

The Evolution and History of Human Populations in South Asia

Inter-disciplinary Studies in Archaeology,
Biological Anthropology, Linguistics and Genetics

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12. Interpreting biological diversity in South Asian prehistory: *Early Holocene population affinities and subsistence adaptations*

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Introduction

The goal of this contribution is to provide an integrated synthesis of current research on prehistoric human skeletal remains from South Asia. Data for this study come from dental morphology, as well as from skeletal and dental pathology, and are derived from geographically and chronologically diverse samples. This approach to human biological affinities and subsistence patterns is conducted on the theoretical foundations of organic evolution (Mayr, 1982; Smith, 1993; Gould, 2002). An integrated yet multifaceted approach to population affinities and health in South Asian prehistory will reveal the array of influences that contribute to the complexity of human phenotypic diversity. Evolutionary genetics maintains that phenotypic diversity is the product of complex interactions among forces during ontogeny that include the combined influence of genotypic and environmental factors (Provine, 1971; Ridley, 2004). The deceptively simple yet elegant equation, which

governs ontogenetic development generally is: phenotypic variance = genotypic variance + environmental variance. The simplicity of this equation is misleading. Its role in illuminating gene – environment interaction during ontogeny in real world situations is difficult, yet it provides a conceptual model for the dual approaches adopted in this interpretation of human skeletal and dental diversity in South Asia. In this analysis the more highly heritable and genetically influenced aspects of the dental phenotype, especially morphological variations, are employed in the estimation of biological affinities among prehistoric skeletal samples (Scott and Turner, 1997). Biological attributes whose variability is more directly influenced by the organism's interaction with the environment, such as pathological lesions of the oral cavity and the skeletal system, are analyzed to gain insight into activity patterns, subsistence systems, and dietary behaviors. The value of an integrated dualistic approach to human diversity in South Asian prehistory lies in the greater breadth and depth of understanding that it provides.

This chapter presents results of recent research on the population affinities and health status of early Holocene hunting and foraging peoples of the mid-Ganga plain. The questions and problems that drive the anthropological research reported here are of broad interest to a wide range of scholars. Fundamental issues involving the biological relationships of past human populations include such questions as: How are the early hunters and foragers of the Ganga Plain biologically related to Neolithic people of the greater Indus Plain? What are the biogenetic affinities between the 'Mesolithic' inhabitants of north India and skeletal samples in different regions and prehistoric periods? When interests shift to human – environment interaction in prehistory, a rather different set of research questions become relevant. How do local environments and subsistence systems impact dietary patterns and health status? Do subsistence and diet have discernibly different consequences on males and females?

Answers to these distinctive kinds of questions rely on different, yet complementary classes of data. One data set is comprised of over two dozen polymorphic genetically determined variations in dental morphology. The other consists of proliferative and degenerative pathological lesions that can be recognized in skeletal and dental tissues. These two data sets inform us about population affinities and health status, respectively, but they typically are not equally well preserved or manifested in single specimens. Normal patterns of tooth wear and pathological lesions, such as dental caries and antemortem tooth loss, are destructive in nature and gradually obliterate genetically informative morphological traits expressed on the tooth crown. A demographic effect is present here too, in which younger individuals yield more complete evidence of genetically influenced variables in the primary and permanent dentition. By contrast, older individuals in a skeletal series often do not preserve genetically informative biological traits well or in

abundance, because they are worn away or destroyed by pathological processes. Nevertheless, individuals from older age classes yield informative clues regarding environmental effects that yield insight into diet and health, ecology and disease.

Research Materials

The human remains on which this study is based come from four distinct chrono-cultural clusters. The focus of this analysis is referred to as the Mesolithic Lake Culture Complex. The remaining clusters are arranged in temporal sequence, from early to late, and provide comparative data for interpreting and evaluating biological attributes of the early Holocene, Mesolithic Lake Culture group (see Figure 1 for site locations). The five chrono-cultural clusters consist of the following:

- 1) Hunter/forager samples, from the Ganga Plain with 'Mesolithic' artifact associations (Uttar Pradesh, India). This sample consists of a total of 94 specimens from three main sites, including Sarai Nahar Rai (ca. 10,000 BP; n = 15), Mahadaha (ca. 4000 BP; n = 32), and Damdama (8500 BP; n = 47).
- 2) Early farming village samples from the site of Mehrgarh in the Kachi Plain (Baluchistan Province, Pakistan). These early farming sites produced a total sample of 163 specimens from two mortuary sites: an early Chalcolithic cemetery sample (ca. 6500 BP; n = 70) and a Neolithic cemetery sample (ca. 8000 BP; n = 93).
- 3) Urban farmers of the Indus Valley Civilization (Punjab Province, Pakistan). This mature phase sample was excavated and analyzed in 1987–1988 and consists of the Harappa cemetery R-37 sample (ca. 4500 BP; n = 90) and a subsequent addition to the sample made in 1994, known as the pottery yard sample (n = 5) yielding a total 95 specimens.
- 4) Northwest frontier sites with evidence of iron. Human remains from Sarai Khola

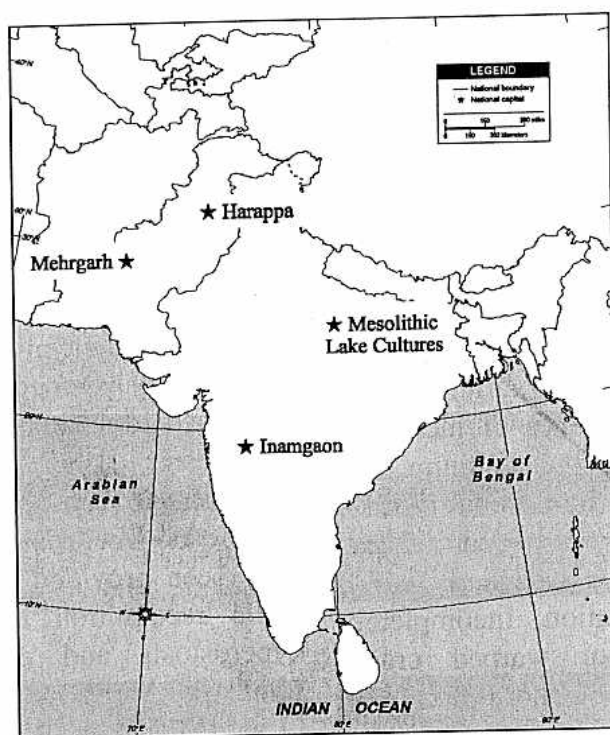


Figure 1. Map of site locations (modified from DeBlij and Muller, 2002)

(ca. 2000 BP; $n = 46$) are better preserved, but fewer in number than skeletons from Timargarha (ca. 3000 BP; $n = 80$). These sites provide a combined early Iron Age sample of 126 specimens.

- 5) Post-Harappan mixed subsistence early farmers of the Deccan Plateau with Chalcolithic material culture (Maharashtra, India). The thoroughly analyzed, primary site is Inamgaon (ca. 3350-2650 BP; $n = 185$). While other Deccan Chalcolithic sites have yielded human remains, the samples from Chandoli, Daimabad, and Nevasa are neither as abundant or well studied as the sample from Inamgaon.

Collectively, these skeletal samples total 663 individuals. Data from numerous additional sites are available, and have been analyzed by the author, yet are not included here due to small sample sizes, fragmentary condition or unique features of demography, geography or chronology that preclude their usefulness in this study. While one sample (from Harappa) was excavated and prepared for study by the author and colleagues, other samples

were analyzed in either museum or field repositories. One important component of the research reported here is that all dental attributes, including morphological variations and pathological lesions were systematically examined by the author employing a single set of uniform methods. Therefore, issues of inter-observer variability and differing systems of classification or methodological technique are obviated – improving the reliability of inter-sample comparisons.

Analytical Methods

The synthetic approach to understanding skeletal and dental variation in living and prehistoric populations of South Asia requires an array of analytical methods. Two complementary sets of methods are used: one for classifying variation in tooth crown morphology, and another for recognizing and diagnosing the disease processes responsible for causing pathological lesions of the skeleton and dentition.

Dental Morphology

The estimation of biological affinities among populations requires observing traits whose variable expression is controlled primarily by genetic variation. Populations that are similar for many independently controlled traits with high heritability are inferred to have close genetic affinities. When skeletal preservation is excellent, assessment of biological relationships from phenotypic variation may involve systematic observation of metric or non-metric variations of the cranium and postcranial skeleton. The monsoonal climate and post-burial environments of many South Asian archaeological sites frequently result in poor skeletal preservation. Incompletely preserved, fragmented or warped crania preclude accurate measurement or observation of non-metric variations. These concerns are exemplified at Damdama where most skulls are damaged beyond measurement (Figure 2), leaving the osteologist with small study samples rendering estimates of biological distance that are biased or unreliable. My research focuses on dental remains for this and several other practical and theoretical reasons. Teeth preserve well in archaeological contexts, even when crania are severely damaged, and details of dental morphology are clearly preserved (Figure 5, below). They present an abundant number of independent polymorphic variations of the tooth crown and root that are easily recorded. Morphological dental traits have a highly variable range of phenotypic expression that is under moderate to high levels of genetic influence. In addition, dental morphology can be observed and trait frequencies tabulated for living and prehistoric populations and direct comparisons of many trait frequencies can be computed with different multivariate statistical techniques. Systematic observation and classification of 25 morphological traits of the permanent teeth were conducted according to the guidelines of the Arizona State University Dental Anthropology System (Turner et al., 1991; Scott and

Turner, 1997). A sub-set of ten morphological traits are used in this study.

