconds ($f[M_1/M_2]= 9.118$). The least overrepresentation of retained Y-grooves occurs among the Iron Age Indus Valley occupants of Sarai Khola ($f[M_1/M_2]= 2.000$) and the Kuzali period Central Asian occupants of Djarkutan ($f[M_1/M_2]= 2.143$). There appears to be little regional effect in the difference in the relative retention of the Y-groove across the two mandibular molars, except for inhabitants of west-central India, where all of the samples (except the urban mixed caste sample from Pune) are marked by relatively low overrepresentation of the Y-groove on the first molar.

The Madaklasht are marked by a moderate rate of retention of the Y-groove on the second molar (f= 26.4%; $f[M_1/M_2]= 3.069$), which stands in contrast to the much greater loss of this groove among and consequent greater over-representation of the Y-groove on the first molar among Khowars ($M_2$ f= 18.6%; $f[M_1/M_2]= 4.935$), a rate second only to that found among the Late Chalcolithic inhabitants of Harappa. Overall, the Madaklasht are marked by a pattern of Y-groove retention most like that seen among the high-status Maratha ($f[M_1/M_2]= 3.244$) and to the prehistoric inhabitants of Inamgaon from west-central India ($f[M_1/M_2]= 3.135$), to tribal Chenchus from southeast India ($f[M_1/M_2]= 3.115$), to the Djarkutan period Central Asian occupants of Djarkutan ($f[M_1/M_2]= 2.893$), and to the Neolithic Indus Valley inhabitants of Mehrgarh ($f[M_1/M_2]= 2.837$). The Madaklasht differ markedly in the pattern of Y-groove retention—not only from the Khowar, but also from the Late Chaclolithic Indus Valley inhabitants of Harappa ($f[M_1/M_2]= 9.118$), the Kuzali period inhabitants of Djarkutan ($f[M_1/M_2]= 2.143$), and from the Iron Age Indus Valley inhabitants of Sarai Khola ($f[M_1/M_2]= 2.000$).

### RETENTION OF THE HYPOCONULID

As noted in the companion paper (Hemphill et al 2010), retention of the hypoconulid (C5) on the occlusal surface of the mandibular molars is considered the conservative condition among members of the superfamily *Hominoidea* (Gregory and Hellman 1926; Swindler 1976). Analysis of variance across all samples **(Table 3)** reveals there is significant heterogeneity in the retention of the hypoconulid on the first mandibular molar (CSPNLM1). Retention of the hypoconulid occurs with the highest frequency among the Gompadhompti Madigas (GPD), a low-status Hindu caste from southeast India, where this cusp is retained in 98.8% of individuals **(Table 2)**. Lowest frequencies occur among the Iron Age Indus Valley occupants of Sarai Khola, where this cusp is retained among only 60% of individuals **(Fig. 4c)**.

Standing at odds to expectations of evolutionary tooth crown simplification over time, chi-square analysis **(Table 3)** indicates that retention of the hypoconulid is significantly more common among the 10 living samples (avg.= 0.922) than among the 10 prehistoric samples (avg.= 0.809). Also running contrary to these expectations is the fact that the range in hypoconulid frequency is greater among the prehistoric samples (range= 0.352) than among the living samples (range= 0.137).

When considered by region, highest average frequencies of hypoconulid retention on the first mandibular molar occur among the living ethnic groups of southeast India (avg.= 0.974), for these three groups are marked by the highest frequencies for hypoconulid retention among all of the samples considered (GPD= 98.8%; CHU= 97.9%; PNT= 95.6%). Second highest average frequencies occur among the inhabitants of west-central India (avg.= 0.881), followed by prehistoric Central Asians (avg.= 0.821). Lowest average frequencies of hypoconulid retention on the first mandibular molar are found among the prehistoric inhabitants of the Indus Valley (avg.= 0.797). Tukey's HSD **(Table 3)** indicates that the significant differences in hypoconulid retention prevalence among samples is driven solely by the higher frequencies found among southeast Indian groups relative to samples from all other regional aggregates.

Similar to retention of the Y-groove, intraregional variation in hypoconulid retention on the first mandibular molar divides the four regions into two regional samples of living individuals (except for INM), who are marked by higher average frequencies accompanied by lower levels of intraregional variation (southeast Indians: sd= 0.033; west-central Indians: sd= 0.046;), and the two regional samples dominated by prehistoric samples, which are marked by lower average frequencies accompanied by higher levels of intraregional variation (Central Asians: sd= 0.123; Indus Valley: sd= 0.123). So uniformly high is the retention rate of the hypoconulid on the first molar among the southeast Indian samples that the two prehistoric sample aggregates are marked by a level of intraregional variation that is over seven times (Indus Valley= 7.328; Central Asians= 7.360) greater than among these living inhabitants of southeast India.

Ranked ninth among the 20 samples considered, the Madaklasht feature a relatively moderate frequency of hypoconulid retention on the first mandibular molar (89.8%) that is somewhat higher than their Hindu Kush counterparts, the Khowars (86.7%). As such, they are most similar to the Neolithic Indus Valley occupants of Mehrgarh (90.7%) and to the Mahars, a low-status caste from west-central India (MRH: 88.5%). Chi-square analysis (Table 4) indicates the Madaklasht have significantly lower prevalence of hypoconulid retention than the three living ethnic groups of southeast India (f>95%), as well as from the Iron Age sample from Sarai Khola and the Kuzali period occupants of Djarkutan.

Overall, retention of the conservative hypoconulid occurs far less often (avg.= 15.9%) and varies less across samples (sd= 0.069) on the second mandibular molar (CSPNLM2) than on the first molar (avg.= 86.5%; sd= 0.078), a result consistent with findings worldwide (Scott and Turner 1997:51). Nevertheless, analysis of variance across all samples reveals there is significant heterogeneity in the frequency of hypoconulid retention on the second molar **(Table 3)**. Retention occurs with greatest frequencies among the Gompadhompti Madigas, a low-status caste from southeast India (37.2%) and the urban mixed caste sample from Kolkata (36.2%), while the lowest frequency occurs among the Late Chalcolithic Indus Valley inhabitants of Harappa, where none of the second molars were observed to possess a hypoconulid (Table 2, Fig. 4d).

Chi-square analysis **(Table 3)** reveals that, as for the first molar, overall frequencies of hypoconulid retention on the second molar are significantly higher among the 10 living samples (avg.= 0.240) than among the 10 prehistoric samples (avg.= 0.079). However, variation in hypoconulid retention on the second molar among the 10 living samples (sd= 0.085) is greater than among the 10 living samples (sd= 0.054). Highest average frequencies of hypoconulid retention are found among members of the living ethnic groups of southeast India (avg.= 0.296) followed by the inhabitants of west-central India (avg.= 0.193). By contrast, the two regional aggregated samples composed of prehistoric samples are marked by much lower frequencies (Indus Valley: avg.= 0.078; Central Asians: avg.= 0.058).

The pattern of intraregional variation in hypoconulid retention on the second molar differs from that observed for the first molar. Whereas, in the first molar, the two prehistoric samples were marked by lowest frequencies and highest intraregional regional variation, this is not the case for the second molar. Instead, levels of intraregional variation are highest among the living ethnic groups of southeast India (sd= 0.069), followed closely by variation among the prehistoric inhabitants of the Indus Valley (sd= 0.064). Intraregional variation among inhabitants of west-central India (sd= 0.054) is somewhat less than that seen among prehistoric Indus Valley dwellers, but prehistoric Central Asians stand apart from members of all other regions by exhibiting an extremely low level of intraregional variation (sd= 0.010) in hypoconulid retention on the second molar.

Tukey's HSD (Table 3) provides a trichotomy of regional aggregates that differ significantly in hypoconulid retention prevalence on the second molar. Ethnic groups from southeast India (as well as the mixed urban caste sample from Kolkata) stand apart with relatively high frequencies of hypoconulid retention. Hindu Kush highlanders and ethnic groups of west-central India are marked by moderate frequencies, while the prehistoric samples from Central Asia and the Indus Valley stand apart with significantly lower frequencies for retention of the hypoconulid on the second molar.

Ranked sixth among the 20 samples, the Madaklasht retain the hypoconulid on the second molar with a frequency of 22.5%, a rate nearly double that seen among Khowars (12.5%). The Madaklasht are most similar in the frequency of hypoconulid retention on the second molar to the high-status Pakanati Reddis (23.9%) and tribal Chenchus (27.7%) from southeast India (23.9%), as well as to the tribal Madia Gonds from west-central India (20.3%) and the Late Bronze/Early Iron Age Indus Valley inhabitants of Timargarha (17.6%). Chi-square analysis **(Table 4)** indicates the Madaklasht are marked by significantly lower prevalence of hypoconulid retention relative to low-status caste Gompadhompti Madigas (37.2%) from southeast India and the urban mixed caste sample from Kolkata (36.2%). By contrast, the Madaklasht have significantly higher prevalence of hypoconulid retention on the second molar relative to the Neolithic inhabitants of Mehrgarh, the Late Chalcolithic inhabitants of Harappa, and to all prehistoric Central Asian samples, except the Molali period occupants of Djarkutan.

All samples are marked by higher frequencies of retention of the conservative hypoconulid on the mandibular first molar than on the second molar. However, as with retention of the Y-groove, the degree to which hypoconulids are overrepresented on first molars relative to seconds differs markedly. The greatest loss of hypoconulids on second molars relative to first molars occurs among the Djarkutan period Central Asian occupants of Djarkutan, where hypoconulids are found on over 17 times as many first molars as seconds ($f[M_1/M_2]$= 17.143). The least under-retention occurs among urban mixed caste sample from Kolkata ($f[M_1/M_2]$= 2.602) and among the low-status caste Gompadhompti Madigas from southeast India ($f[M_1/M_2]$= 2.656).

Overall, greatest loss of the hypoconulid on the second molar relative to the first occurs among the prehistoric samples from Central Asia (DJR: $f[M_1/M_2]$= 17.143; SAP: $f[M_1/M_2]$= 16.107; MOL:

$f[M_1/M_2]$= 15.379; KUZ: $f[M_1/M_2]$= 9.333) and the two prehistoric samples from Mehrgarh (NeoMRG: $f[M_1/M_2]$= 14.814; ChlMRG: $f[M_1/M_2]$= 10.435). With the sole exception of the urban mixed caste sample from Pune ($f[M_1/M_2]$= 3.255), loss of the hypoconulid on the second molar relative to the first occurs with moderate frequency among the west-central Indians (f = 4.6% - 6%). Loss of the hypoconulid on the second molar relative to the first occurs with rather low frequencies among the samples from southeast India (f= 2.7% – 4%). Thus, there appears to be a significant regional effect in the difference in the relative retention of the hypoconulid across the two mandibular molars, where prehistoric Central Asians stand apart from all other samples, except the two earliest prehistoric samples from Mehrgarh, by possessing mandibular molars that are marked by relatively high under-retention of the hypoconulid on the second molar.

The Madaklasht are marked by a relatively high rate of retention of the hypoconulid on the second molar (f= 22.5%; $f[M_1/M_2]$= 3.990), which is markedly different from the greater loss suffered by Khowars ($M_2$ f= 12.5%; $f[M_1/M_2]$= 6.938). Overall, the Madaklasht are marked by a pattern of Y-groove retention most like that seen among the samples from southeast India, while retention rates among Khowars are more like those seen among west-central Indians.

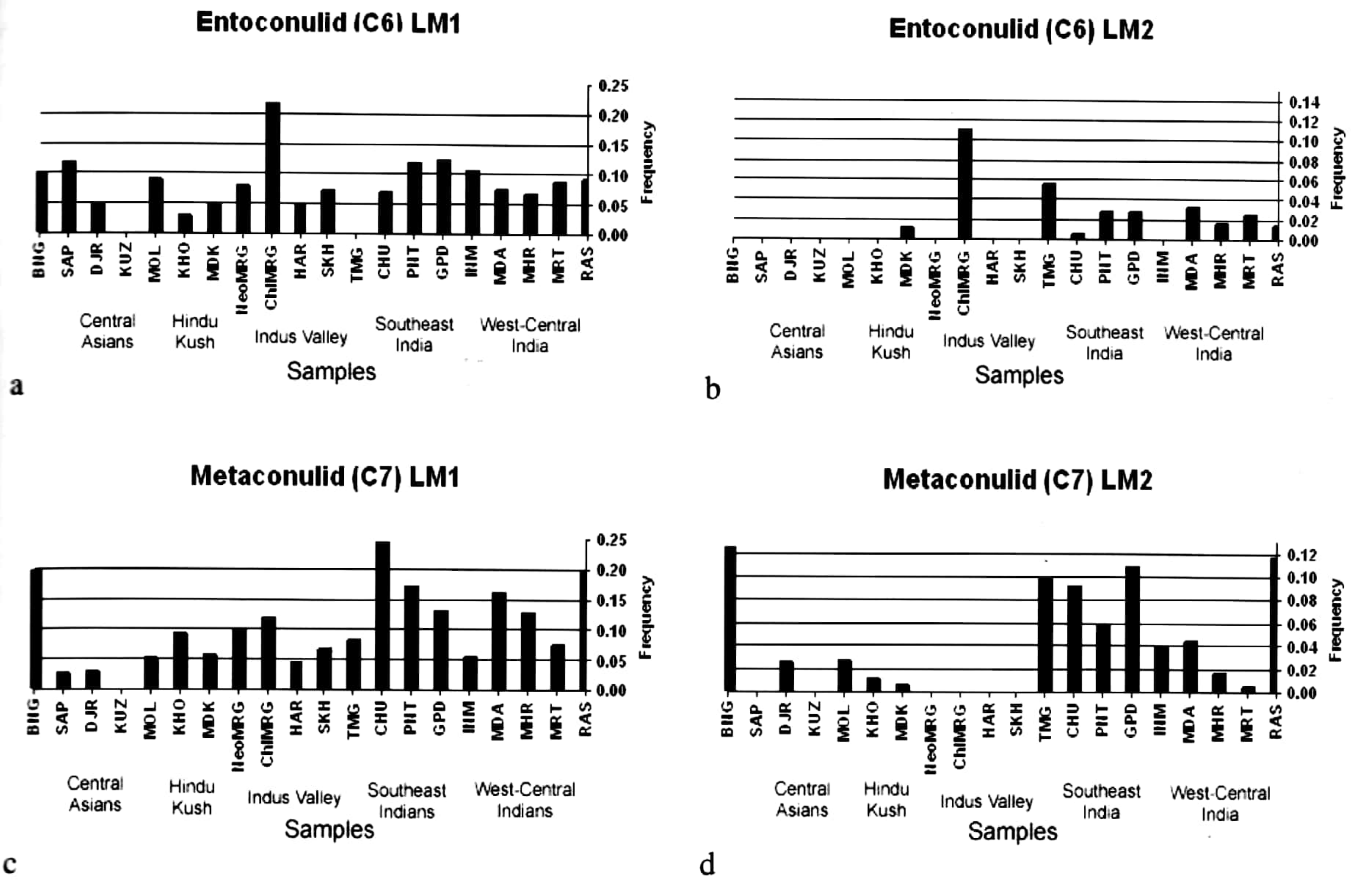



Fig 5 Frequencies of accessory cusps among mandibular posterior teeth. Living samples in alphabetical order by geographic region from left to right. Archaeologically derived sampled in temporal order by geographic region. Sample abbreviations and geographic region assignment from Table 1.a.) Entoconulid (C6) LM1, b.) Entoconulid (C6) LM2, c.) Metaconulid (C7) LM1, d.) Metaconulid (C7) LM2.