Paleopathology

The recognition and scoring of skeletal pathology follows standards established and adhered to by practitioners in the field. The primary sources for identifying and diagnosing pathological skeletal lesions include reference volumes by Ortner and Putschar (1981), Buikstra and Ubelaker (1994), Roberts and Manchester (1995), and Aufderheide and Rodriguez-Martín (1998). Supplemental guidelines for paleopathological analysis have been provided by Lovell (1997, 2000), while recognition and scoring of porotic hyperostosis and cribra orbitalia follows standards developed by Stuart-Macadam (Stuart-Macadam, 1989, 1992). Recognition and characterization of muscle attachment sites, or entheses, follows standards described by Hawkey and Merbs (1995) with attention to the concerns expressed by Robb (1998; Robb et al., 2001). Recognition of degenerative joint diseases, or osteoarthritis, rely on protocols established by Jurmain (1999), in which osteophytic lipping, porosity and eburnation were separately recorded.

Bioarchaeological Foundations and Archaeological Context of Research

This study of skeletal and dental variation in early Holocene north India is part of a larger and long term research agenda devoted to understanding the dynamics of biocultural transformation in ancient India. In the 1980s, the primary focus of bioarchaeological study was human skeletal and dental remains from Pakistan, including the Neolithic and Chalcolithic levels at Mehrgarh (Baluchistan Province), and from the Bronze Age cemetery at Harappa (Punjab Province). This prior research was devoted to descriptive and analytic aspects of variation in tooth size and morphology (Lukacs, 1986;

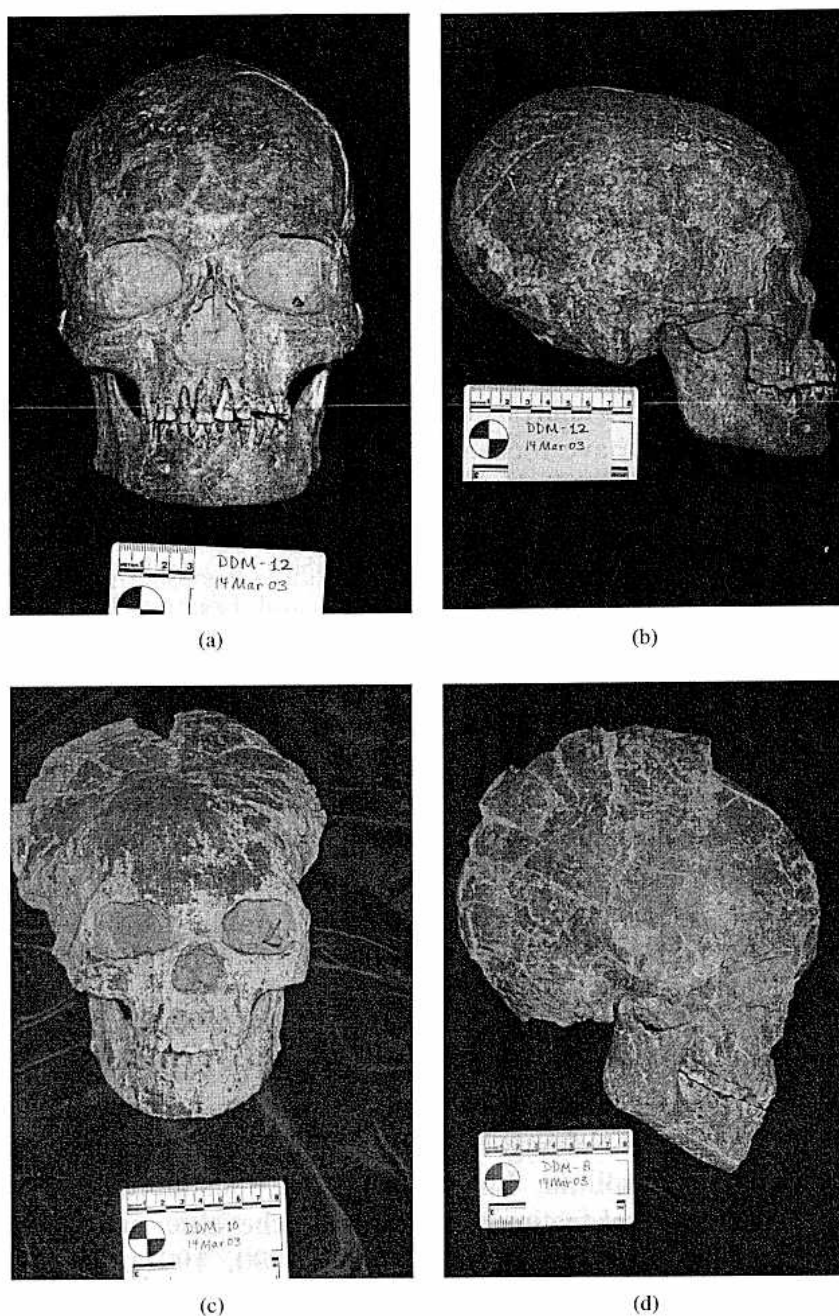


Figure 2. Variation in cranial preservation at Damdama, including well preserved skulls (a, b) and skulls affected by postmortem distortion (c, d). a) frontal view, and, b) right lateral view of DDM 12, a well-preserved, middle-aged adult female. c) Postmortem vertical compression (occipital-parietal) of DDM 10, and adult female. d) Postmortem lateral compression (occipital-parietal) of DDM 8, an adult male

Lukacs and Hemphill, 1991), dental wear patterns (Lukacs and Pastor, 1988, 1990), as well as multiple components of dental paleopathology (Lukacs, 1985; Lukacs et al., 1985; Lukacs and Minderman, 1992). Dental

paleopathology at Harappa and a diachronic assessment of dental diseases yielded evidence for a decline in oral health with agricultural intensification in the greater Indus Valley (Lukacs, 1992).

Research on the bioarchaeology of human remains from Mesolithic Lake Culture sites of the Ganga Plain is extensive and on-going. Comprehensive analyses have been published on the skeletons from Sarai Nahar Rai (Kennedy et al., 1986) and Mahadaha (Kennedy et al., 1992). Preliminary reports on the dentition and stature of the Damdama series (Lukacs and Pal, 1993) confirm a phenotypic pattern similar to that described for Sarai Nahar Rai and Mahadaha. More recently, the analysis of human remains from Damdama have focused on aspects of skeletal pathology and subsistence patterns (Lukacs and Pal, 2007) and on issues of variation in stature and skeletal robusticity in response to activity levels and adaptation to climate (Lukacs and Pal, 2003). The research results reported in this study are built on this foundation of prior research and comprise the first inter-regional comparison of variation in dental morphology and skeletal and dental pathology between pene-contemporaneous early Holocene populations of the greater Indus Valley and middle Ganga Plains.

The site of Damdama is located in the middle Ganga Plain, 72 km NNE of the modern city of Allahabad (lat. 26°10' N; long. 82°10' E). Sister-sites are located nearby: Mahadaha – 5 km SSE and Sarai Nahar Rai – 40 km SW of Damdama. Mesolithic Lake Culture sites are similar in several features:

- 1) in geo-ecological setting they are situated on locally elevated ground adjacent to remnant ox-bow lakes; 2) in lithic technology all belong to the geometric microlithic tradition; and, 3) in site inventories they are all aceramic, and yield representative samples of fauna, stone and bone tools, and human burials. The antiquity of Mesolithic Lake Culture sites is problematic for several reasons, but recent AMS ¹⁴C dates derived from human bone samples suggest an early Holocene antiquity for Damdama (8865 and 8640 BP; Lukacs et al., 1996). Absolute dates for Sarai Nahar Rai and Mahadaha are more variable and controversial,

yet all show a level of relative homogeneity in cultural inventory and biological attributes that suggests these sites are sampling one regional population.

The Mehrgarh site complex is situated in the Kachi Plain on flat alluvium, 15 m above the active Bolan River (lat. 29° 28' N; long. 67° 39' E). At the western-most margin of the greater Indus Valley, Mehrgarh is adjacent to the Bolan Pass, about 8 km from the front of the Harboi Hills, and 30 km SW of the modern town of Sibi. A multi-phase site, culture history at Mehrgarh begins in the Neolithic (ca. 8000 BP), and continues through early Chalcolithic (6500 BP), to late Chalcolithic (4500 BP; Jarrige and Lechavellier, 1980). Cemeteries are similarly located within the living area at both sites, though the depth of burial features at Neolithic Mehrgarh (maximum = 11.0 m) is substantially greater than the depth of deposition at Mesolithic Lake Culture sites: Damdama (1.50 m), Mahadaha (0.60 m), Sarai Nahar Rai (0.06).