## PRESENCE OF THE ENTOCONULID (C6)

Analysis of variance across all samples **(Table 3)** reveals there is significant heterogeneity in the frequency of the entoconulid on the first mandibular molar (C6LM1). The entoconulid occurs with greatest frequency among the Early Chalcolithic Indus Valley inhabitants of Mehrgarh (21.7%). Lowest frequencies occur among the Late Bronze/Early Iron Age Indus Valley occupants of Timargarha and among the Kuzali period Central Asian occupants of Djarkutan where none of the first molars of individuals recovered from these sites exhibit development of the entoconulid **(Table 2, Fig. 5a)**. Chi-square analysis **(Table 3)** reveals that the entoconulid on the first molar occurs with slightly higher frequencies among the 10 living samples (avg.= 0.082) than among the 10 prehistoric samples (avg.= 0.079), but this difference is not statistically significant. Nevertheless, both the amount of inter-sample variation and the range of that variation are far higher among prehistoric samples (sd= 0.063; range= 0.217) than among living samples (sd= 0.029; range= 0.093).

When considered by geographic region, it is clear the living ethnic groups of southeast India (avg.= 0.105) are marked by higher average frequencies relative to samples from the other three regions (west-central: avg.= 0.086; Indus Valley= 0.084; Central Asia= avg.= 0.065). Tukey's HSD **(Table 3)** indicates that only the separation between Hindu Kush highland samples, marked by very low frequencies, and living ethnic groups from southeast India, who are marked by relatively high frequencies, are statistically significant. Intraregional variation reveals a pattern in which the two samples dominated by living individuals (west-central: sd= 0.015; southeast: sd= 0.030) are marked by considerably less intraregional variation than the prehistoric samples (Central Asia: sd= 0.081; Indus Valley: sd= 0.052). In fact, intraregional variation is particularly marked for the prehistoric Indus Valley samples, running from nearly four (3.979) to over five times (5.240) higher than that seen among west-central and southeast peninsular Indians.

Ranking 15th among the 20 samples, the Madaklasht feature a relatively low frequency of entoconulid development (5.1%), but one that is higher than that found among the Khowar (3.1%). As such, the Madaklasht are marked by frequencies that are virtually identical to those observed among the Djarkutan period Central Asian occupants of Djarkutan (5%) and to the Late Chalcolithic Indus Valley inhabitants of Harappa (5%). Chi-square analysis (Table 4) indicates the Madaklasht are marked by significantly lower entoconulid prevalence on the first mandibular molar than caste Hindu samples from southeast India (GPD: 12.4%; PNT= 12.1%) and the Early Chalcolithic Indus Valley occupants of Mehrgarh (21.7%).

The entoconulid is only found on the second mandibular molar (C6LM2) among half of the samples included in this **(Table 2)**. Consequently analysis of variance **(Table 3)** indicates there is an insignificant level of heterogeneity across samples. Among those samples where the entoconulid is found on the second molar, frequencies are highest among the Early Chalcolithic Indus Valley inhabitants of Mehrgarh (11.1%) and are least common among Chenchu tribals from southeast India (0.5%). Overall frequencies of the entoconulid on the second molar are identical and hence, non-significant **(Table 3)**, between prehistoric and living samples (1.7%). Nevertheless, variation is three times greater among the 10 prehistoric samples (sd= 0.037) than among the 10 living samples (sd= 0.012).

When considered by regional group, highest average frequencies for the entoconulid on the second molar are found among the prehistoric inhabitants of the Indus Valley (3.3%); but this is misleading, for the only sample in this regional aggregate that expresses the entoconulid on the second molar are the Early Chalcolithic inhabitants of Mehrgarh. Among members of the remaining regions, entoconulid frequencies on the second molar are higher among living ethnic groups of southeast India (avg.= 2.1%) than among inhabitants of west-central India (avg.= 1.8%), while none of the prehistoric samples from Central Asia exhibit any presence of the entoconulid on the second molar.

Intraregional variation among the prehistoric inhabitants of the Indus Valley is far higher than among samples of the other regions for the reason noted above. Intraregional variation is nearly identical and minimal among the living ethnic groups of southeast India (sd= 0.013) and inhabitants of west-central India (sd= 0.012) and, of course, there is no intraregional variation among the prehistoric samples from Central Asia in which none of the samples exhibits any development of the entoconulid.

The Madaklasht evince development of the entoconulid on the second molar with a frequency of 1.2%, a rate second lowest among those samples marked by development of this trait on the second molar, but a rate higher than that seen among the Khowars, where the entoconulid is completely absent. The Madaklasht are most similar in entoconulid frequency on the second molar to the urban mixed caste sample from Pune (1.5%) and the low-status caste Mahars of west-central India (1.7%). The Madaklasht differ strongly, but not significantly **(Table 4)**, from the Early Chalcolithic Indus Valley inhabitants of Mehrgarh (11.1%) in the frequency of entoconulid development on the second molar.

All samples, except the post-Harappan Indus Valley occupants of Timargarha ($M_1$= 0.0%, $M_2$= 5.6%), are marked by higher frequencies of the entoconulid on the mandibular first molar than on the second molar. However, the degree to which entoconulids are represented on first molars relative to seconds differs markedly across samples. The greatest relative overrepresentation on first molars occurs among the tribal Chenchu of southeast India, where entoconulids are present 13 times more often on first molars than on second molars. Overrepresentation is also high in the urban mixed caste sample from Pune (RAS: (f[$M_1/M_2$]= 6.277), but is relatively low among the Early Chalcolithic Indus Valley inhabitants of Mehrgarh (f[$M_1/M_2$]= 1.957). The Madaklasht are marked by a moderate rate of entoconulid presence on the second molar (f= 1.2%; f[$M_1/M_2$]= 4.195) relative to that seen on the first molar, which is markedly different from the complete absence of this accessory cusp on the second molar among the Khowars, but which occurs with frequencies similar to those found among the low-status Gompadhompti Madigas of southeast India (f[$M_1/M_2$]= 4.275) as well as the low-status Mahars from west-central India (f[$M_1/M_2$]= 3.948).

### PRESENCE OF THE METACONULID (C7)

Analysis of variance **(Table 3)** across all samples reveals that there is significant heterogeneity in the frequency of metaconulid (C7) on the mandibular first molar (C7LM1). The metaconulid occurs with greatest frequency upon the first molar among the Chenchu tribals of southeastern India, where this accessory cusp was found in 24.6% of individuals **(Table 2)**. The metaconulid was found in lowest frequency among the Kuzali period Central Asian occupants of Djarkutan, where none of the first molars of individuals recovered from this site exhibited development of the metaconulid **(Fig. 5c)**. Chi-square analysis **(Table 3)** indicates that the metaconulid on the first molar occurs with significantly higher frequencies among the 10 living samples (avg.= 0.147) than among the 10 prehistoric samples (avg.= 0.058). Likewise, inter-sample variation and the range of that variation are also higher among the living samples (sd= 0.060; range= 0.189) than among the prehistoric samples (sd= 0.036; range= 0.120).

As was found for the entoconulid, when considered by geographic region, it is clear that average frequencies are far higher among samples of living ethnic groups from southeast India (avg.= 0.184) than among inhabitants of west-central India (avg.= 0.125) and samples of prehistoric individuals from either the Indus Valley (avg.= 0.083) or, especially, Central Asia (avg.= 0.027). In a departure from what was observed for the entoconulid, intraregional variation reveals a pattern in which the two samples dominated by living individuals (west-central: sd= 0.141; southeast: sd= 0.112) are marked by considerably more intraregional variation in metaconulid presence than those regions represented solely by archaeologically-derived individuals (Indus Valley: sd= 0.075; Central Asia: sd= 0.051). Tukey's HSD analysis **(Table 4)** indicates that significant differences among geographic aggregates serve to separate living ethnic groups from southeast India from individuals of all other geographic regions.

As with the entoconulid, the Madaklasht possess this accessory cusp with relatively low frequency (5.7%), but in contrast to the entoconulid, this frequency is only slightly higher than half the frequency with which the metaconulid is observed among the Khowar (9.3%). As such, the Madaklasht are marked by frequencies that are virtually identical to those observed among the prehistoric inhabitants of Inamgaon (5.6%). Chi-square analysis **(Table 4)** indicates the Madaklasht have significantly lower metaconulid frequency on the first mandibular molar than Chenchu tribals of southeast India, the urban mixed caste samples from Kolkata (BNG: 19.7%) and Pune (RAS: 19.7%), as well as from high-status caste Pakanati Reddis of southeast India (17.1%), Madia Gond tribals (16.4%) and low-status Mahars (13.1%) of west-central India.

The metaconulid is found on the second mandibular molar (C7LM2) in 14 of the samples included in this analysis. Nevertheless, analysis of variance **(Table 3)** reveals there is significant heterogeneity in the expression of this trait across all samples. Among those samples where it is found, frequencies are highest among the two urban mixed caste samples from Kolkata (12.5%) and Pune (11.8%) and are least common among the Madaklasht (0.6%) and high-status caste Marathas from west-central India (0.5%). Chi-square analysis **(Table 3)** reveals that overall frequencies of the metaconulid on the second molar are significantly greater among living samples (avg.= 5.9%). All samples of living individuals included in this analysis feature at least *some* presence of this accessory trait. By contrast, average frequencies among prehistoric samples are not only lower (avg.= 1.9%) but six of the 10 prehistoric samples are marked by a complete absence of this trait. This finding is likely a consequence of the generally smaller sample size of these archaeologically derived samples and serves as a note of caution about drawing firm conclusions concerning biological relatedness between samples based on such low frequency traits. Not surprisingly, living samples are also marked by a greater degree of inter-sample variation in metaconulid frequencies (sd= 0.049), relative to prehistoric samples (sd= 0.032).

When considered by geographic region, highest average frequencies for the metaconulid on the second molar are found among the living ethnic groups of southeast India (avg.= 8.8%), followed by inhabitants of west-central India (avg.= 4.5%) and prehistoric inhabitants of the Indus Valley (2%). Frequencies of the metaconulid on the second mandibular molar are of lowest average frequency among prehistoric Central Asians (1.3%); which is a bit misleading, for the two samples in which any presence of this trait is found, it is found in frequencies that exceed 2.5% (MOL: 2.8%, DJR= 2.8). Levels of intraregional variation divide the regional samples into two groups, those with relatively high internal variation (Indus Valley: sd= 0.045; west-central India: sd= 0.044), and those marked by relatively low internal variation (southeast India: 0.025; Central Asia: sd= 0.015). Tukey's HSD **(Table 3)** yields a significant separation of southeast Indians from all other regional aggregates.

As noted above, the Madaklasht exhibit the lowest frequencies of metaconulid development among those samples that show evidence of this trait on the second molar. As such, frequencies are somewhat lower than among the Khowar (1.1%) and stand out as significantly different from the urban mixed caste sample from Kolkata, where this trait occurs in over 12% of individuals observed, all three of the ethnic groups from southeast India, as well as the Late Bronze/Early Iron Age Indus Valley sample from Timargarha.

All samples, except the Late Bronze/Early Iron Age Indus Valley occupants of Timargarha ($M_1$= 8.3%, $M_2$= 10%: 1.200) are marked by higher frequencies of the metaconulid on the mandibular first molar than on the second molar. However, the degree to which metaconulids are represented on first molars relative to seconds differs markedly across samples. The greatest relative overrepresentation on first molars occurs among high-status Marathas from west-central India, where metaconulids are present nearly 15 times more often on first molars than on second molars ($M_1$= 7.6%, $M_2$= 0.5%, f[$M_1$/$M_2$]= 14.924). Overrepresentation is also high among the Madaklasht ($M_1$= 5.7%, $M_2$= 0.06%, f[$M_1$/$M_2$]= 9.261), Khowars ($M_1$= 9.3%, $M_2$= 1.1%, f[$M_1$/$M_2$]= 8.372) and low-status caste Mahars from west-central India ($M_1$= 13.1%, $M_2$= 1.7%, f[$M_1$/$M_2$]= 7.723), while overrepresentation is of a moderate degree among Madia Gond tribals ($M_1$= 16.4%, $M_2$= 4.4%, f[$M_1$/$M_2$]= 3.694) from west-central India, as well as high-status caste Pakanati Reddis ($M_1$= 17.1%, $M_2$= 6.0%, f[$M_1$/$M_2$]= 2.834).and tribal Chenchus from southeast India ($M_1$= 24.6%, $M_2$= 9.3%, f[$M_1$/$M_2$]= 2.653).

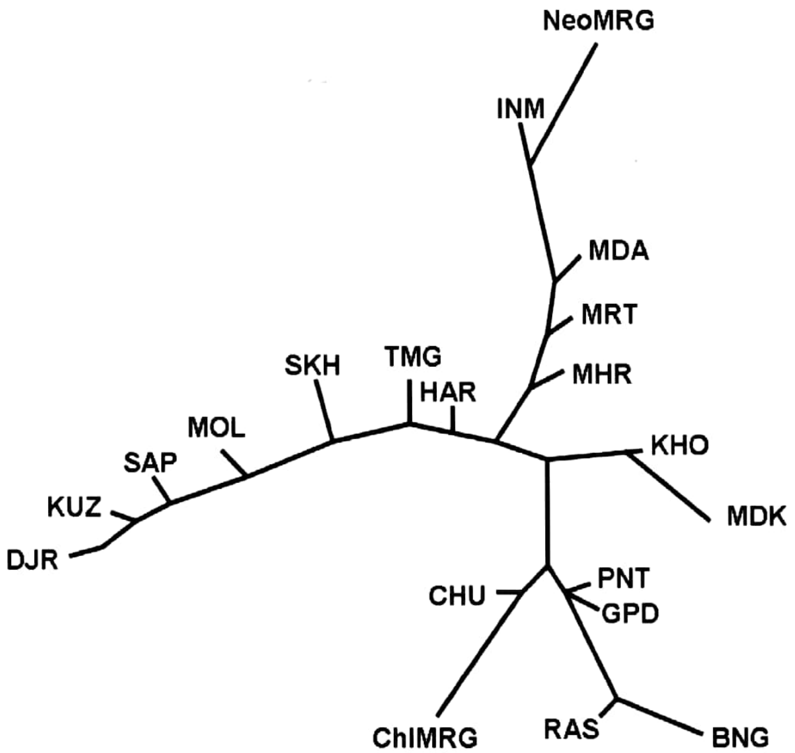



Fig 6 Neighbour-joining cluster analysis of Smith's pairwise MMD values based on 17 tooth-trait combinations (sample abbreviations from Table 1).

*Multivariate Variation*

NEIGHBOUR-JOINING CLUSTER ANALYSIS **(FIG. 6)**

A neighbour-joining dendrogram places the Madaklasht (MDK) in the centre of the right side of the array with closest affinities to their Hindu Kush highland counterparts, the Khowars (KHO). Together these two Hindu Kush highland samples are identified as possessing equidistant affinities to members of living ethnic groups from west-central peninsular India (MHR, MRT, MDA), located in the centre of the array, and members of living ethnic groups from southeast peninsular India (CHU, GPD, PNT), located in the lower centre of the array. Affinities are somewhat more distant with the prehistoric Indus Valley samples from Harappa (HAR) and Timargarha (TMG).

Prehistoric Central Asians, located on the left side, are identified as possessing closest affinities to one another. 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-Late Chalcolilthic 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 to 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 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).

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). The two samples from the Hindu Kush highlands are found in the lower right and they both occupy rather isolated positions. Both the inhabitants of Madaklasht (MDK) and Khowars (KHO) are identified as possessing closer affinities to the Late Chalcolithic Indus Valley sample from Harappa (HAR) than to one another. In the case of the Madaklasht, they depart rather markedly in multidimensional phenetic space from the Harappans along a unique vector away from all other samples included in this comparison.

The four prehistoric Central Asian samples (DJR, KUZ, MOL, SAP) occupy an isolated position on the left side. These samples exhibit fairly close affinities to one another, but are strongly separated from all other 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 neighbor-joining cluster analysis, the earlier sample (NeoMRG) is identified as possessing closest affinities to inhabitants of west-central peninsular India. However, multidimensional scaling suggests affinities are closer to living Madia Gond tribals (MDA) than to the prehistoric sample from Inamgaon (INM). Nevertheless, multidimensional scaling is consistent with neighbor-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 neighbor-joining cluster analysis. The two mixed caste urban samples (BNG, RAS) occupy unexpected positions adjacent to one another among the living Dravidian-speaking samples from southeastern India.

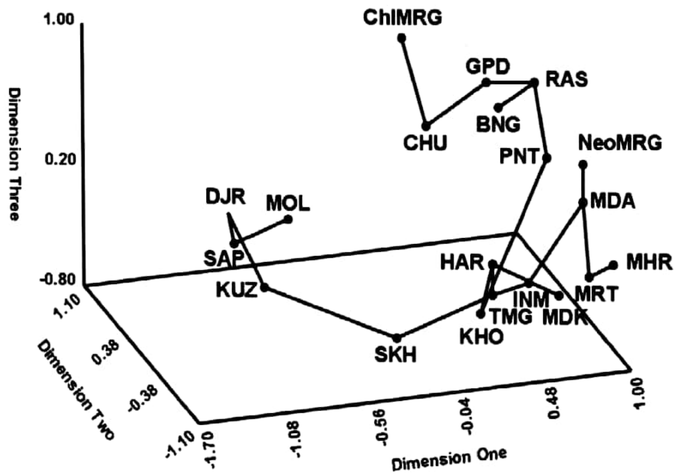



Fig 7 Multidimensional scaling of Smith's pairwise MMD values based on 17 tooth-trait combinations.

## Principal Coordinates Analysis (Fig. 8)

The first three principal coordinate axes account for 88.3% of the total variance. Principal coordinates analysis yields results only moderately consistent with those obtained by neighbour-joining cluster analysis and multidimensional scaling. Located in the lower left, the two samples of living Hindu Kush highlanders occupy an unexpected phenetic position intermediate between living ethnic groups of west-central India on the one hand (MHR, MRT, MDA), and living ethnic groups of southeastern India on the other (PNT, GPD, CHU). In contrast to results obtained by neighbour-joining cluster analysis and multidimensional scaling, principal coordinates analysis suggests it is the Khowars, rather than the Madaklasht, who occupy an isolated position relative to all other samples. The odd phenetic position occupied by both the Madaklasht and the Khowars suggest that members of these two ethnic groups share little biological affinities to one another, or to any of the other samples included in this comparative study.

Located on the far right side, the four prehistoric samples from Central Asia (MOL, DJR, KUZ, SAP) are once again identified as possessing rather close affinities to one another, but are strongly isolated from all other samples. 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 Early 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). 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).

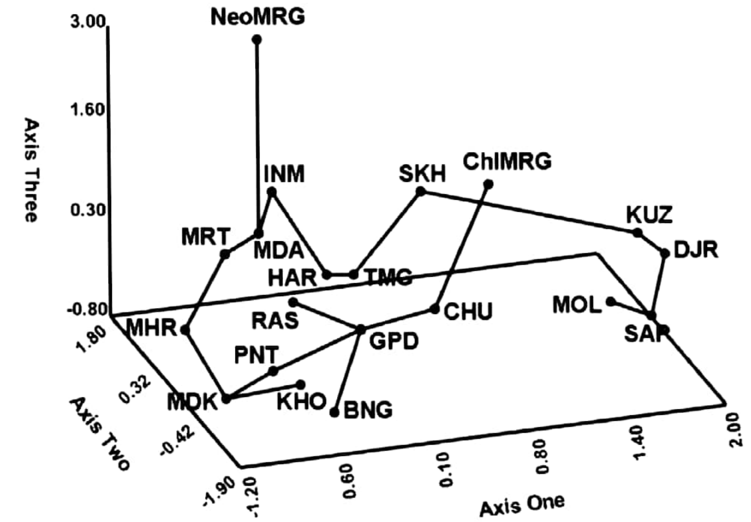



Fig 8 Principal coordinates analysis of Smith's pairwise MMD values based on 17 tooth-trait combinations (sample abbreviations from Table 1).

## Discussion

*Should Trait Consideration be Limited to "Key" Teeth?*

Some researchers opt to compare as large a battery of tooth-trait combinations as possible from within a practical framework often delimited by trait fixation, absence, or low observation counts (Coppa et al 1998; Hemphill and Lukacs 1991; Menabe et al 1992; Scuilli 1979). The rationale often expressed in such cases is that there is no *a priori* reason to assume that any specific tooth-trait combination is inherently superior than any other for identifying the pattern of phenotypic differentiation among an array of samples. In fact, such researchers (Hemphill in press b; Lukacs and Hemphill 1991) emphasize that the specific battery of traits found to be most useful for phenetic analysis will vary depending upon the array of samples included in such an analysis.

Other researchers opt to employ a selective battery of traits that use observations from key and distal teeth (Greene 1982; Haeussler et al 1989; Higa et al 2003; Irish and Turner 1990; Palomino et al

1977; Sofaer et al 1972; Turner 1985; 1987; Turner and Bird 1981). Often this is done to 'maximize' the sensitivity of the trait battery for distinguishing between samples, or to recognize that variation tends to occur more often among either the key or distal tooth within a given morphogenetic field. However, *which* traits and *which* tooth-trait combinations actually 'maximize' sensitivity for identification of phenetic differences and the patterning of such differences are likely to vary, not only with the battery of samples considered, but also within that very battery of traits. That is, while a specific tooth-trait combination may work well to distinguish between samples as a whole, it may also be the case that a particular tooth-trait combination, while not distinguishing between the majority of samples, may provide a crucial distinction between a single sample pair or a small subset of sample pairs.

Still others focus on morphological trait frequencies found on only the key tooth of a morphogenetic field (Scott and Dahlberg 1982; Scott et al 1983; Sofaer et al 1972; Turner 1976). Obviously considering but one tooth per trait eliminates the problem of bias potentially introduced by scoring the same trait on multiple members of the same morphogenetic field. Building upon the same logic behind the individual count method of Scott (1973; 1977; 1980; see also Scott and Turner 1997), in which the greatest degree of expression, regardless of side, is considered the score for that individual under the assumption that this procedure reflects the maximum genetic potential for each trait (Scott and Turner 1997; Turner 1985; Turner et al 1991), such researchers assert that trait expressions on the key teeth have a lower environment contribution to variance (Dahlberg 1945; Sofaer et al 1971; 1972). From this, some researchers assume that phenetic analyses that rely upon key teeth provide the best, or most reliable, indicators of genetic differentiation (Scott and Dahlberg 1982).

If such claims are true, that earlier developing key teeth within morphogenetic fields provide a clearer less 'muted' genetic signal than later developing key teeth, patterns in trait prevalence should demonstrate that less environmentally compromised key teeth ought to be marked by higher trait prevalence than distal teeth. Of the 17 tooth-trait combinations considered across the 20 samples in the current analysis, eight involve assessments of the same trait on both key and distal members of the same morphogenetic field. As expected, key teeth tend to be marked by higher trait prevalence than distal teeth. However, when trait prevalence within morphogenetic fields is considered by sample, not all samples exhibit the expected preponderance of trait prevalence on the key tooth. Of the eight traits scored on multiple teeth, four conform to the expectation of uniformly higher prevalence on the key tooth than on the distal tooth, while an equal number do not. Those that exhibit uniformly higher prevalence on the key tooth relative to the distal tooth across all 20 samples include hypocone development on the maxillary molars, presence of the entoconulid on the mandibular molars, as well as retention of the conservative Y-groove and hypoconulid on these same teeth. The four traits that fail to yield a uniform preponderance of trait prevalence on the key tooth are shovelling and median lingual ridge development on the maxillary incisors, presence of the metaconule on the maxillary molars, and the presence of the metaconulid on the mandibular incisors.

Shovelling prevalence is higher on the central incisor in 13 of the 20 samples **(Figs. 2a,b)**. In one sample (SKH) no shovelling was observed on either tooth. In the remaining seven samples, prevalence on the lateral incisor exceeds that found on the central incisor. All of these are prehistorically derived samples and the minimum number of observations possible for this trait range from a low of seven among the Late Bronze/Early Iron Age occupants of Timargarha to 25 among the Molali period inhabitants of Djarkutan. The surfeit of shovelling on the lateral incisor relative to the central incisor ranges from a low of 2.5% among the Late Chalcolithic inhabitants of Harappa to a high of 35.9% among the Molali period inhabitants of Djarkutan. The correlation between excess frequency of shovelling on the lateral incisor relative to the central incisor is low (r= 0.204) and insignificant (p= 0.660).

Median lingual ridge development occurs with greater prevalence on the central incisor in 16 of the 20 samples **(Figs. 2c,d)**. In the remaining four samples, prevalence is higher on the lateral incisor. Of these four samples, three are prehistorically derived samples, while the fourth is the mixed caste urban sample from Kolkata. The minimum number of observations for this trait range from 13 to 71 individuals. The excess of median lingual ridge development on the lateral incisor relative to the central incisor ranges from a low of 0.6% among the Djarkutan period inhabitants of Djarkutan to a high of 27.5% among the Kuzali period inhabitants of this same site. The correlation between excess frequency of median lingual ridge development on the lateral incisor relative to the central incisor is negative, low (r= -0.389) and insignificant (p= 0.611).

The metaconule appears along the distal margin of the first maxillary margin with greater prevalence than on the second molar in 14 of the 20 samples **(Figs. 3c,d)**. In the remaining six samples, prevalence is higher on the later developing second molar. Four are prehistorically derived samples, while three are samples of living individuals. These latter samples include the two Hindu Kush highland samples, Khowars and the Madaklasht, as well as one of the samples from west-central India, the tribal Madia Gonds from eastern Maharashtra. The minimum number of observations for this trait range from 18 to 147 individuals. The surfeit of metaconule development on the second molar relative to the first ranges from a low of 0.4% among the Molali period inhabitants of Djarkutan and the Jorwe period inhabitants of Inamgaon to a high of 8.8% among the Madaklasht. The correlation between excess frequency of median lingual ridge development on the lateral incisor relative to the central incisor is negative, low (r= -0.026) and insignificant (p= 0.956).

The metaconulid appears along the lingual surface of the first mandibular molar more often than on the second molar in all but one sample **(Figs. 5c,d)**. The sole exception is the late Bronze/early Iron Age sample from Timargarha. Two individuals were found to possess the metaconulid on the first molar and two individuals were found to possess this accessory cusp on the second molar. Because the number of observations are fewer for the second molar (n= 20) than for the first (n= 34), prevalence on the former ($M_1$= 10.0%) is slightly higher than the latter ($M_2$= 8.3%).