Burials exhibit significant differences in structural features, position of the deceased, and funerary accoutrements. Detailed description of Neolithic excavations and funerary practices at Mehrgarh includes an account of pit and wall construction, placement of the skeleton, and inferences derived from the sequential postmortem decomposition of joints (Lechevallier and Quivron, 1981, 1985; Sellier, 1990, 1992). A general description of Mesolithic Lake Culture settlements and burials (Pal 1986, 1992, 1994) document the close association of hearths, artifacts, and burials at Damdama and Mahadaha. Site-specific burial descriptions, line drawings and photographs are available for Sarai Nahar Rai (Sharma, 1973) and Mahadaha (Pal, 1985). Particular attention has been given to variation in the orientation and position of skeletons in five double burials and one triple burial at Damdama (Pal, 1988). Table 1 provides a comparison of the main features of human burials at Neolithic Mehrgarh and

Table 1. Comparison of burial features in early Holocene Indus and Ganga samples

Burial Feature	Neolithic Mehrgarh – Indus	Mesolithic Lake Culture – Ganga (Damdama, Mahadaha, Sarai Nahar Rai)
Structures	Mud brick wall	Ovoid pit
Orientation of body	East-west	East-west
Placement of body	Flexed, on left side, facing south head to east	extended, supine head to the west
Grave goods	Common: body ornaments (turquoise) bitumen lined basket polished stone adze lithics: blades and cores	few: body ornaments (antler, bone) lithics fauna
Example	MR 3-153 (Figure 3b)	DDM-38 (Figure 3a)

among the Lake Culture complex of the Ganga Plain. Representative burials from Neolithic Mehrgarh (MR 3-153) and Mesolithic Damdama (DDM-38) are provided in Figure 3. Note the absence of structural features and burial goods in the Mesolithic Lake Culture burial from Damdama. The overall impression derived from this comparison of burial features is one of greater cultural complexity and more developed material culture at Neolithic Mehrgarh than among the Mesolithic Lake Culture sites.

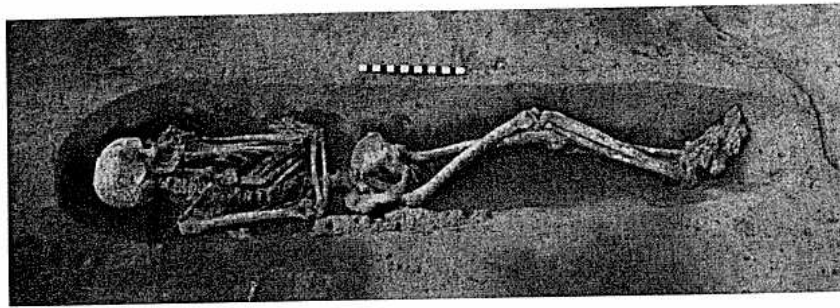
Research Results

Dental Morphology and Biological Distance

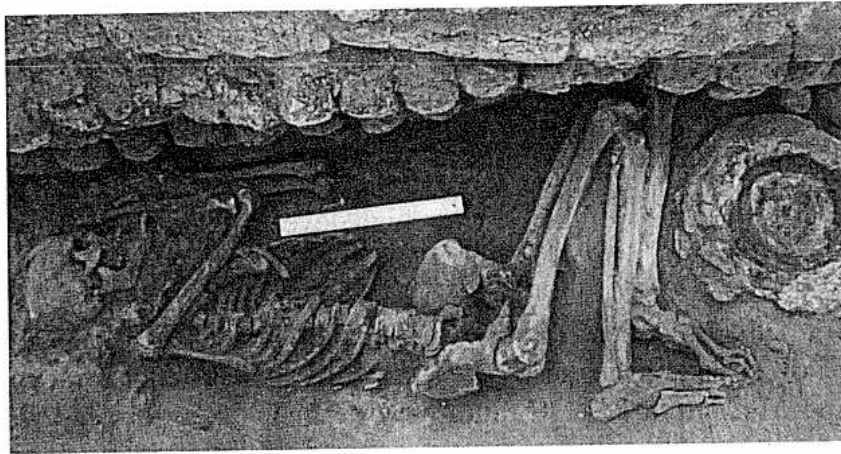
Morphological features of the Mesolithic Lake Culture dentition are documented and trait frequencies compared with data from Neolithic Mehrgarh. The degree of phenetic similarity in dental morphology is the basis for inferring the degree of biological affinity between these skeletal samples and between the Mesolithic Lake Culture sample and other prehistoric samples in South Asia. Homogeneity in the bio-cultural attributes of Mesolithic Lake Culture sites constitutes the basis for pooling dental morphological observations from Damdama, Mahadaha, and Sarai Nahar Rai for this analysis. In addition, the

high level of dental attrition documented in these series limits the number of individuals from whom morphological data could be attained (Lukacs and Pal, 1993). Dental data from Mahadaha and Sarai Nahar Rai alone, were inadequate to accurately characterize dental trait frequencies. The new morphological data from Damdama permit the first accurate descriptive and comparative evaluation of Mesolithic Lake Culture dental morphology.

Schematic comparison of dental crown trait frequencies for maxillary and mandibular teeth from Mesolithic Lake Culture sites and Neolithic Mehrgarh are presented in Figures 4a and 4b, respectively. Note the similarity in overall pattern of trait frequencies. Significant differences in dental morphology were found in 2 of 13 maxillary dental attributes and 3 of 14 mandibular traits. In maxillary traits, Neolithic Mehrgarh tends to have slightly higher frequencies of shovelling, interruption grooves (I2), and molar traits (hypocone, Carabelli's trait and metaconule), yet significant differences occur in only two traits: *tuberculum dentale* (I2) and the metaconule (M2). In mandibular dental traits, Mesolithic Lake Culture sites tend to have greater frequencies of the Y occlusal groove pattern and accessory molar cusps (C-6 and C-7), while 5 cusped molars are more frequent at Mehrgarh (M1 and M3).



(a)



(b)

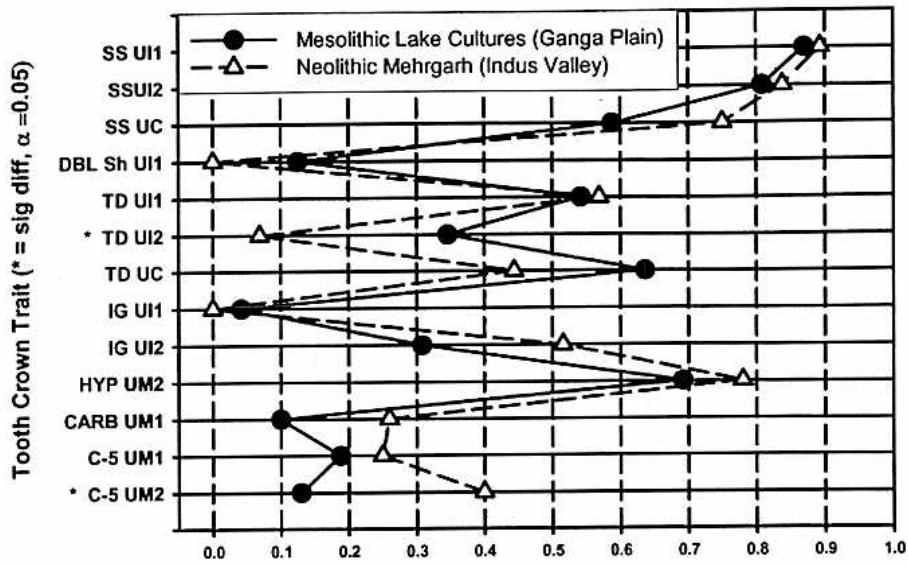
Figure 3. Comparison of burials: 'Mesolithic' Damdama and 'Neolithic' Mehrgarh. a) Damdama burial 38 (DDM 38). Oriented east-west in a supine position, this specimen has legs slightly flexed, the left arm tightly flexed and the right arm flexed 90° . Note the absence of funerary goods. b) Neolithic Mehrgarh burial 153. Oriented east-west, this individual was placed on their left side, facing south, against a hand-made mud brick wall. Arms and legs are flexed. Burial goods include a bitumen-lined basket (on right, adjacent to tibiae); a ground and polished stone axe, and body adornments (small turquoise pieces) are present, but not visible in the photograph

Three lower molar traits are significantly different between groups: five cusped M3, Y groove M3, and the entoconulid (C-6, M3). Examples of dental preservation at Damdama, as well as representative morphological traits of the maxillary and mandibular dentition are provided in Figures 5 and 6, respectively.