The majority of cases involving a reversal of the expected preponderance of trait prevalence on the key tooth relative to the distal member of the same morphogenetic field occur for archaeologically derived samples. Such samples tend to be small in number. One might be tempted to conclude that departures from the expected surfeit of trait presence on key teeth relative to distal teeth are nothing more than a statistical artefacts caused by small sample size. Two observations run counter to such a conclusion. First, samples in which trait prevalence is higher for the distal tooth rather than the key tooth are not limited to archaeologically derived samples. The best example of this in the current study is the metaconule where half of the non-conforming samples are those of living individuals. Second, a correlation analysis demonstrates that there is no strong relationship between the number of observations for a particular trait and the degree to which trait prevalence on the key tooth is surpassed by prevalence on its distal counterpart. Such results suggest departures from key tooth trait preponderance are not a inhabitants of Djarkutan. The surfeit of shovelling on the lateral incisor relative to the central incisor ranges from a low of 2.5% among the Late Chalcolithic inhabitants of Harappa to a high of 35.9% among the Molali period inhabitants of Djarkutan. The correlation between excess frequency of shovelling on the lateral incisor relative to the central incisor is low (r= 0.204) and insignificant (p= 0.660).

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Instead, such results not only run counter to a simple key tooth-distal tooth dichotomy in phenotypic expression of morphological traits, such results also suggest that these "gradients" in trait prevalence within morphogenetic fields may be as informative in and of themselves, if not more informative, than assessments of simple trait prevalence itself (Harris and Harris 2007; Hemphill in press b). Thus, 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). It is proposed here that differential prevalence of morphological traits between early developing key teeth and late developing distal teeth within the same morphogenetic field offer the same potential for reconstructing the biological histories of such populations. Consequently, trait frequencies need to be considered for both key and distal teeth found within specific morphogenetic fields.

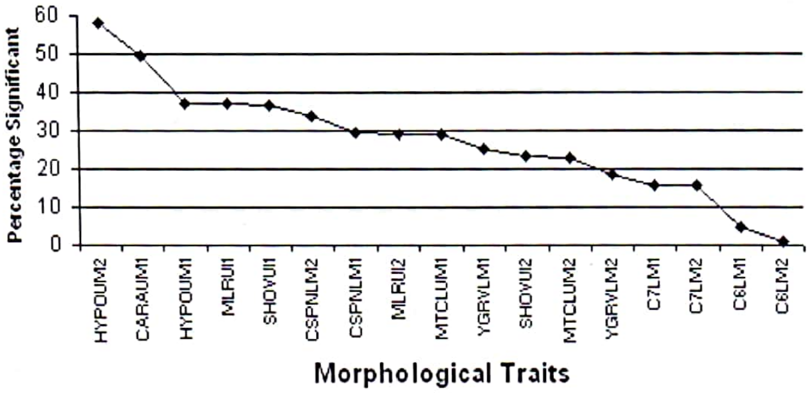


Fig 9 Utility of specific tooth-trait combinations for differentiating between samples based on the number of significant differences between sample pairs.

*Which Tooth-Trait Combinations are Most Useful for Distinguishing between Samples?*

It is well-known that some tooth-trait combinations vary more and some vary less across samples (see Scott and Turner 1997). It is also the case that which particular traits are most variable among samples depends upon the set of samples considered in a specific comparative analysis (Hemphill in press b). The two-step trait selection process advocated by Irish (2010) and by Harris (2008; Harris and Sjovøld 2004) resulted in elimination of 54 tooth-trait combinations. The remaining battery of 17 tooth-trait combinations, nine maxillary and eight mandibular, was retained for comparative purposes.

Chi-square analysis between sample pairs was used to determine the significance of variation in these tooth-trait combinations. A total of 190 pairwise comparisons were possible for each tooth-trait combination. Tooth-trait combinations found to be significantly different are listed in Table 4 by pairwise contrast. **Figure 9** provides an illustration of the percentage of pairwise contrasts that differ significantly for each of the 17 traits, with the tooth-trait combination marked by the greatest proportion of significant differences on the left and the trait with lowest proportion of significant differences on the right.

The number of significant differences ranges from a high of 110 pairwise contrasts (58%) for hypocone development on UM2 to a low of two for the entoconulid on LM2 (1.1%). Other traits providing high levels of differentiation among sample pairs include Carabelli's trait on UM1 (94 contrasts: 49.5%), hypocone development on UM1 (71 contrasts: 37.4%), median lingual ridge development on UI1 (71 contrasts: 37.4%), shovelling on UI1 (70 contrasts: 36.8%), and retention of the hypoconulid on LM2 (64 contrasts: 33.7%). Traits providing lesser differentiation among samples include retention of the hypoconulid on LM1 (56 contrasts: 29.5%), median lingual ridge development on UI2 (55 contrasts: 28.9%), presence of the metaconule on UM1 (55 contrasts: 28.9%), retention of the Y-groove on LM1 (48 contrasts: 25.3%), shovelling on UI2 (44 contrasts: 23.2%), and presence of the metaconule on UM2 (43 contrasts: 22.6%). Traits providing rather poor overall differentiation among samples include retention of the Y-groove on LM2 (35 contrasts: 18.4%), presence of the metaconule on LM1 (30 contrasts: 15.8%) and LM2 (30 contrasts: 15.8%), and the presence of the entoconulid on LM1 (9 contrasts: 4.7%).

When considered by position within specific morphogenetic fields, it is clear the majority of traits in which both the key and distal members of a field are contrasted between sample pairs that key teeth are marked by a greater number of significant differences. There are only two exceptions, retention of a fully developed hypocone on UM2 and retention of the hypoconulid on LM2. The former represents the single tooth-trait combination marked by the greatest number of significant differences across the 20 samples considered in this analysis, while the latter ranks sixth. Those traits in which the key tooth is found to be marked by more significant differences than the distal tooth range from those marked by high numbers of significant differences (median lingual ridge development on UI1 [4th], shovelling on UI1 [5th]) to those marked by the fewest such differences (metaconulid on LM1 [14th], entoconulid on LM1 [16th]). When considered by average rank order, although there are more tooth-trait combinations in which the key tooth differs significantly in a greater number of samples, their average rank score (9.67) indicates that key tooth dominated contrasts tend to occur among traits that distinguish among samples to a lesser degree than those tooth-trait combinations in which significant differences among distal teeth outnumber those on the key tooth (3.5). Such findings provide further evidence that trait frequencies need to be considered for both key and distal teeth found within specific morphogenetic fields.

The battery of tooth-trait combinations considered in this comparative analysis included nine traits found among maxillary teeth and eight traits found among mandibular teeth. When considered by rank order by the number of significant differences between sample pairs it is clear that maxillary traits provide a greater ability to distinguish among samples than traits found on the mandibular teeth. Maxillary traits account for the top five tooth trait combinations, and of the top ten all but three (cusp number on LM1 and LM2, Y-groove on LM1) are maxillary. Conversely, the five traits that differ least among samples are all mandibular and of the bottom eight tooth-trait combinations all but two (shovelling on UI2, metaconule on UM2) are mandibular. Not surprisingly, a contrast of average rank score shows maxillary traits to have a much higher value (6.11) than mandibular traits (12.25). Such findings indicate that among these prehistoric and living samples from Central and South Asia, morphological traits found among maxillary teeth provide greater phenetic separations between samples than mandibular traits.

Results are less marked when trait sensitivity is considered between anterior and posterior teeth. This may be partly due to the fact that far fewer traits (four) found on the anterior teeth were considered relative to the posterior teeth (13 traits). The top three traits are all found among the posterior teeth (full hypocone development on UM1 and UM2, Carabelli's trait on UM1) as are the traits with the six lowest number of significant differences among samples (metaconule on UM2, Y-groove on LM2, entoconulid on LM1 and LM2, metaconulid on LM1 and LM2). Overall, average rank scores indicate that morphological traits found on the anterior teeth (7.0) only slightly outperform traits found in the posterior teeth (9.6). This finding is important, given that due to post-depositional factors archaeological derived samples are often characterized by an underrepresentation of anterior teeth, for such results indicate that no marked bias is introduced when prehistoric samples are considered alongside samples obtained from populations of living ethnic groups.

*Do the Samples Reflect Regional Structure?*

An issue of equally great importance as trait selection in biological distance analyses concerns the impact of geographic propinquity upon gene flow between populations. An array of genetic studies suggest the Indian subcontinent served as a major corridor for dispersal of early modern humans out of Africa into East Asia, Southeast Asia and beyond (Barnabas et al 2006; Basu et al 2003; Chaubey et al 2007; Kivisild et al 2003; Templeton 2002). Some of these studies also suggest that the population history of the myriad ethnic groups of South Asia was the product of initial colonization in the Pleistocene followed by long-standing *in situ* continuity of local populations (Kivisild et al 2003; Metspalu et al 2004; S. Roychoudhury et al 2000; Sengupta et al 2006). Further, other proponents of what may be termed the Long-Standing Continuity Model (LSCM) maintain that the Hindu Kush and Himalayan Mountains served as effective barriers that discouraged any subsequent and significant introduction of new genes into the subcontinent (Sahoo et al 2006; but see Krithika et al 2009). Noting that the majority of Indian haplogroups reflect 10,000 – 15,000 years of isolation, some LCSM proponents assert these ages attest to the antiquity of regional differentiation, thereby ruling out any major migratory events *within* the subcontinent since the end of the Pleistocene (Kennedy et al 1984). Consequently, patterning of biological affinities may be a reflection of simple isolation-by-distance (Ayala 1982; Epperson 1993; Falconer 1981; Hartl and Clark 1997; Hedrick 2000; Manel et al 1993; Sokal and Wartenburg 1983), in which, due to the constraints of travel, marital partners should be preferentially recruited nearby. Hence, with the passage of time, populations closest temporally and geographically should be most similar biologically.

Analysis of the 17 tooth-trait combinations across the 20 samples considered in this analysis **(Figs. 2-5)** yield a consistent pattern in which samples that come from the same geographic region tend to exhibit greater similarities in trait prevalence than those that belong to different regions (see also Hemphill in press b). This pattern holds true for a regional aggregate composed of archaeologically derived individuals of different temporal contexts from Central Asia, for an aggregate composed solely of living individuals (southeast India), as well as an aggregate composed of both prehistoric and living individuals (west-central India). There is, however, one glaring exception in which there is a repetitive pattern of greater intraregional variation that results in some samples being identified by the multivariate data reduction techniques as possessing closer affinities to samples from other geographic regions **(Figs. 6-8)**. This anomalous region is composed of the samples of prehistoric individuals from the Indus Valley.

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Morphological traits of the permanent maxillary teeth among the prehistoric occupants of the Indus Valley exhibit a considerable range of variation between samples. Shovelling prevalence is all across the board **(Figs. 2a,b)**. The level of intraregional variation across the prehistoric samples from the Indus Valley is four to eight times and four and a half to ten times higher than that observed across samples of the other geographic regions for the central and lateral incisor, respectively. Prevalence is highest for the two temporally distinct samples from Mehrgarh, yet while the earlier Neolithic sample is like peninsular Indian samples with higher prevalence on the central than on the lateral incisor, this pattern is reversed for the later Early Chalcolithic inhabitants of this site. Frequencies are distinctly lower among the Late Chalcolithic inhabitants of Harappa and Late Bronze/Early Iron Age inhabitants of Timargarha, but in both samples relative frequencies between the central and lateral incisor are like those of the Early Chalcolithic sample from Mehrgarh. The latest prehistoric sample from Sarai Khola is devoid of shovelling on both central and lateral incisors. Given such heterogeneity in shovelling prevalence by tooth, it is no surprise that prehistoric Indus Valley are also unique in expressing markedly different gradients in shovelling presence across the two maxillary incisors, with one (NeoMRG) exhibiting a preponderance of expression on the central incisor, three exhibiting equivalent frequencies on the two incisors (ChlMRG, TMG, SKH), and another featuring higher prevalence on the lateral incisor relative to the central incisor (HAR).

A broadly similar pattern is observed for median lingual ridge development **(Figs. 2c,d)**. Prehistoric inhabitants of the Indus Valley express the greatest internal variation for ridge development on both the central and lateral incisor. Further, these samples are also marked by a temporal trend of increasing parity in median lingual ridge frequencies across the two maxillary incisors from the Neolithic through the Late Chalcolithic, which is then followed by a complete absence of this trait on the lateral incisor in the two post-Chalcolithic samples.

A different pattern emerges with retention of fully developed hypocones **(Figs. 3a,b)**. Full retention on the firstmaxillary molar occurs universally among the two Chalcolithic period samples (ChlMRG, HAR), while retention rates on the first molar among the remaining samples are among the lowest of the 20 samples considered. On the secondmaxillary molar, retention of a fully developed hypocone occurs with one of the highest frequencies among the Early Chalcolithic inhabitants of Mehrgarh, but retention occurs at relatively moderate to low frequencies in all other samples. Carabelli's trait on the first maxillary molar **(Fig. 3c)** occurs at frequencies that range from relatively high (ChlMRG) to moderate (HAR, TMG), to low (NeoMRG, SKH). Prevalence of the metaconule **(Figs. 3c,d)** is not only variable among samples of prehistoric occupants of the Indus Valley, but exhibits different temporal trends on the first maxillary molar than on the second. On the first molar, metaconule prevalence ranges from relatively moderate to high, increasing from the Neolithic sample from Mehrgarh to the Chalcolithic sample from this same site, reaching a peak prevalence among the Late Chalcolithic inhabitants of Harappa, dropping markedly among the Late Bronze/Early Iron Age inhabitants of Timargarha, only to rebound to second highest frequencies among all samples in the Iron Age sample from Sarai Khola. By contrast, metaconule prevalence on the second molar is marked by a temporally progressive decline from the Neolithic through the Iron Age, with one exception. Timargarha, in which there is no expression of the metaconule on any second molars.

Samples of the prehistoric occupants of the Indus Valley also exhibit considerable heterogeneity in the prevalence of Y-groove retention on the first and second mandibular molars **(Figs. 4a,b)**. Retention rates on the first molar are moderate among the Late Chalcolithic inhabitants of Harappa and the Neolithic inhabitants of Mehrgarh, respectively. By contrast, retention on first molars of the three remaining samples occurs at the lowest relative frequencies of all comparative samples, except for the Kuzali period inhabitants of Djarkutan. Retention rates on the second molar follow a completely different pattern. Ranging from relatively high (SKH) to moderate (NeoMRG, ChlMRG) to low (HAR, TMG), there is no consistent temporal trend across samples. Indus Valley samples stand apart from samples of other geographic regions by exhibiting the greatest relative decline in hypoconulid retention prevalence from the first to the secondmandibular molar **(Figs. 4c,d)**. Apart from the early Chalcolithic occupants of Mehrgarh, who stand apart from all other samples with the highest relative prevalence of the entoconulid on both first and second molars **(Figs. 5a,b)**, and the Late Chalcolithic/Early Iron Age occupants of Timargarha, where the entoconulid is completely absent on the first molar but shows up with second highest relative presence on the second, entoconulid prevalence among the remaining Indus Valley samples are marked by moderate frequencies on the first molar accompanied by complete absence on the second. Prehistoric inhabitants of the Indus Valley stand apart from samples of all other regions in possessing dentitions marked by moderate frequencies of the metaconulid on the firstmandibular molar **(Fig. 5c)**, coupled with complete absence of this cusp on the second molar **(Fig. 5d)**.