A comparison of dental trait frequencies at Mesolithic Lake Culture sites and Neolithic Mehrgarh with five key South Asian prehistoric samples is designed to reveal similarities and differences in trait expression, and by inference biological affinity. Morphological trait frequencies for all seven groups are presented in Table 2. A chi-square test reveals that 54.5% (6/11) of maxillary dental

traits and 30% (3/10) of mandibular traits compared are significantly different among groups. In order to facilitate inter-group comparison of trait expression, standardized frequencies with mean = 0 and standard deviation = 1 were computed using the STANDARD procedure of SAS-PC (ver 8.0). Standardized frequencies of selected tooth crown traits are presented for four maxillary (Figure 7) and four mandibular (Figure 8) traits across all seven samples (see Table 3 for data). Arranged in approximate chronological order from left (earliest) to right (latest) these groups are: Mesolithic Lake Cultures (Damdama, Mahadaha, Sarai Nahar Rai; Ganga sample); Neolithic Mehrgarh (Indus

Dental Trait Frequencies: Maxillary Teeth



Dental Trait Frequencies: Mandibular Teeth

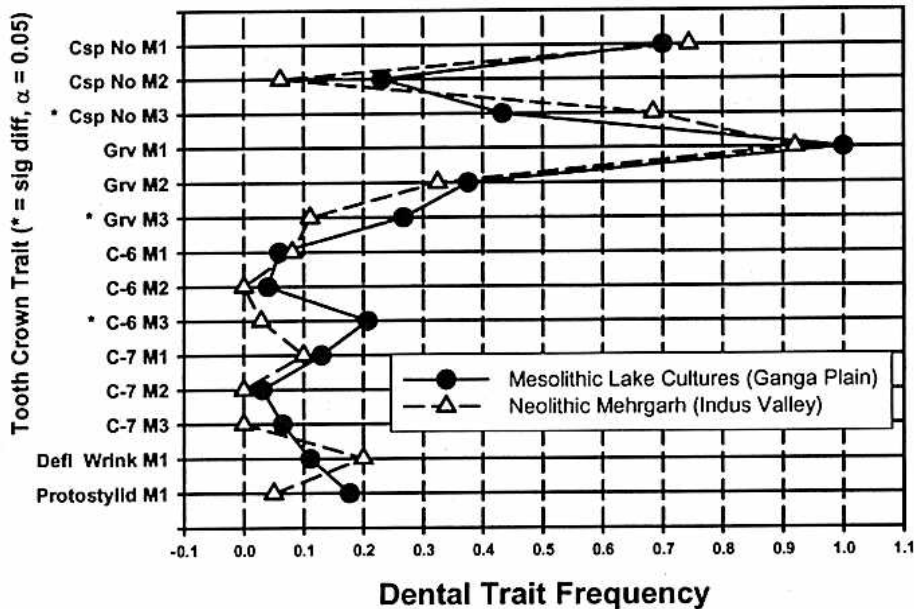


Figure 4. Dental morphology trait frequencies: Mesolithic Lake Cultures (Ganga Plain) and Neolithic Mehrgarh (Indus Valley) compared

sample); Chalcolithic Mehrgarh; Harappa; Inamgaon; Timargarha; and Sarai Khola.

In maxillary incisor traits (Figure 7), Mesolithic Lake Cultures and Neolithic Mehrgarh – Indus show strong positive deviations for I1 shovelling, but express divergent deviations in marginal interruptions for I2, with Mesolithic Lake Culture

sites exhibiting a negative and Neolithic Mehrgarh a positive deviation. In maxillary molar morphology the Ganga Mesolithic Lake Culture and Indus samples share negative deviations for Carabelli's trait (M1), though the Lake Culture sample is more strongly negative than the Indus sample. Expression of the metaconule (M1) is divergent as well, with

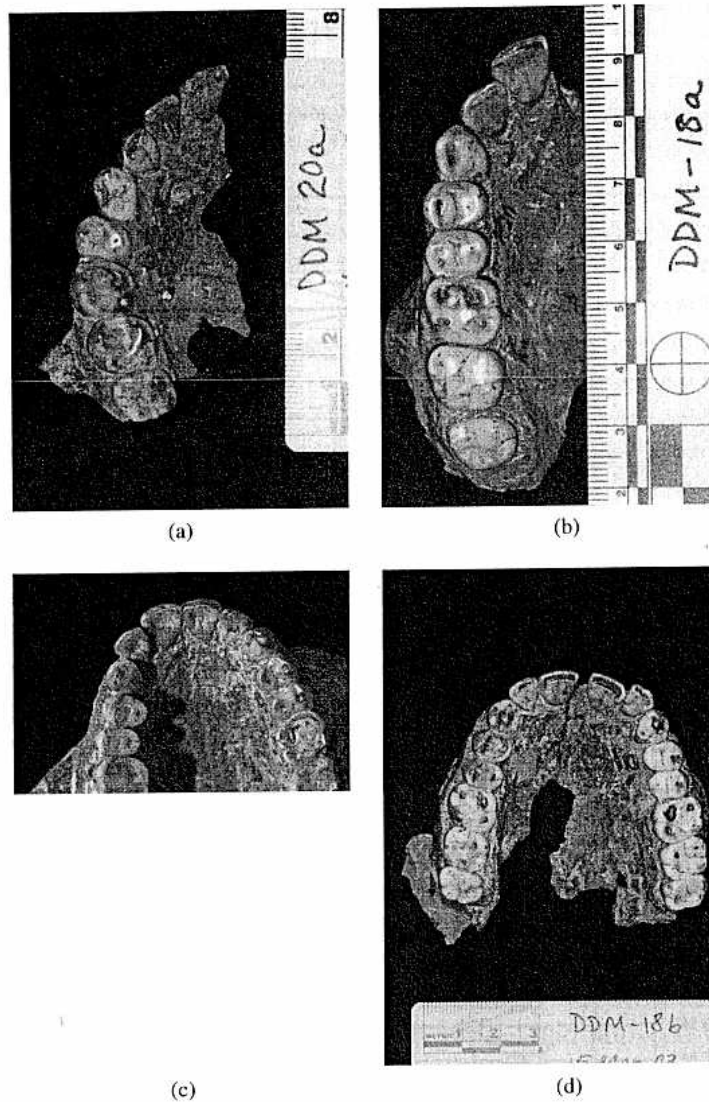


Figure 5. Morphological variation in the maxillary dentition of early Holocene foragers from Damdama, Mesolithic Lake Cultures. a) DDM 20a. Right maxillary dentition (young adult female). Note rotated premolar and C-5 (metaconulid) lower arrow. b) DDM 18a. Right maxillary dentition (young adult male). Note simple incisors (no shovel, no tuberculum dentale). c) DDM 36a. Anterior maxillary dentition (young adult male). Note shoveling of incisor teeth and well-developed tuberculum dentale (arrows). d) DDM 18b. Maxillary dentition (young adult male). Note simple incisors and well-developed hypocones (arrows)

moderately negative values for Mesolithic Lake Culture sites and a slightly negative deviation for Neolithic Mehrgarh, the Indus sample. Mandibular molar traits (Figure 8) display different patterns as well, with 5 cusped second molars exhibiting a strong positive deviation in the Ganga sample and a modest negative deviation in the Indus sample, however both groups express moder-

ately positive deviation for the Y occlusal groove pattern in LM2. Variation in the expression of accessory lower molar cusps is greater for cusp 7 (the metaconulid), for which Mesolithic Lake Culture sites exhibit a positive deviation while the Indus sample from Neolithic Mehrgarh shows a moderately negative deviation. By contrast, the Mesolithic Lake Culture and Neolithic Mehrgarh samples

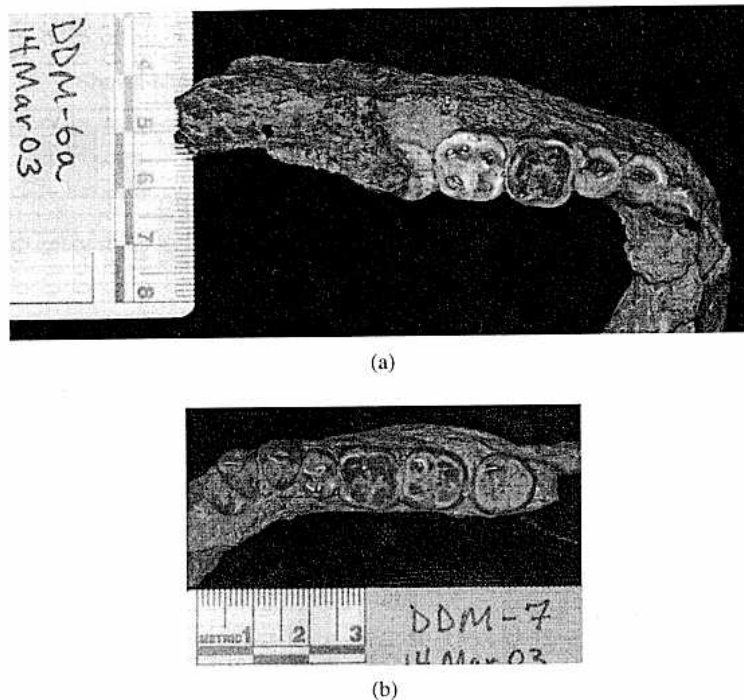


Figure 6. a) The right mandible of DDM 6a, an adult female. Note the heavy wear on M1 and the five cusped M2. b) The right mandibular dentition of DDM 7, an adult male. Note the Y groove pattern of M1 and M2, and the large size and presence of five cusps on M3

are more similar in their expression of accessory cusp 6 (the entoconulid), which exhibits modest and small negative deviations, respectively. Overall the Mesolithic Lake Culture dentition exhibits frequent but low grades of incisor and canine shoveling, low frequencies of double shovel and interruption grooves, while maxillary molars display low frequencies for Carabelli's trait, hypocone reduction, and the metaconule (Cusp 5). Mandibular dental traits common among Mesolithic Lake Culture samples include low levels of incisor shoveling and the distal canine accessory ridge, molarized second premolar (P4), and the presence large second lower molar teeth with the Y occlusal groove pattern and five cusps (Lukacs and Hemphill, 1992).

The relationship among South Asian prehistoric skeletal samples was preliminarily assessed using Ward's minimum variance cluster analysis (Ward, 1963). Ward's cluster technique is widely used in

anthropological bio-distance studies. It is hierarchical, agglomerative and reliably yields clusters that accurately represent known group relationships. Clustering is based on standardized dental trait frequencies and the results are presented in Figure 9. Note the relatively close biological relationship between Neolithic Mehrgarh (8000 BP; Baluchistan) and Inamgaon (3350–2650 BP; Deccan Plateau). These groups are more closely related to one another than either is to the Mesolithic Lake Culture group. This triad – Neolithic Mehrgarh, Inamgaon, and the Mesolithic Lake Culture – is collectively distinct from, and distantly related to, other South Asian prehistoric dental samples. While close affinities exist between Harappa and Chalcolithic Mehrgarh, and between Sarai Khola and Timargarha, all four of these groups are only distantly linked with the Mesolithic Lake Culture, Neolithic Mehrgarh and the Inamgaon cluster. The cluster pattern derived from standardized trait frequencies

Table 2. Dental morphology trait frequencies – prehistoric South Asia

Dental Trait	Tooth	Mesolithic Lake Culture			Neolithic Mehrgarh			Chalcolithic Mehrgarh			Harappa			Inamgaon			Timargarha			Sarai Khola		
		P	N	f	P	N	f	P	N	f	P	N	f	P	N	f	P	N	f	P	N	f
Antiquity (BP)		8700			8000			6500			4500			3350-2650			3000			2000		
Shovel-shape	UJ1	20	23	0.870	25	28	0.893	21	25	0.840	10	18	0.556	22	24	0.917	1	7	0.143	3	9	0.333
	UJ2	21	26	0.808	31	37	0.838	21	24	0.875	10	16	0.625	13	19	0.684	2	7	0.286	2	9	0.222
<i>Tuberculum dentale</i>	UJ1	13	24	0.542	15	26	0.577	14	25	0.560	8	12	0.667	14	25	0.560	3	8	0.375	2	9	0.222
	UJ2	9	26	0.346	2	29	0.069	7	24	0.292	6	13	0.462	1	20	0.050	0	7	0.000	0	9	0.000
Interruption Groove	UJ1	1	24	0.042	0	27	0.000	2	21	0.095	1	16	0.063	0	25	0.000	1	8	0.125	1	10	0.100
	UJ2	8	26	0.308	16	31	0.516	10	22	0.455	6	15	0.400	7	20	0.350	4	7	0.571	1	10	0.100
Hypocone Size	UM1	25	25	1.000	35	42	0.833	22	22	1.000	16	16	1.000	27	41	0.659	17	22	0.773	11	14	0.786
	UM2	18	26	0.692	2	41	0.049	10	18	0.556	2	18	0.111	0	20	0.000	0	13	0.000	2	13	0.154
Carabelli's	UM1	2	20	0.100	7	27	0.259	11	18	0.611	4	9	0.444	13	40	0.325	9	18	0.500	2	9	0.222
	UM1	3	16	0.188	7	28	0.250	5	19	0.263	6	13	0.462	6	41	0.146	4	19	0.211	3	9	0.333
Metaconule (C-5)	UM2	3	23	0.130	10	25	0.400	6	18	0.333	4	16	0.250	3	20	0.150	0	13	0.000	2	14	0.143
	LM1	14	20	0.700	39	43	0.907	20	23	0.870	17	20	0.850	32	39	0.821	19	25	0.760	9	15	0.600
Cusp Number	LM2	6	26	0.231	3	49	0.061	2	24	0.083	0	33	0.000	4	24	0.167	3	17	0.176	1	15	0.067
	LM1	17	17	1.000	23	25	0.920	15	21	0.714	15	17	0.882	32	35	0.914	12	17	0.706	5	7	0.714
Y-Groove Pattern	LM2	9	24	0.375	12	37	0.324	6	22	0.273	3	31	0.097	7	24	0.292	3	18	0.167	5	14	0.357
	LM1	1	17	0.059	3	37	0.081	5	23	0.217	1	20	0.050	4	37	0.108	0	22	0.000	1	14	0.071
Entoconulid (C-6)	LM2	1	25	0.040	0	44	0.000	1	23	0.043	0	28	0.000	0	24	0.000	1	18	0.056	0	15	0.000
	LM1	3	23	0.130	4	40	0.100	3	25	0.120	1	22	0.045	2	36	0.056	2	24	0.083	1	15	0.067
Metaconulid (C-7)	LM1	1	32	0.031	0	43	0.000	0	24	0.000	0	28	0.000	1	25	0.040	2	20	0.100	0	15	0.000
	LM2																					

P = present; N = sample size; f = frequency

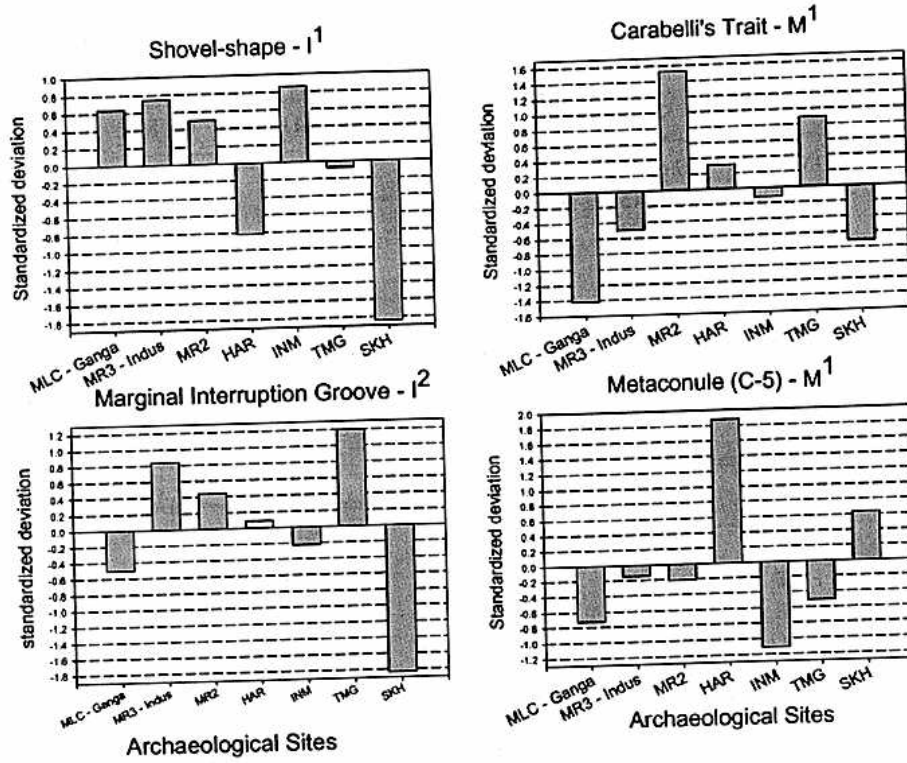


Figure 7. Standardized frequencies of selected polymorphic traits: maxillary teeth