Multivariate assessment of morphological trait expression with neighbour-joining cluster analysis confirms the unique heterogeneity of prehistoric Indus Valley samples. While the Late Chalcolithic sample from Harappa and the Late Bronze/Early Iron Age sample from Timargarha are shown to have rather close affinities, affinities to the latest of the Indus Valley samples, Sarai Khola is more distant. In fact, the sample from Sarai Khola is identified by neighbour-joining cluster analysis as possessing nearly equal affinities to the latest prehistoric sample from Central Asia, Molali phase inhabitants of Djarkutan, as to the temporally proximate Indus Valley sample from Timargarha. The two temporally distinct samples from Mehrgarh are identified as possessing no affinities, either to one another, or to the other three samples from the Indus Valley. Instead, the Neolithic inhabitants of Mehrgarh are identified as a phenetic outlier to the samples from west-central India, while the later Early Chalcolithic sample from this site is identified as possessing closer affinities to the living ethnic groups from southeast India.

This heterogeneity in phenetic affinities among the prehistoric samples from the Indus Valley is corroborated by multidimensional scaling **(Fig. 7)**. The samples from Harappa and Timargarha, located in the lower right of the array, exhibit close affinities to one another. The Early Iron Age sample from Sarai Khola occupies an isolated position in the centre of the array midway between the samples from Harappa and Timargarha on the one hand, and the Central Asian samples on the other. The Neolithic inhabitants of Mehrgarh exhibit closest affinities to west-central Indians, while the Early Chalcolithic sample from Mehrgarh, found in the upper centre, stands out as an isolate with no close affinities to any of the other samples.

Principal coordinates analysis **(Fig. 8)** adds additional emphasis to the observations drawn from the three-dimensional plot yielded by multidimensional scaling. That is, the phenetic proximity of

Harappa and Timargarha is confirmed, as is the unique phenetic isolation of the Early Chalcolithic sample from Mehrgarh. Intriguingly, while the minimum spanning tree identifies that this phenetically isolated sample has closest affinities to tribal Chenchus, it may be observed that the Late Chalcolithic inhabitants of Mehrgarh are nearly equally separated in phenetic space from the latest of the Central Asian samples, Molali period inhabitants of Djarkutan. It is with regard to the phenetic affinities possessed by the Neolithic inhabitants of Mehrgarh that principal coordinates analysis yields additional insight. This sample, while identified as possessing closest affinities to samples from west-central peninsular India, actually stands out as an isolate in phenetic space with no close affinities to any of the other samples.

When dental traits among prehistoric inhabitants of the Indus Valley are considered from both univariate and multivariate perspectives it is clear that these samples are not drawn from a single regional population. Instead, the consistently high level of intraregional variation in trait prevalence, the heterogeneity in trait gradients across multiple teeth within the same morphogenetic field, and the lack of phenetic cohesiveness, coupled with the tendency of some samples to be identified as possessing affinities to members of other regional aggregates or as outliers in phenetic space suggest these samples are drawn from several populations with different genetic profiles. A total of fivepopulations appear to be represented. The first is represented by the Neolithic sample from Mehrgarh, which is identified as a population isolate or as possessing distant affinities to west-central Indians. The second is represented by the Early Chalcolithic sample from Mehrgarh, which appears to be a population isolate relative to all of the other samples considered in this analysis. The fourth is represented by the Late Chalcolithic sample from Harappa and the Late Bronze/Early Iron Age sample from Timargarha, which exhibit affinities to one another. The fifth is represented by the Iron Age sample from Sarai Khola. This may be a population descended from that represented by Harappa and Timargarha, but one thathas experienced substantial gene flow from another population.

When considered against current models for the population of history of South Asia as a whole and Pakistan in particular, it may be that the Neolithic sample from Mehrgarh is representative of the original population of *Homo sapiens* that dispersed out of Africa during the Middle Pleistocene (Kivisild et al 1999 a,b; 2003; McElreavy and Quintana-Murci 2005; Passarino et al 1996; Sahoo et al 2006) and which appears to be represented by an underlying structure found within the gene pool found in the Indian subcontinent today (Metspalu et al 2011; Reich et al 2009; see also Hemphill in press b).

The situation for the later Early Chalcolithic sample from Mehrgarh is more complex. This study fails to find the close phenetic affinity between this sample and the later Chalcolithic sample from Harappa identified in previous studies (Hemphill 2009; Hemphill et al 1991; 1997; 1998; Lukacs and Hemphill 1991; Lukacs et al 1998). Instead, the Early Chalcolithic sample appears to be a phenetic isolate that, contrary to models that call for a dispersal of proto-Elamo-Dravidian-speakers from southwestern Iran through the Indus Valley to peninsular India (see McAlpin 1974; 1981; Quintana-Murci et al 2001), exhibit no consistently close phenetic affinities to living Dravidian-speaking populations of southeast India (McElreavey and Quintana-Murci 2005; Metspalu et al 2004; Sengupta et al 2006).

The consistent finding with regard to phenetic affinities among prehistoric Indus Valley samples is the close affinities between the Late Chalcolithic sample from Harappa and the Late Bronze/Early Iron Age sample from Timargarha. Such a finding runs directly counter to models that call for the introduction of Indo-Aryan languages into the subcontinent during the mid-2nd millennium BC (Erdosy 1995; Hiebert 1994; 1998; Hiebert and Lamberg-Karlovsky 1999; Kuzmina 1998; Parpola 1995). Although recent genetic studies have identified Y-chromosome variants that have been attributed to Central Asians in peninsular Indian populations (Bamshad et al 2001; Mukherjee et al 2001; Roychoudhury et al 2000; Thanseem et al 2006; Wells et al 2001), the results of this study suggest that any such entry of Central Asian genes, if it even occurred at all (seeSahoo et al 2006; Sharma et al 2006), must have occurred no earlier that the late first millennium BC and is reflected by the mild rapprochement between the latest of the Indus Valley prehistoric samples, Sarai Khola, and the latest of the Central Asian samples, the Molali period occupants of the BMAC urban centre of Djarkutan.

*Are There Consistent Regional Differences among Samples?*

HINDU KUSH HIGHLANDERS

Beginning with the maxillary teeth, Hindu Kush highland samples express moderate levels of shovelling on both central and lateral incisors, with frequencies somewhat higher for the Madaklasht than for Khowars **(Figs. 2a,b)**. A similar pattern occurs for median lingual ridge development **(Figs. 2c,d)** and for retention of fully developed hypocones on the first and second maxillary molars **(Figs. 3a,b)**. Hindu Kush highlanders are marked by some of the highest prevalence for Carabelli's trait and in a reversal of shovelling, medial lingual ridge development and retention of fully developed hypocones, it is the Madaklasht, rather than the Khowar, who have higher prevalence of Carabelli's trait. Hindu Kush highlanders stand apart from samples from the other three regions by possessing maxillary molars in which the metaconule is found at moderate to low frequencies on both first and second molars.

Turning to traits assessed among mandibular teeth, Hindu Kush highlanders, with rather moderate relative prevalence compared to samples from other geographic regions, do not stand out as remarkable. However, when expression of the Y-groove is compared between the Madaklasht and the Khowar there are marked differences (see below). Khowars are marked by high prevalence of Y-groove retention, both in relation to all other samples, and especially in respect to the Madaklasht. However, this high prevalence of Y-groove retention on the first molar among Khowars is coupled one of the lowest frequencies of retention of this trait on the second molar. By contrast, the Madaklasht, while expressing only moderate prevalence of Y-groove retention on the first molar, retain this trait on the second molar at one of the higher frequencies. Hindu Kush highlanders stand apart from members of other regional aggregates by possessing mandibular molars that are marked by moderate to high levels of hypoconulid retention on the first molar, coupled with moderate frequency of retention on the second molar. Hindu Kush highlanders have relatively low prevalence of the entoconulid on the first molar. Prevalence is much lower on the secondmolar among the Madaklasht and entoconulids are completely absent among Khowars. Hindu Kush highlanders express the metaconulid with greater prevalence on the first molar than on the second, and in both cases prevalence is higher among Khowars than among the Madaklasht.

When Hindu Kush highlanders are contrasted with prehistoric Central Asians, the tooth-trait combinations with the greatest number of significant differences between samples of these two regions are exclusively maxillary and include median lingual ridge development on the central incisor, Carabelli's trait on the first molar, and retention of fully developed hypocones on the second molar. From **Figure 10a**, it may be seen that Hindu Kush samples stand apart from prehistoric Central Asians by possessing relatively high frequencies of median lingual ridge development on UI1 (60.6% - 70.2%) and Carabelli's trait on UM1 (52.1% - 66.9%) coupled with low relative frequencies for full development of the hypocone on UM2 (10.0% - 24.6%). Prehistoric Central Asians exhibit the exact opposite pattern; that is, relatively low prevalence of median lingual ridge development on UI1 (15.4% - 39.1%) and retention of a fully developed hypocone on UM2 (50.0% - 71.9%), coupled with relatively high prevalence for Carabelli's trait on UM1 (10.0 – 36.1%).

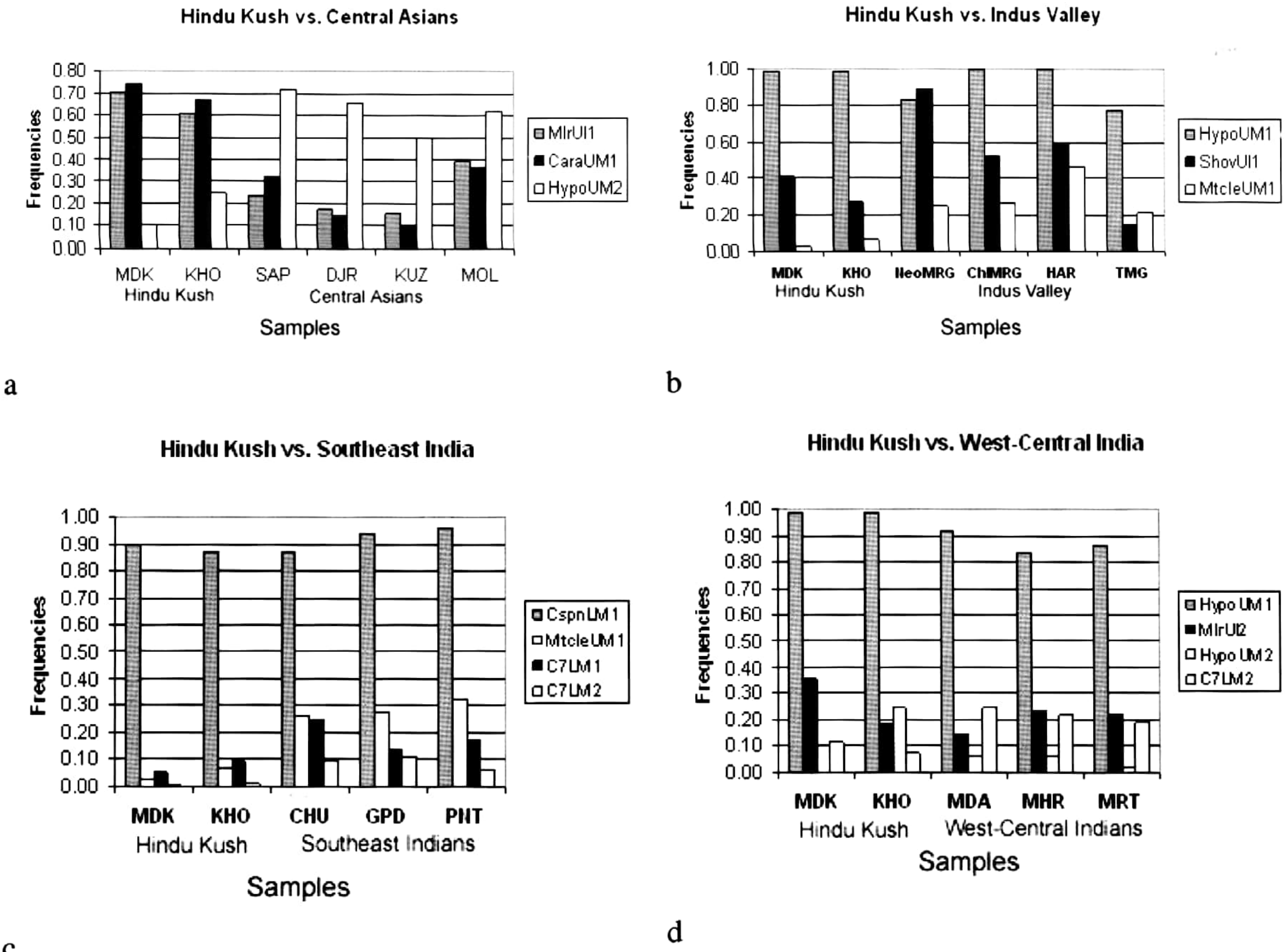


Fig 10 Contrasts of tooth-trait combinations with the highest number of significant differences detected by chi-square analysis between Hindu Kush highlanders and members of other geographic regions. Sample abbreviations and geographic region assignment from Table 1.a.) Hindu Kush vs. Central Asians, b.) Hindu Kush vs. Indus Valley, c.) Hindu Kush vs. Southeast Indians, d.) Hindu Kush vs. West-Central Indians.