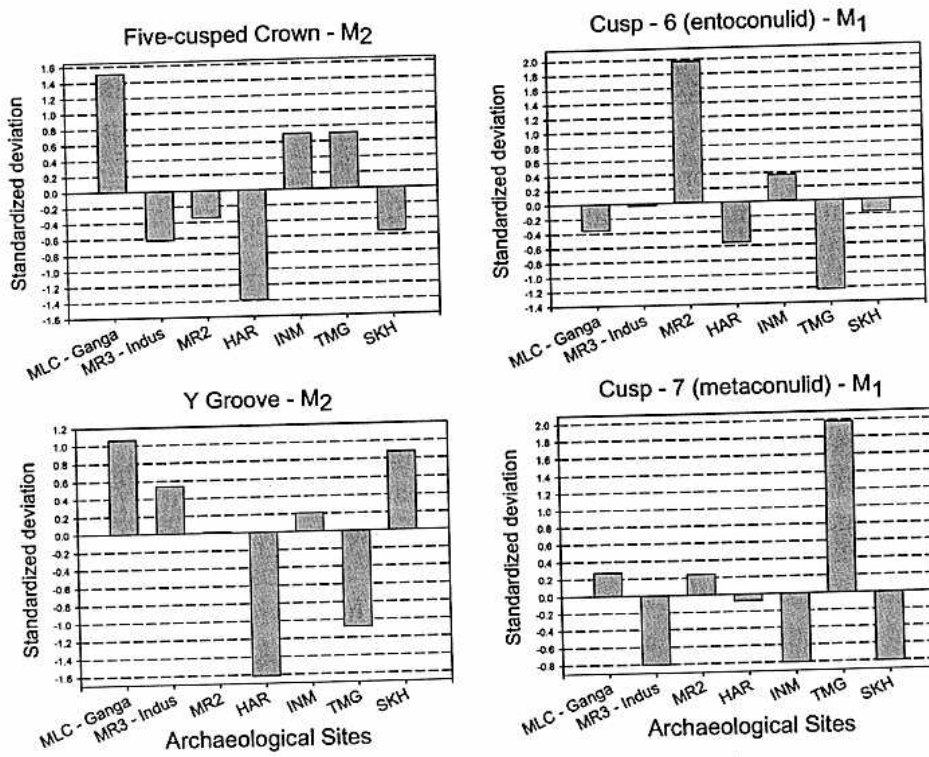


Figure 8. Standardized frequencies of selected polymorphic traits: mandibular teeth

Table 3. Standardized deviations for selected morphological dental traits

Standardized Frequencies: Maxillary dental traits				
Site	SS I1	IG I2	CAR M1	C5 M1
MLC	0.63688	0.50095	1.41384	0.72806
MR3	0.74452	0.83785	0.49618	0.14364
MR2	0.50025	0.44229	1.53122	0.02060
HAR	0.81426	0.09195	0.31478	1.88238
INM	0.85455	0.22921	0.11738	1.11293
TMG	0.08072	1.19304	0.89099	0.51275
SKH	1.84121	1.83497	0.70959	0.63560

Standardized Frequencies: Mandibular dental traits				
Site	CNO5M2	YGR M2	ENC6 M1	MTC7 M1
MLC	1.50656	1.060410	0.35845	0.27316
MR3	0.62187	0.54027	0.03094	0.80468
MR2	0.34432	0.01067	1.97478	0.23947
HAR	1.39048	1.61559	0.55516	0.07831
INM	0.70183	0.20507	0.36674	0.80468
TMG	0.70183	1.07795	1.22400	1.97974
SKH	0.55355	0.87712	0.17297	0.80468

Key to site abbreviations: MLC = Mesolithic Lake Cultures (Damdama, Mahadaha, Sarai Nahar Rai); MR 3 = Neolithic Mehrgarh; HAR = Harappa; MR 2 = Chalcolithic Mehrgarh; INM = Inamgaon; TMG = Timargarha; SKH = Sarai Khola.

Key to dental trait abbreviations: SS I1 – shovel-shape upper central incisor; IG I2 – Interruption groove upper lateral incisor; CAR M1 – Carabelli's trait upper first molar; C5 M1 – cusp 5 (metaconule) upper first molar; CNO5 M2 – cusp number lower second molar; YGR M2 – Y groove pattern lower second molar; ENC6 M1 – cusp 6 (entoconulid) lower first molar; MTC7 M1 – cusp 7 (metaconulid) lower first molar.

are in close agreement with previous studies (Lukacs, 1986) that found close affinities between Neolithic Mehrgarh and Inamgaon, a Chalcolithic site in peninsular west India. This analysis differs somewhat from prior studies (Lukacs and Hemphill, 1991) in displaying a closer linkage between Mesolithic Ganga Plain sites (Damdama, Mahadaha, Sarai Nahar Rai) and the cluster comprised of Neolithic Mehrgarh and Inamgaon.

Paleopathology: Clues to Health and Nutrition

Were semi-nomadic hunters and foragers of Damdama and the Lake Culture Complex healthy and well nourished? Is there evidence of environmentally induced physiological stress? Skeletal and dental indicators of health

and nutrition were observed to answer these questions. Teeth and gnathic elements were examined for evidence of developmental or degenerative pathological lesions. Crania were examined for evidence of cribra orbitalia, and porotic hyperostosis (iron deficiency anemia), while postcranial remains were inspected for evidence of osteoarthritis (degenerative joint disease), and periostitis (a proliferative bone response, evidence of non-specific infection). Cranial and postcranial elements were scrutinized for evidence of trauma, including fractures, dislocations, wounds, and cut-marks. Vascular impressions of the tibia and hypertrophy of entheses were also systematically analyzed. Sample sizes fluctuate dramatically for skeletal and dental afflictions due to the role diagenetic and taphonomic factors

Ward's Cluster - Standardized Frequencies

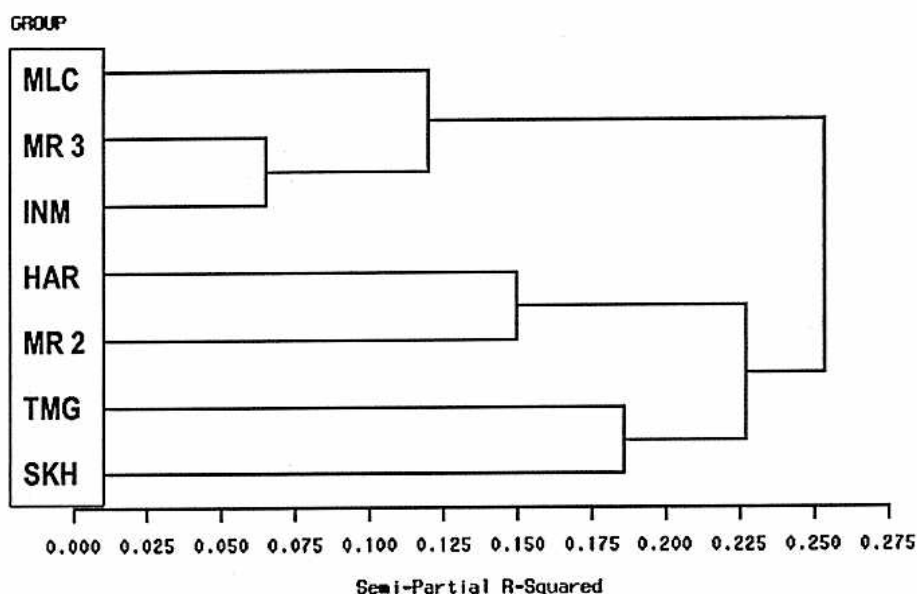


Figure 9. Ward's cluster based on standardized frequencies of dental morphological traits with significant inter-group differences. Abbreviations: MLC = Mesolithic Lake Culture; MR 3 = Neolithic Mehrgarh; MR 2 = Chalcolithic Mehrgarh; HAR = Harappa; INM = Inamgoan; TMG = Timargarha; SKH = Sarai Khola

play in influencing differential preservation of dental and skeletal elements.

Meaningful comparative analysis of the frequency of skeletal and dental lesions requires close attention to demographic variables of the groups under comparison. While some investigators make age-specific comparisons of lesion frequency, a viable alternative for small samples is testing for significant differences in demographic profiles. Although the Mesolithic Lake Culture sites analyzed here differ slightly in mean age, no significant inter-site differences in mean age at death were found between Damdama, Mahadaha and Sarai Nahar Rai ($p < 0.05$; Lukacs and Pal, 1993:751).

Pathological Lesions of Skeletal and Dental Remains

The prevalence of pathological dental lesions in the Damdama skeletal series was documented by prior research, but is included here to provide a holistic and comparative picture of health (Lukacs and Pal, 1993). The dental pathology profile of the Mesolithic Lake Culture and

Neolithic Mehrgarh are graphically compared in Figure 10; the supporting data are provided in Table 4. Dental caries rates are low, exposure of the pulp chamber is also rather low but caused by heavy dental wear, and evidence of systemic developmental growth disruption – as indicated by linear enamel hypoplasia – is common. A chi-square test of the prevalence of dental lesions at Mesolithic Lake Culture sites and Neolithic Mehrgarh reveals significant differences in five of the seven traits compared. Some of the difference may result from the more fragmentary nature of the Mehrgarh gnathic remains, which has a higher representation of isolated teeth. Consequently small sample size may contribute to the low rate of alveolar recession and dental abscesses at Mehrgarh. Lower rates of dental caries at Neolithic Mehrgarh are attributable to naturally fluoridated water in the Kachi Plain (Lukacs et al., 1985). The higher frequency of pulp exposure among Mesolithic Lake Culture samples results from greater rates of

Pathological Dental Lesions: 'Mesolithic' Lake Cultures (including DDM), and Neolithic Mehrgarh (MR 3).

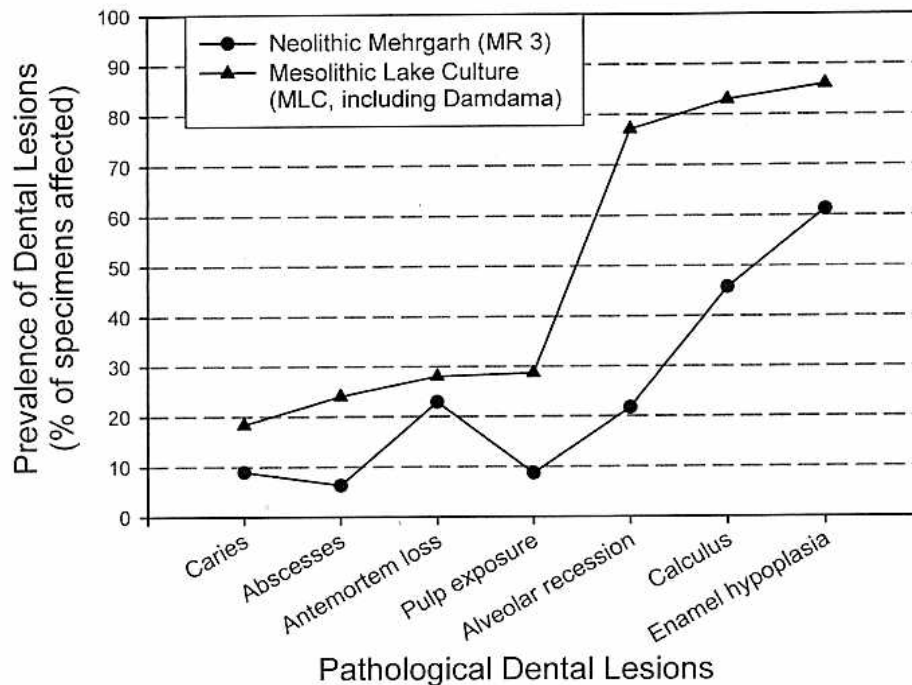


Figure 10. Dental pathology profile at Damdama

dental wear from the coarse diet associated with a hunter and gatherer subsistence.

The most frequent pathological dental lesion in both samples is enamel hypoplasia.

Observed as transverse lines on the outer enamel surface, hypoplasia is evidence of

deficient enamel formation and suggests that physiological disruptions in growth among

Table 4. Dental pathology of Ganga Mesolithic and Neolithic Mehrgarh compared

Dental Lesion	Ganga Plain Mesolithic				Neolithic Mehrgarh	
	DDM		MLC		MR 3	
	+/n	%	+/n	%	+/n	%
Caries	5/35	14.3	9/49	18.4	8/89	9.0
Abscesses	9/35	25.7	12/50	24.0	3/48	6.3
Antemortem loss	10/35	28.6	14/50	28.0	11/48	22.9
pulp exposure	11/35	31.4	14/49	28.6	8/92	8.7
Alveolar recession	27/33	81.8	37/48	77.1	10/46	21.7
Calculus	30/35	85.7	39/47	83.0	42/92	45.7
Enamel hypoplasia	30/32	93.6	37/43	86.0	57/93	61.3

MLC (Mesolithic Lake Cultures) = frequencies for Damdama (DDM) and Mahadaha (MDH) combined and arranged in ascending frequency.

children were common among early farmers of the Kachi Plain and semi-nomadic hunters and foragers of the Ganga Plain. Despite frequent disruptions to growth in childhood, the tall stature attained by Mesolithic Lake Culture men and women shows that periodic stress was balanced by flush periods that allowed for significant amounts of catch-up growth (Lukacs and Pal, 2003, 2007).

Results for skeletal pathology, trauma and other skeletal variations are presented in Tables 5 and 6, respectively. A significant finding of this study is the absence of pathological lesions for several morbid conditions indicative of nutritional and infectious disease. Lesions of the cranial vault, including: cribra orbitalia and porotic hyperostosis, and lesions of the postcranial long bones, such as periostitis were not observed in the Damdama skeletal series. None of these key indicators of nutritional and infectious disease have been reported for either Mahadaha (Kennedy et al., 1992) or Sarai Nahar Rai (Kennedy et al., 1986). Evidence of osteoarthritis was present, but rare. Osteoarthritis of the temporomandibular joint was lacking from the glenoid fossa of the temporal bone, but present on the mandibular condyle of one specimen (DDM 1, an adult female). This condition has also been reported in two specimens from

Mahadaha (MDH 19 and 21, both older adult females) indicating that masticatory stress at the temporomandibular joint affected some individuals of Mesolithic Lake Culture (Lukacs and Hemphill, 1992). These observations are consistent with high rates of dental wear, abscesses due to heavy masticatory forces and high rates of pulp exposure. In general, vertebrae were poorly preserved and under-represented in the sample, however osteophytes were observed in three of seven specimens. Osteoarthritis of the appendicular skeleton is low in frequency and was observed bilaterally in the elbows of one individual (DDM-1, an adult female) and in the hand of another (metacarpals, DDM-12, adult female).

The skeletal analysis, including cranial and postcranial trauma, vascular impressions, and enthesial hypertrophy are presented in Table 6, and briefly discussed below.

Traumatic lesions were absent from all observable cranial remains, but three individuals preserved evidence of postcranial fractures: a) a compression fracture of the ninth thoracic vertebra (DDM 1); b) a simple fracture of a left ulna (DDM 24); and, c) a simple fracture of the right fibula (DDM 23). The latter injury was associated with multiple markers of dysfunction in the right leg including a prominent exostosis of

Table 5. Prevalence of pathological skeletal lesions at Damdama

Lesion Name	N _{affected}	N _{observed}	% affected
Cribra orbitalia	0	15	0.0
Porotic hyperostosis	0	30	0.0
Periostitis	0	40	0.0
<i>Osteoarthritis</i>			
Temporomandibular joint (glenoid fossa)	0	14	0.0
Temporomandibular joint (mandibular condyle)	1	12	8.3
Vertebral osteophytosis	3	7	42.9
Appendicular osteoarthritis	3	33	9.1

Key: N_{affected} = number of specimens in which lesion was present;
N_{observed} = total number of specimens observed.

Table 6. Prevalence of pathological lesions and skeletal variations at Damdama

Variation	N _{affected}	N _{observed}	% affected
Cranial Trauma	0	20	0.0
Post-Cranial Trauma	3	36	8.3
Vascular Impressions	5	21	23.8
Enthesial Hypertrophy	18	33	54.6

Key: N_{affected} = number of specimens in which lesion was present;
N_{observed} = total number of specimens observed.



Figure 11. Vascular channels, features also known as vascular impressions or vessel tracks, on lateral aspect of the diaphysis of the left (lower) and right (top) tibiae of DDM 2. Four channels are easily viewed on each tibia

the posterior superior aspect of the femoral diaphysis.

Vascular impressions (channels, cortical grooves, vessel tracks) are shallow grooves on the cortical surface of long bone diaphyses, analogous to surficial grooves on the frontal bone (see Hauser and DeStefano, 1989). In humans they are most commonly found on the lateral (sub-periosteal) surface of the tibial diaphysis. DDM 2 presents numerous well demarcated vascular channels on right and left tibiae (Figure 11). Five of 21 specimens (23.8%) exhibited one or more vascular impressions on either the right, left or both tibia. While the functional significance of

such grooves remains unclear, the Damdama sample shows no significant difference by side, but suggests significant differences by sex – 5 of 10 females exhibit vascular impressions (7/15 tibiae; 46.7% of female tibiae), while none of 11 males exhibit the trait (0/14 tibiae). In a rare study of vascular impressions, Wells (1963a, 1963b) reports a frequency of 52.6% (n = 300) of tibiae affected in his Anglo-Saxon sample and reports no significant inter-sex difference. Like frontal grooves, vascular channels may indicate disharmony in the growth rate of different tissues. Exuberant bone growth, combined with slower development of neural or vascular

tissues, may impose localized restriction in proliferation of sub-periosteal osseous tissues thereby creating sinuous or linear channels on the cortical surface. Vascular grooves, may mimic peri- or postmortem cutmarks or toothmarks, and have been observed on the lateral ramus of large bovid humeri (wildebeest) by Shipman and Rose (1984). Accurate description and diagnosis is required if mis-identification of these surface features of cortical bone is to be avoided (see Buikstra and Ubelaker, 1994:108, and Figure 77).

Entheses are sites throughout the skeleton where muscles attach to bone by tendon. Entesial hypertrophy was systematically evaluated as an indicator of skeletal function and activity, and as one factor contributing to the perception of 'skeletal robusticity'. Entesial hypertrophy was observed at multiple loci throughout the skeleton and 54% of specimens displayed entesial hypertrophy at one or more sites. Common loci of entesial hypertrophy include the forearm: proximally near the elbow at the supinator crest and radial tuberosity, and distally at the pronator quadratus insertion. The most prominent site of entesial hypertrophy is on the posterior proximal surface of the tibia, where the soleal line is developed into a rugose welt-like swelling or in more extreme instances into a ridge-like crest from which the soleus muscle originates. Hypertrophy of the soleal line is a marker of plantar flexion related to high mobility, and is equally well developed in the Damdama series among males and females and among young and old individuals (Lukacs and Pal, 2003).