When Hindu Kush highlanders are compared to prehistoric inhabitants of the Indus Valley, the tooth-trait combinations with the greatest number of significant differences between samples of these two regions are again exclusively maxillary and include shovelling on the central incisor, retention of a full hypocone on the first molar, and the presence of the metaconule on this same tooth. From **Figure-10b**, Hindu Kush samples stand apart from prehistoric Indus Valley samples by possessing uniformly high frequencies of fully developed hypocones on the first molar (98.3% – 98.5%), whereas samples from the Indus Valley vary from a high of universal retention among the Chalcolithic inhabitants of Mehrgarh and Harappa to a low of 77.3% among the late Bronze/Early Iron Age inhabitants of

Timargarha. Hindu Kush highlanders possess maxillary central incisors that have a relatively moderate prevalence of shovelling (27.0% - 40.8%). In marked contrast, prehistoric inhabitants of the Indus Valley are either marked by relatively high prevalence of shovelling on UI1 (52.0 – 89.3%), very low prevalence (14.3%), or no shovelling at all (SKH). Finally, Hindu Kush highlanders are marked by relatively low prevalence for the metaconule on UM1 (2.8% - 6.8%), while all of the prehistoric Indus Valley samples possess this accessory cusp with greater frequency (21.1% - 46.2%). **Figure 10b** also illustrates the marked intraregional variation found among the prehistoric Indus Valley samples described in greater detail in the results section above. Three different patterns may be identified by the three tooth-trait combinations that serve to distinguish them from Hindu Kush highlanders. The earliest sample from aceramic Neolithic levels at Mehrgarh stands out as unique by coupling a fair amount of hypocone reduction on UM1 with the highest prevalence of shovelling on UI1 found among Indus Valley samples. By contrast, the Early Chalcolithic sample from Mehrgarh and the Late Chalcolithic sample from Harappa are both marked by high prevalence of full hypocone development coupled with relatively moderate prevalence of shovelling on UI1. The two most recent samples from Timargarha and Sarai Khola express a third variation in which their dentitions couple a fair amount of hypocone reduction on UM1 with little to no expression of shovelling on UI1.

When Hindu Kush highlanders are contrasted with the three samples of living ethnic groups from southeast India, the tooth-trait combinations with the greatest number of significant differences between samples of these two regions are dominated by traits occurring among the mandibular teeth. The four most distinguishing include retention of the hypoconulid on LM1 (CSPNLM1), presence of the metaconule on UM1, and the presence of the metaconule on both LM1 and LM2. From **Figure 10c**, it may be seen that Hindu Kush samples stand apart from the southeast Indian samples by possessing all four traits at lower frequencies. Differences in relative prevalence between members of these two regions are greatest for the presence of the metaconulid on LM2 (Hindu Kush avg.= 0.9%; Southeast India avg.= 8.8%), followed closely by the presence of the metaconule on UM1 (Hindu Kush avg.= 4.8%; Southeast India avg.= 28.5%), with differences in retention of the hypoconulid on LM1 being by far the least distinctive (Hindu Kush avg.= 88.3%; Southeast India avg.= 97.4%).

In marked contrast to the comparison with ethnic groups from southeast India, when Hindu Kush highlanders are compared to prehistoric and living samples from west-central India, the tooth-trait combinations with the greatest number of significant differences between samples of these two regions are dominated by maxillary traits. These include retention of a fully developed hypocone on UM1 and UM2, development of the median lingual ridge on UI1, and the presence of the metaconulid on LM2. From **Figure 10d**, Hindu Kush samples stand apart from west-central Indian samples by possessing uniformly high frequencies of fully developed hypocones on UM1 (98.3% – 98.5%), whereas samples from west-central India, with one notable exception (RAS, see below), have greater prevalence of hypocone reduction, especially among the prehistoric inhabitants of Inamgaon (34.1%). The opposite pattern is observed for the presence of the metaconule on UM2, for frequencies are higher among west-central Indian samples (15.0% - 24.6%) than among the two Hindu Kush samples (7.8% - 11.6%). The remaining tooth-trait combinations are marked by a pattern in which only one of the Hindu Kush samples stand apart as distinctive from west-central Indians, while the other does not. For retention of a fully developed hypocone on UM2, the inhabitants of Madaklasht, like their counterparts from west-

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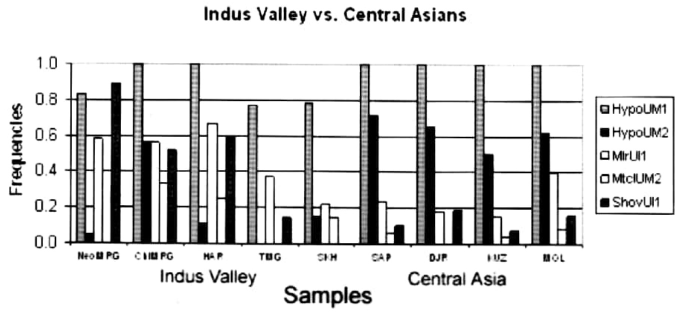


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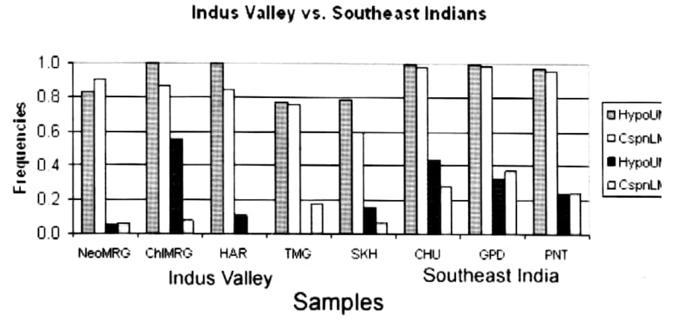


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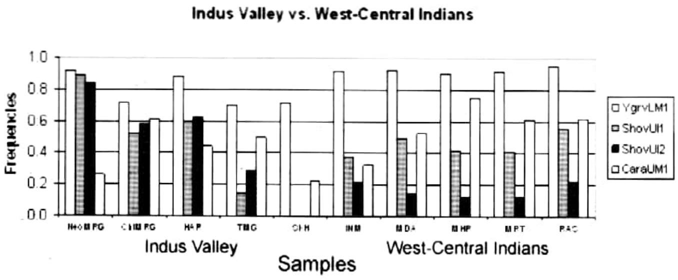



c

Fig 11 Contrasts of tooth-trait combinations wi the highest number of significant differenc detected by chi-square analysis betwe prehistoric inhabitants of the Indus Vall and members of other geographic regior Sample abbreviations and geographic regi assignment from Table 1. a.) Indus Vall vs. Central Asians, b.) Indus Valley v Southeast Indians, c.) Indus Valley vs. We Central Indians

## PREHISTORIC INDUS VALLEY INHABITANTS

When the dentitions of prehistoric inhabitants of the Indus Valley are contrasted with those possessed prehistoric Central Asians, the five tooth-trait combinations with the greatest number of significa differences between these samples are all found on the maxillary teeth. These traits include shovelli and median lingual ridge development on UI1, retention of a fully developed hypocone on UM1 a UM2, as well as the presence of the metaconule on UM2. From **Figure 11a**, prehistoric inhabitants the Indus Valley are distinguished from their prehistoric counterparts in Central Asia by possessi maxillary first and second molars that retain fully developed hypocones with greater prevalence, but t patterning for the two teeth differs. For UM1, retention of a fully developed hypocone occurs wi lowest prevalence in the earliest (NeoMRG: 83.3%) and two most recent samples (TMG: 77.3%; SK 78.6%), while fully developed hypocones occur universally among individuals of the two Chalcolith era samples (ChlMRG, HAR). By contrast, retention of a fully developed hypocone occurs universal among all Central Asian samples. For UM2, with one notable exception (ChlMRG: 55.6%), occurren of a fully developed hypocone among prehistoric inhabitants of the Indus Valley occurs rare (NeoMRG: 4.9%; HAR: 11.1%) or not at all. By contrast, prehistoric Central Asians retain a fu developed hypocone on UM2 far more often (50.0% - 71.9%). The occurrence of shovelling and medi lingual ridge development on UI1, as well as the presence of the metaconule on UM2, follows generally opposite pattern. That is, prevalence is higher for each of these traits among Neolithic and Chalcolithic inhabitants of the Indus Valley (SHOVUI1: 52.0% - 89.3%; MLRUI1: 56.0% - 66.7%; MTCLUM1: 25% - 40%) than among their counterparts from Central Asia (SHOVUI1: 0% - 18.8%; MLRUI1: 15.4% - 39.1%; MTCLUM1: 0% - 8.1%), while frequencies among post-Chalcolithic Indus Valley samples (SHOVUI1: 0% - 14.3%; MLRUI1: 23.5% - 37.5%; MTCLUM1: 0% – 5.9%) are quite similar to those observed among Central Asians. Running counter to the claims of Kennedy and coworkers (1984), such results suggest that the biological history of the Indus Valley is not one of uninterrupted continuity. Instead, post-Chalcolithic samples are marked by trait frequencies more like those seen among prehistoric Central Asians. Though some might interpret such shifts in trait prevalence as indicative of a model that calls for an invasion of Central Asian populations into the Indus Valley during the mid-2ndmillennium BC (Erdosy 1995; Kuzmina 1998; Parpola 1995), these shifts are neither of sufficient comprehensiveness nor completeness to signal significant gene flow into Indus Valley populations from Central Asia (see also Hemphill in press b).

When the dentitions of prehistoric inhabitants of the Indus Valley are contrasted to those possessed by members of living ethnic groups of southeast India, the four tooth-trait combinations with the greatest number of significant differences between these samples derive equally from maxillary and mandibular teeth. Focused solely on the prevalence of conservative retentions, samples from these two regions differ in the extent to which the maxillary molars retain fully developed hypocones and their mandibular molars retain the hypoconulid. From **Figure 11b**, prehistoric inhabitants of the Indus Valley are distinguished from southeast Indians, who are characterised by near universal retention of a fully developed hypocone on UM1 (97.3% - 99.5%), by possessing maxillary first molars that exhibit varying frequencies of hypocone reduction. As noted in the contrast with prehistoric Central Asians, while universal retention is observed among Chalcolithic era inhabitants of the Indus Valley (ChlMRG, HAR), this is not the case for the populations that precede (NeoMRG: 83.3%) and ante-date them (TMG: 77.3%, SKH: 78.6%). A similar pattern is observed for UM2. Overall, with one notable exception (ChlMRG: 55.6%), prehistoric inhabitants of the Indus Valley possess dentitions in which retention of a fully developed hypocone occurs with far lower prevalence (0% - 11.1%) than observed among members of living ethnic groups of southeast India (23.5% - 42.8%). Turning to the mandibular teeth, the hypoconulid is nearly universally retained among southeast Indians on LM1 (95.6% - 98.8%), but among prehistoric inhabitants of the Indus Valley hypoconulid retention occurs with lower prevalence (60.0% - 90.7%) and the disparity between samples of the two regions increases from the earliest to the latest prehistoric sample. Retention of the hypoconulid occurs with less frequency on LM2 among samples from both regions, but in all cases the prevalence of hypoconulid retention is higher among living southeast Indians (23.9% - 37.2%) than among prehistoric individuals recovered from the Indus Valley (0% - 17.6%).

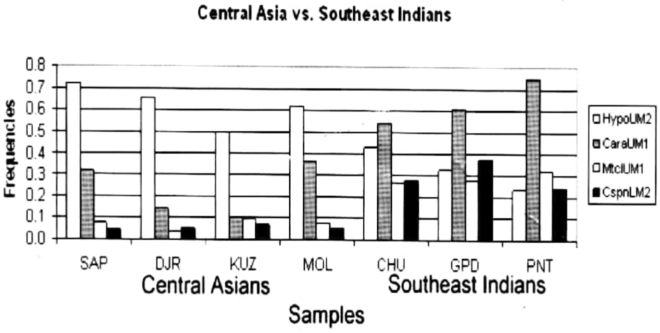
When the dentitions of prehistoric individuals from the Indus Valley are compared to those of prehistoric and living individuals from west-central India, the four tooth-trait combinations with the greatest number of significant differences between these samples mostly derive from the maxillary teeth. These traits include shovelling on UI1 and UI2, Carabelli's trait on UM1, and retention of the conservative Y-groove on LM1. From **Figure 11c**, shovelling occurs with greater overall prevalence among the prehistoric Indus Valley samples than among inhabitants of west-central India. This is true for both the central and the lateral incisor. However, with regard to the former, shovelling prevalen declines precipitously over time, such that the two latest samples are marked by low (TMG: 14.3%) complete absence of shovelling (SKH). A broadly similar pattern occurs for the lateral incisor, except this case prevalence in the sample from Timargarha (28.6%) remains higher than that seen among any the samples from west-central India (12.2% - 22.4%). In contrast to shovelling, retention of t conservative Y-groove occurs with lesser prevalence (70.6% - 92.0%) among prehistoric Indus Vall samples than among the west-central Indian samples (90.6% - 97.4%). Unlike shovelling, frequencies Y-groove retention exhibit a discernible trend over time. Prevalence of Carabelli's trait on UM1 similar between the two regions. However, among the prehistoric samples from the Indus Valle Carabelli's trait prevalence is lowest in the earliest (NeoMRG: 25.9%) and latest samples (SKH: 22.2% lower that that seen among both living and prehistoric inhabitants of west-central India (32.5% - 74.9%

PREHISTORIC CENTRAL ASIANS

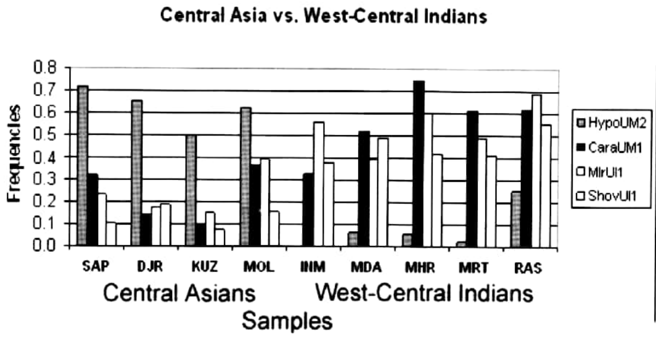
Starting once again with the maxillary dentition, prehistoric Central Asians stand apart from members the other three regional aggregates by having maxillary incisors that feature relatively low prevalence shovelling on the central incisor, coupled with higher prevalence on the lateral incisor **(Figs. 2a,b)**. similar patterning is found for median lingual ridge development **(Figs. 2c,d)**. Prehistoric Central Asia are also distinctive in possessing maxillary molars that are marked by no reduction of the hypocone the first molar, coupled with the relatively lowest prevalence for reduction on the second molar **(Fi 3a,b)**. By contrast, Central Asians possess first molars with some of the lowest prevalence of Carabell trait, coupled with first and second molars with low prevalence of the metaconule **(Figs. 3c-e)**.

Prehistoric Central Asians, like prehistoric inhabitants of the Indus Valley, possess mandibu molars that exhibit great variability from sample to sample in the frequency of Y-groove retention. T two earliest samples are marked by high (DJR) to moderate (SAP) prevalence of the Y-groove on t first molar **(Fig. 4a)**, while the two later samples (KUZ, MOL) are marked by some of the low frequencies for the Y-groove. This pattern is nearly reversed on second molars **(Fig. 4b)**. Now it is t earliest and latest samples that are marked by relatively low prevalence, while temporally intermedi samples (DJR, KUZ) have some of the highest frequencies for retention of the Y-groove. Prehisto Central Asians stand apart from all other samples, except the two prehistoric samples from Mehrga being marked by relatively high under-retention of the hypoconulid on the second molar. Prehisto Central Asians stand apart from other samples by possessing mandibular molars that express t entoconulid with comparable frequencies to peninsular Indians on the first molar **(Fig. 5a)**, but completely devoid of expression on the second molar **(Fig. 5b)**. Likewise, prehistoric Central As stand apart from samples of other geographic regions by possessing mandibular molars that tend express the metaconulid at low frequencies on both first and second molars **(Figs. 5c,d)**.

When the dentitions of prehistoric Central Asians are contrasted with those possessed by three samples of living ethnic groups from southeast India, the tooth-trait combinations with the great number of significant differences between samples of these two regions are dominated by tra occurring among the maxillary teeth. The four most distinguishing combinations include retention of hypocone on UM2, presence of Carabelli's trait and the metaconule on UM1, and retention of hypoconulid on LM2 (CSPNLM2). From **Figure 12a**, prehistoric Central Asians stand apart fr southeast Indians by possessing maxillary second molars that retain fully developed hypocones w greater prevalence (Central Asia: 50.0% - 71.9%; southeast India: 23.5% - 62.2%), but whose maxill first molars have markedly lower prevalence of both Carabelli's trait (Central Asia: 10.0% - 36.1%; southeast India: (54.4% - 74.7%) and the metaconule (Central Asia: 3.4% - 9.5%; southeast India: 26.2% - 31.9%). In contrast to retention of fully developed hypocones on UM2, retention of the hypoconulid on its isomere (LM2) occurs with far lower prevalence among Central Asians (4.9% - 7.1%) relative to their counterparts from southeast India (23.9% - 37.2%). With respect to these four tooth-trait combinations, it is clear that differences are greatest between the earliest of the prehistoric samples from Central Asia, Sapalli tepe, and high-status Pakanati Reddis, while similarities are closest between the latest of the Central Asian samples, Molali period occupants of Djarkutan, and the tribal Chenchus of central Andhra Pradesh. This patterning of similarities and differences between inhabitants of these two regions is somewhat different than that yielded by chi-square analyses of all 17 tooth-trait combinations and likely reflects less of the volatile effects wrought by the much smaller sample sizes for the archaeologically derived samples from Central Asia.




a

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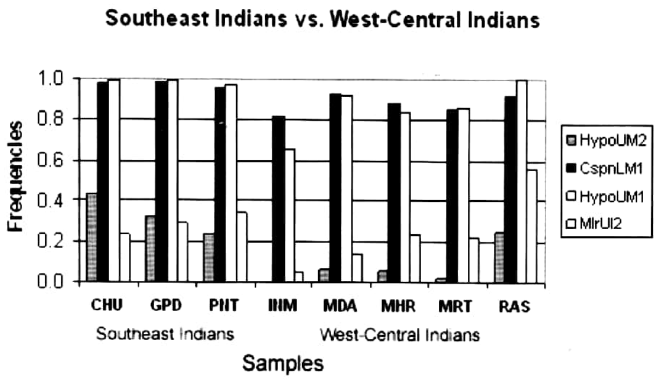


c

Fig 12 Contrasts of tooth-trait combinations with the highest number of significant differences detected by chi-square analysis between prehistoric Central Asians and members of other geographic regions as well as between ethnic groups of Southeast India and West-central India. Sample abbreviations and geographic region assignment from Table 1. a.) Central Asians vs. Southeast Indians, b.) Central Asians vs. West-Central Indians, c.) Southeast Indians vs. West-Central Indians.

When the dentitions of prehistoric Central Asians are compared to those possessed by prehistoric and living ethnic groups of west-Central India all four tooth-trait combinations with the greatest number of significant differences are maxillary traits. These include shovelling and median lingual ridge development on UI1, possession of Carabelli's trait on UM1, and retention of a fully developed hypocone on UM2. From **Figure 12b**, prehistoric Central Asians stand apart from west-central Indian samples by exhibiting far lower frequencies of shovelling (7.7% - 18.8%) and median lingual ridge development on UI1 (15.4% - 39.1%) than west-central Indians (SHOVUI1: 37.5% - 55.2%; MLRUI1:

39.2 – 69.1%). By contrast, prehistoric Central Asians are distinguished from west-central Indians by a much higher prevalence of retaining a fully developed hypocone on UM2 (Central Asians: 50.0% - 71.2%; west-central Indians: 0% - 6.5%). Differences in Carabelli's trait prevalence are less marked between prehistoric Central Asians (10.0 % - 36.1%) and west-central Indians (32.5% - 74.9%), with prevalence actually being somewhat higher in the latest of the prehistoric samples from Central Asia, the Molali period occupants of Djarkutan (36.1%), than among the prehistoric inhabitants of Inamgaon (32.5%).

### Southeast Indians

The maxillary dentition of ethnic groups from southeast India is marked by relatively moderate prevalence of shovelling on the central incisors **(Fig. 2a)**, coupled with low relative prevalence of shovelling on the lateral incisor **(Fig. 2b)**. A similar pattern is observed for median lingual ridge development **(Figs. 2c,d)**. Retention of fully developed hypocones occurs at very high prevalence the first maxillary molar **(Fig. 3a)**, while fully developed hypocones occur with moderate relative prevalence on the second **(Fig. 3b)**. Carabelli's trait occurs at fairly high prevalence on the first molar **(Fig. 3c)**. The metaconule occurs at relatively moderate frequency overall, being consistently more common on first molars **(Fig. 3d)** than on second molars **(Fig. 3e)**.

Members of the southeast Indian ethnic groups included in this analysis possess mandibular molars that reflect some of the highest retention rates for the Y-groove on both first and second mandibular molars **(Figs. 4a,b)**. The same is also true for retention of the hypoconulid **(Figs. 4c,d)**, as well as entoconulid and metaconulid presence on these same teeth **(Fig. 5)**.

### West-Central Indians

Morphological trait frequencies in both the maxilla and mandible among the ethnic groups from west-central India included in this analysis exhibit numerous similarities, but also some differences, relative to their counterparts from southeast India. Like ethnic groups from southeast India, west-central ethnic groups possess maxillary anterior teeth characterised by moderate prevalence of shovelling on the central incisor **(Fig. 2a)** accompanied by lesser prevalence on the lateral incisor **(Fig. 2b)**. However, differences occur between ethnic groups of the two geographic regions in the expression of median lingual ridge development. While both groups are marked by similar prevalence of this trait on the central incisor **(Fig. 2c)**, west-central Indians, especially the archaeologically derived individuals from Inamgaon, have lesser prevalence of median lingual ridge development on the lateral incisor **(Fig. 12c)**. It is with respect to full development of the hypocone that ethnic groups of the two regions differ most markedly in maxillary trait frequencies **(Fig. 12c)**. Ethnic groups from west-central India, especially the archaeologically derived individuals from Inamgaon, are marked by lower prevalence of full hypocone development on the first maxillary molar. The sole exception to this pattern is the mixed caste urban sample from Pune (RAS). Differences in the prevalence of full hypocone development are even greater for the second molar. While ethnic groups from southeastern India manifest frequencies between 23.5% and 54.4%, prevalence among west-central Indians is far lower, ranging from completely absent among the prehistoric individuals from Inamgaon to 6.5% among tribal Madia Gonds. Once again, the exception is the mixed caste urban sample from Pune, in which 25% of second molars feature a fully developed hypocone. Presence of the metaconule on both first and second maxillary molars **(Figs. 3d,e)** occurs with similar prevalence among ethnic groups of west-central India as described for ethnic groups from southeast India with one exception, the archaeologically derived individuals recovered from Inamgoan, in which prevalence is lower for both teeth.

Turning to the mandible, the Y-groove occurs on the first molar **(Fig. 4a)** with similar prevalence among the ethnic groups of west-central India as described for ethnic groups from southeast India above. One interesting difference, however, is that while tribal Chenchus represented the ethnic group with lowest prevalence of the Y-groove on the first molar, among west-central Indian groups tribal Madia Gonds stand out as possessing the Y-groove on the first molar with the greatest frequency of any of the peninsular Indian samples included in this analysis. Members of west-central Indian ethnic groups stand apart from their southeast Indian counterparts in exhibiting a greater fall-off in Y-groove retention prevalence on the second molar **(Fig. 4b)**. Once again, an exception to this pattern is the mixed caste urban sample from Pune. A similar pattern occurs for retention of the hypoconulid on these same teeth **(Fig. 12c)**. Entoconulid presence on the first molar **(Fig. 5a)** occurs with lesser overall presence among west-central Indian ethnic groups than ethnic groups of southeast India, but there is considerable overlap between the individual samples. By contrast, presence of the entoconulid on the second molar **(Fig. 5b)** occurs with equal prevalence among ethnic groups of the two regions, except for the prehistoric occupants of Inamgaon where no entoconulids were observed on the second molar. Ethnic groups of west-central India may be distinguished from their west-central Indian counterparts by their lesser overall prevalence of the metaconulid, especially on the second molar **(Figs. 5c,d)**. A glaring exception to this pattern, however, is once again, the mixed urban caste sample from Pune.

*Are Mixed Caste Samples Distortive?*

Another issue of equal importance as trait selection and regional structure in biological distance analyses concerns which taxonomic unit is most appropriate for such studies. Throughout South Asia the strictures of the caste system have, over the course of the last several millennia, led to an atomisation of the gene pool into small mendelian populations (Reich et al 2009; Metspalu et al 2011). Further, even with the development of modern transportation, marital distances within the subcontinent tend to be short leading to a significant degree of isolation-by-distance (Ayala 1982; Falconer 1981; Hartl and Clark 1997; Hedrick 2000). Given high levels of within-caste endogamy, coupled with low rates of inter-caste exogamy and short marital distances, it stands to reason that local populations composed of individuals from the same sub-caste of Hindus, of the same self-identifying ethnic group in Islamic Pakistan, and of the same tribal entity among non-Hindu tribal populations represent the correct taxonomic unit for biological distance analysis.

The dataset employed in the current analysis includes samples of two self-identifying ethnic populations from Islamic Pakistan, four samples of local Hindu sub-caste populations from southeast and west-central India, two tribal populations from the same regions, as well as two urban mixed caste samples from Kolkata and Pune. The latter, because it can be compared to samples of local Hindu sub-caste populations and a single tribal population of the same region of India, permits assessment of whether use of individuals from an array of castes results in a distortion of dental morphology trait frequencies.

The neighbour-joining tree **(Fig. 6)** yielded by cluster analysis places the mixed caste urban sample from Pune along a branch in the lower right of the array where it is strongly separated from the other west-central Indian samples. In fact, the neighbour-joining tree suggests that the urban mixed cas sample from Pune shares closest affinities to the urban mixed caste sample from Kolkata, wi secondary affinities to the two Dravidian-speaking Hindu caste samples from southeast India. Su results are not only surprising, they are markedly discordant in the face of the pattern of geographic regionality that characterises most of the other regional samples (see above and Hemphill in press t Similar results are obtained with multidimensional scaling **(Fig. 7)**. The urban mixed caste sample fro Pune occupies a position in the upper right of the array and the minimum spanning tree suggests close affinities are not with the other samples from west-central India, found on the right side of the array, b with the urban mixed caste sample from Kolkata and to the two Hindu caste samples from southea India. The three-dimensional plot obtained by principal coordinates analysis **(Fig. 8)** places the urb mixed caste sample from Pune in an isolated position in the centre of the array. This sample appears have no close phenetic affinities to any of the other samples included in this analysis. The urban mix caste sample from Kolkata occupies a similarly isolated position. Together, then, these three multivaria data reduction techniques consistently identify the urban mixed caste sample from Pune as anomalou having no affinities to other samples from the same region of India, and possessing distant, discorda affinities to samples that differ markedly with regard to language and geography.

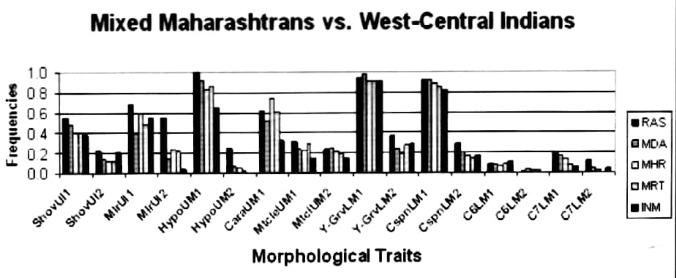


Fig 13 Contrast of all 17 tooth-trait frequencies between the urban mixed caste sample from Pune ("Mixe Maharashtrans") and other samples from West-Central India. Sample abbreviations from Table 1, morphological trait abbreviations from Table 2.

To understand exactly what is driving the anomalous phenetic position of the urban mixed cas sample from Pune, frequencies for all 17 tooth-trait combinations are contrasted against a sample prehistoric individuals recovered from the Jorwe period site of Inamgaon, to samples of individual drawn from a high-status (Marathas) and low-status Hindu caste (Mahars), as well as a sample of trib Madia Gonds. The results of this contrast are provided in **Figure 13**. The urban mixed caste sample fro Pune stands out by possessing the highest frequencies for 11 tooth-trait combinations, including all those found among the anterior teeth. This sample is also marked by highest frequencies for retention the hypoconulid on LM1 and by the second highest frequency for Carabelli's trait on UM1, th metaconule on UM2, and retention of the Y-groove on LM1. Only for two of the 17 tooth-tra combinations considered, the presence of the entoconulid on LM1 and LM2, does the urban mixed cast sample from Pune *not* stand apart from the other samples from west-central India.

Examination of **Table 4** reveals that the urban mixed caste sample from Pune is separated b more significant differences from the other samples from west-central India than any other sample. Th least distinct sample is the archaeologically derived sample from Inamgaon, separated from the thre group-specific samples (MDA, MHR, MRT) by two significant differences, but is separated from th urban mixed caste sample by four combinations. When consideration is limited to samples of living individuals, the number of significant differences separating the three group-specific samples ranges from a low of three between the two Hindu caste samples (MHR, MRT), to a high of nine separating the urban mixed caste sample from Pune from high-status Marathas.

When considered by specific tooth-trait combination, three combinations were found to separate significantly the urban mixed caste sample from Pune from all other west-central Indian samples. These include retention of a fully developed hypocone on UM1 and UM2, as well as median lingual ridge development on UI2. Another tooth-trait combination, presence of the metaconulid on LM2, separates significantly the urban mixed caste sample from Pune from the three group-specific samples of living ethnic groups. Four tooth-trait combinations separate the urban mixed caste sample from two of the three group-specific samples of living ethnic groups. Shovelling on UI2 and retention of the hypoconulid on LM2 separate the urban mixed caste sample significantly from low-status Mahars and high-status Marathas, while median lingual ridge development on UI1 and retention of the Y-groove on LM2 separate the urban mixed caste sample significantly from tribal Madia Gonds and low-status Mahars. Shovelling on UI1 separates the urban mixed caste sample significantly from high-status Mahars, while Carabelli's trait on UM1 separates the urban mixed caste sample significantly from the prehistoric occupants of Inamgaon.

This analysis consistently shows the urban mixed caste sample from Pune to be anomalous relative to other samples from west-central India. Trait frequencies are remarkably high for most traits and gradients of trait expression across key and distal teeth within a specific morphogenetic field are markedly different from those found among the three group-specific west-central Indian samples. When the mixed caste sample from Pune is compared to samples from Central Asia, the Indus Valley, southeast India and to a mixed caste urban sample from Kolkata, it shares no affinities to other samples from west-central India. Instead, it either shares inexplicable affinities to the other mixed caste urban sample from Kolkata and to Dravidian-speaking caste Hindus of southeast India, or it occupies an isolated position in phenetic space with no close affinities to any other sample. The similarities in phenetic affinities also found for the urban mixed caste sample from Kolkata, suggest that both samples are distorted by including individuals from an array of biologically meaningful entities. Thus, it appears clear; samples that mix individuals of different meaningful biological entities (*i.e.*, tribes, self-identifying ethnic groups, Hindu sub-castes) distort trait frequencies, thereby rendering biological distance analyses that rely upon such frequencies biologically meaningless for the reconstruction of the biological history of the various tribes, ethnic groups, and castes of South Asia.

*Are the Madaklasht an Intrusive Group into Northern Pakistan?*

If the Madaklasht oral tradition of external origins and relatively recent migration to their current location in northern Pakistan is true, the Madaklasht should not exhibit close biological affinities to any of thenon-Hindu Kush highland groups included in this analysis. If is also true that the inhabitants of Madaklasht have not intermarried to any significant extent with outside groups, then they should also be distinct from their closest neighbours, the Khowars, who are the numerically dominant ethnic group in Chitral District.

The neighbour-joining tree **(Fig. 6)** yielded by cluster analysis shows that samples of most, but not all (see above), regional groups are marked by closest affinities to other members of the same regional group. This is illustrated by all of the prehistoric samples from Central Asia being located along a single branch on the right side of the array and by four of the five samples from west-central India being located in the upper right. The Khowars and the Madaklasht are depicted as occupying a single branch with fairly close affinities to one another in the centre-right. Both are shown to have nearly equidistant phenetic affinities to west-central Indians, southeast Indians, and to prehistoric inhabitants of the Indus Valley. Such results could indicate long-standing isolation of both groups in the mountains of Chitral, or could be indicative that both groups are intrusive into the region.

The three-dimensional plot yielded by multidimensional scaling **(Fig. 7)** places the Madaklasht and the Khowars in the lower-right of the array. The minimum spanning tree suggests that both groups share closer affinities to the Late Chalcolithic sample from Harappa than to one another. Both samples depart from the phenetic space occupied by the sample from Harappa toward the foreground away from all other samples and away from one another. This plot suggests affinities between the Madaklasht and their neighbours the Khowars are not particularly close. Further, the unique directionality of departure of the samples in multidimensional phenetic space suggests that one or both may be intrusive into northern Pakistan. The three-dimensional plot obtained from principal coordinates analysis **(Fig. 8)** places the Madaklasht and the Khowars in the lower left. These two samples are identified by the minimum spanning tree as possessing closest affinities to one another, but they are clearly isolated in phenetic space from all other samples.

Together, then, these three data reduction techniques suggest the Madaklasht and the Khowars share *some* affinities to one another and are distinctively set apart from both prehistoric and living samples from Central Asia, the Indus Valley, and peninsular India. However, these data reduction techniques differ in their depiction of the phenetic proximity of these two Hindu Kush highland samples to one another. Neighbour-joining cluster analysis suggests affinities are close, multidimensional scaling suggests they are markedly divergent, while principal coordinates analysis suggests their affinities are of but moderate intensity.

All 17 tooth-trait combinations are compared to provide additional insight into what is driving the similarities and differences in the phenetic affinities of the two Hindu Kush highland samples. This comparison is provided in **Figure 14** and serves to highlight similarities and differences between the Madaklasht and the Khowars.

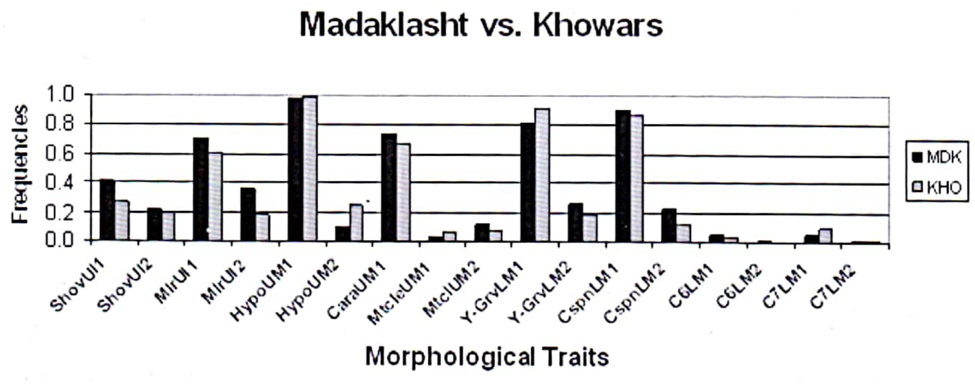


Fig 14 Contrast of all 17 tooth-trait frequencies between the Madaklasht and Khowars. Sample abbreviations from Table 1, morphological trait abbreviations from Table 2.

The Madaklasht are marked by higher frequencies for 11 tooth-trait combinations, including all four combinations occurring on the maxillary anterior teeth. The Madaklasht also have higher prevalence for Carabelli's trait, the metaconule on UM2, retention of the hypoconulid on both LM1 and LM2, as well as possession of the entoconulid on these same teeth. The Khowar possess higher trait frequencies for only four tooth-trait combinations. These include retention of full hypocone development on UM2, retention of the hypoconulid on LM1, presence of the metaconule on UM1 and the presence of the metaconulid on LM1. Two tooth-trait combinations occur at virtually identical frequency in the two samples: retention of a fully developed hypocone on UM1 and presence of the metaconulid on LM2. Four tooth-trait combinations differ significantly between the two Hindu Kush highland groups. These include shovelling on UI1 and median lingual ridge development on UI2, both of which occur with higher prevalence among the Madaklasht, as well as retention of a fully developed hypocone on UM2 and the Y-groove on LM1, which are found at higher frequency among Khowars.

Thus, it is clear, the patterning of differences in dental morphology trait frequencies possessed by the Madaklasht and the Khowars not only serve to separate these two ethnic groups from those of peninsular India, but also from the prehistoric populations of Central Asia and the Indus Valley. Consequently, one cannot attribute the origins of either group to an invasion of Central Asians across the Hindu Kush Mountains into the Indus Valley of Pakistan and beyond into the Upper Doab region of India as advocated by proponents of the Aryan Invasion model (Elst 1999; Erdosy 1995; Kuzmina 1998; Misra 1992; Mukherjee et al 2001; Parpola 1995; see also Bryant 2001). Likewise, the absence of phenetic affinities between these Hindu Kush highlanders and prehistoric inhabitants of the Indus Valley render models based upon long-standing local continuity (Kennedy et al 1984; Passarino et al 1996) equally unlikely. Two possibilities remain. It may be that both groups are the product of founder events that occurred at some unknown point in the past and that subsequent isolation has led to the isolation of both groups from the other samples included in this analysis and from one another (see Papiha 1996 for a similar scenario among groups living in the mountainous sub-Himalayan region of Kinnaur District, Himachal Pradesh). Alternatively, either or both groups may represent the entrance of non-local groups into the Hindu Kush highlands from historical seats, perhaps to the west that did not include the Late Bronze Age BMAC population of southern Uzbekistan. Further comparisons of the dental morphology possessed by the inhabitants of Madaklasht to that possessed by such highland ethnic groups as the Wakhis (Hemphill in press b), Swatis (Hemphill 2009b in press b) and Awans (Hemphill 2012) as well as assessments of the allocation of tooth size across the permanent dentition between the inhabitants of Madaklasht (Hemphill 2008) and such highland ethnic groups as Awans (Hemphill 2012), Baltis (Guzman and Hemphill 2012), Shinas (O'Neill and Hemphill 2012), Swatis (Hemphill 2009b), Wakhis (Hemphill in press b; O'Neill and Hemphill 2009; 2010) and Yashkuns (Barton and Hemphill 2012) consistently identify the Madaklasht as possessing closest affinities to Swatis coupled with secondary affinities to all other highland groups, except Baltis. Such results suggest the origins of the ethnic groups occupying the Hindu Kush and Karakoram highlands are complex and may involve long-standing indigenous occupation (Khowars), fairly recent immigration from southern Central Asia (Wakhis) or the highlands of Tibet (Baltis). The Madaklasht, however, as well as the Swatis, do not appear to be either long-standing inhabitants of the Hindu Kush highlands, nor recent immigrants from southern Central Asia or Tibet. Instead, they, like the Swatis, appear to represent fairly recent immigrants to the Hindu Kush highlands whose likely ancestral home is to be found further to the west in Afghanistan.

## Conclusions

This contribution provides a comprehensive investigation of the biological history of the inhabitants of Madaklasht, a small community located in the severe topography of Chitral District, Khyber Pakhtunkhwa Province, in extreme northwestern Pakistan. Differential prevalence of standardized observations of morphological variation of the permanent tooth crown among the Madaklasht were compared, both univariately and multivariately, to a battery of 19 comparative samples. These samples included both archaeologically derived prehistoric individuals as well as living individuals of ethnic groups located in the Hindu Kush highlands of northern Pakistan, southern Central Asia, the Indus Valley of Pakistan, and peninsular India. The conclusions of this research are seven-fold.

1. Systematic and regular departures from the expected pattern of greater trait presence on the 'key' than on the 'distal' teeth within a specific morphogenetic field indicate that differential trait prevalence on these teeth are not a simple consequence of a 'muting' of the genetic signal due to a greater environmental contribution to later developing distal teeth.
2. Since samples were found to differ, not only in trait prevalence, but also in relative trait prevalence between 'key' and 'distal' teeth within morphogenetic fields, this suggests that differences in the gradient of trait expression within a morphogenetic field may be as important, if not more important, than differences in simple trait prevalence.
3. Of the 17 tooth-trait combinations considered, the most discriminating is the frequency of full hypocone development on the second maxillary molar. The least discerning is the presence of the entoconulid (C6) on the mandibular second molar. Overall, among these living and prehistoric samples from Central and South Asia, morphological traits occurring on the maxillary teeth provide greater phenetic separations between samples than traits occurring on the mandibular teeth.
4. There is no simple relationship between crown complexity, as measured by the prevalence of traits that add relief to the crown or are believed to represent conservative retentions, and temporal context. Further, average rank scores indicate that morphological traits that occur on the anterior teeth only slightly outperform traits found on the posterior teeth. These two findings, coupled with the results obtained from multivariate data reduction analyses, indicate that no marked bias is introduced into biological distance analyses when prehistoric samples are considered alongside samples obtained from populations of living ethnic groups.
5. Contrasts between samples grouped by geographic region reveal that no one set of tooth-trait combinations serves to identify similarities and differences both within and between such aggregates. Instead, different mixtures of tooth-trait combinations provide the best discrimination both within and between regional sample sets.
6. The population of South Asia may be examined at myriad population levels. The results obtained in this study indicate samples that include individuals from different socially meaningful entities introduce damaging bias and distort phenetic affinities possessed by such samples. Specifically, the urban mixed caste sample from Pune was found to express elevated trait frequencies that when examined multivariately, yielded a phenetic position that makes no biological sense. Thus to be meaningful for reconstruction of the biological histories of the myriad tribes, self-

identifying ethnic groups of Islamic Pakistan, and sub-castes of Hindu India, local samples of these entities must be the basis for analysis.

7. The Madaklasht, like their Hindu Kush counterparts, the Khowars, are identified as distinct from the other samples included in this analysis, regardless of whether these samples come from southern Central Asia, the Indus Valley of Pakistan, or peninsular India. The three multivariate data reduction techniques disagree over the proximity of the phenetic relatedness between the Madaklasht and the Khowars. From the results presented in this study, these groups may be long-standing residents of the Hindu Kush highlands who have experienced considerable genetic drift through isolation over time, or one or both of them may represent intrusive populations into northern Pakistan. Results obtained from additional studies of dental morphology variation and allocation of permanent tooth size among other ethnic groups of the northern highlands of Pakistan indicate that while the Late Bronze Age inhabitants of the BMA Curban centres of southern Uzbekistan as well as highland populations of Tibet are unlikely sources of Madaklasht, the Madaklasht share affinities to Swatis and both likely owe their origins to populations located further west in Afghanistan.

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