Discussion

This synthetic review documented aspects of human skeletal and dental diversity among semi-nomadic hunters and foragers of the Ganga Plain. These data and their interpretation bear upon two critical features

of current anthropological debate: early human migrations and subsistence and health. Perspectives on these issues that can be derived from South Asian prehistory have the potential to contribute to global discussion of the biological affinities and the origin of modern humans and of how cultural shifts in subsistence and food production impact human health and nutritional status.

Dental Morphology, Biological Affinities, and Dispersal

The biological role of Mesolithic Lake Culture populations in the peopling of South Asia is illuminated by the pattern and frequency of dental morphological traits. The Mesolithic Lake Culture sample exhibits a dental morphological phenotype that is characterized by: a) simple anterior dentition in terms of low frequencies of incisor and canine shoveling, double shovel, *tuberculum dentale*, and marginal interruptions, b) infrequent accessory cusps in the maxillary (low frequency of Carabelli's trait and metaconule) and mandibular molar teeth (low frequency of entoconulid and metaconulid), combined with c) large second lower molars, featuring five cusps and Y occlusal groove patterns. This trait association shares some features in common with Turner's (1990) more generalized Sundadont dental pattern, and displays affinities with both Neolithic Mehrgarh (Baluchistan Province) and Chalcolithic Inamgaon (Deccan Plateau, western Maharashtra). Standardized dental trait frequencies and the cluster analysis derived from them show significant differences between Mesolithic Lake Culture populations and the sub-cluster composed of Harappa and Chalcolithic Mehrgarh. The Mesolithic Lake Culture and Neolithic Mehrgarh samples are most distantly removed from the sub-group comprised of later samples from northern Pakistan, including Sarai Khola and Timargarha.

The Mesolithic Lake Culture dental pattern can also benefit from comparison with an early South Asian pattern of dental variation described by Hawkey (1998, 1999) and given the label "Indodont". In contrast to the early world average for dental trait frequencies, the "Indodont" dental complex is characterized by Hawkey as comprised of a suite of high frequency (shovel shape I^1 , hypocone M^2 , Y-groove M_2 , and four-cusped M_2), average frequency (double shovel I^1 , interruption groove I^2 , cusp 5 - M^1 , parastyle M^3 , six-cusped M_1 , deflecting wrinkle M_1 , protostylid M_1 , and cusp 7 - M_1), and low frequency dental traits (winging I^1 , *tuberculum dentale* I^2 , distal accessory ridge C , Carabelli's trait M^1 ; Hawkey 1998:298).

Dental trait frequencies for three groups provide the basis for the "Indodont" or early South Asian dental complex: a) a Northwest farming and herding group (2 sites; $n = 3-76$ individuals; includes Mehrgarh); b) a Sri Lanka hunter/gatherer group (4 sites; $n = 3-18$ individuals); and, c) northern Indian hunter/gatherer group (6 sites; $n = 4-27$ individuals; includes Mahadaha and Sarai Nahar Rai). Several dental trait frequencies described here for Mesolithic Lake Culture sites (Mahadaha and Sarai Nahar Rai, augmented by new data for Damdama) are comparable with Hawkey's characterization of the India hunter/gatherer group. For example, maxillary dental traits such as *tuberculum dentale* I^2 (0.308 vs. 0.333), cusp 5 - M^1 (0.188 vs. 0.182), Carabelli's trait M^1 (0.100 vs. 0.067), and mandibular traits including cusp 7 - M^1 (0.130 vs. 0.118) and the protostylid (0.177 vs. 0.111) show close similarities. This result may not be surprising since Mahadaha and Sarai Nahar Rai were included along with data for four other geographically dispersed sites in Hawkey's India hunter/gatherer group. Other important traits are more difficult to compare reliably.

In a univariate analysis of 27 dental trait frequencies, Hawkey compared early South Asia with the early world average, yet for 12 of the 27 dental traits, or 44.4% of the comparisons, data for the India hunter/gatherer sample were either unavailable or consisted of sample sizes less than 10. This observation highlights the significance of the present study, since dental trait frequencies for the Mesolithic Lake Culture sites are now based on an average sample size of 23 individuals (n ranges from 16 to 32) per dental trait. This study constitutes a more accurate and meaningful characterization of early hunter/forager dental variation because it is less affected by the bias of small sample size and is based on local breeding populations that are geographically circumscribed and culturally and biologically adapted to a similar riparian environment.

The archaeological and genetic evidence for human dispersal and the origin of modern human behavior in later Pleistocene South Asia was recently reviewed (James and Petraglia, 2005). Data from human biological diversity does not currently play a major role in this discussion (Lukacs and Pal, 2007), nor can dental morphology directly contribute to discussions regarding the early southern dispersal for lack of an adequate later Pleistocene hominin dental record. Nevertheless, research now in progress seeks to construct the dental morphological attributes of a hypothetical early southern dispersing population. Comparative investigation of later Pleistocene African (Irish and Guatelli-Steinberg, 2003) and early Holocene South Asian dental variations will enable a tentative morphological model to be proposed that will permit the biological identity of early dispersers to be recognized and classified as archaic or modern humans. As human skeletal and dental remains with Middle and Late Paleolithic associations are discovered in South Asia their dental attributes can

Table 7. Idealized model of subsistence systems correlates with demography and health

Population Attributes	Subsistence Strategy	
	Hunter-Gatherer/Forager	Agriculture
Size	Small	Large
Density	Low	High
Mobility	High	Low
Dietary Diversity	High	Low
Categories of Disease		
Contagious	Low	High
Dental	Low – moderate	Moderate – high
Infectious	Low	High
Nutritional	Low	High
Parasitic	Variable	Variable
Biological Adaptations and Variations		
Tooth size	Large	Small
Cranial/facial robusticity	High	Low
Post-cranial robusticity	Variable	Variable

be compared with the hypothetical dental morphotype and thereby make a more meaningful and direct contribution to current debates over dispersal and modern human origins in ancient India.

Paleopathology: Health Status and Biological Adaptation

The skeletal and dental evidence for health and nutritional status of early Holocene hunters and foragers of the Ganga Plain make a direct contribution to debates regarding the impact of subsistence shifts on human health and nutrition. Perspectives on the biological consequences of subsistence transitions were initially popularized by Mark Cohen (1989; Cohen and Bennett, 1993) and elaborated by Clark Larsen (Larsen, 1995, 1998). Transition theory contends that the subsistence shift from nomadic hunting and foraging to sedentary agriculture involved several biological costs. The biological toll of changing modes of food acquisition and preparation has been documented for specific geographic regions of the world (Cohen and Armelagos, 1984). A sequel to this influential volume, with greater emphasis on health and subsistence in Asian prehistory will soon be available

(Cohen and Crane-Kramer, 2007; Lukacs, 2007). The stresses of changing subsistence patterns are typically associated with a shift in population attributes (size, density, mobility) that tax a population's adaptive potential and stimulate an increase in contagious, infectious and nutritional diseases, and changes in stature and skeletal robusticity (Table 7). As research on paleopathology and paleodemography across the transition to agriculture becomes better documented, greater variation is evident in how populations adapt to agricultural subsistence (Cohen and Crane-Kramer, 2007).

For example, iron deficiency anemia, an affliction of sedentary agricultural populations, was unknown to humankind during our long history as hunters and foragers prior to about 10,000 years ago (Stuart-Macadam, 1998). Paleopathologists recognize skeletal indications of iron deficiency anemia as thinning and porosity of the external surface of cranial vault (porotic hyperostosis) and as porosity of the bony roof of the eye socket (cribra orbitalia). Dental diseases increase dramatically with the adoption and reliance on processed grains and cereals in the diet (Larsen, 1995). The frequency of

dental caries in particular, increases with the adoption and intensification of agricultural subsistence and with technologically sophisticated food processing procedures (Lukacs, 1992). This decline in dental health with the adoption of agriculture has a greater impact on women, globally (Larsen, 1998) and in prehistoric South Asia, in particular (Lukacs, 1996).

Damdama and the Mesolithic Lake Culture samples described in this study fit the expectation of theoretical models of subsistence and health. Attributes of dental pathology are consistent with a hunting and foraging diet. Dental lesions that are common among Mesolithic Lake Culture sites, such as alveolar recession, abscesses, exposure of the pulp chamber, and high rates of attrition indicate heavy masticatory stresses. These conditions are consistent with robust structural features of the jaws, large tooth size and degenerative osteoarthritis of the temporomandibular joint (Lukacs and Pal, 1993; Lukacs, 2004). Low dental caries rates are consistent with expectations based on the generally coarse, unrefined, and abrasive diet of hunters and gatherers. Women among Mesolithic Lake Culture sites have higher caries rates than men and though this finding is not uncommon the explanation of this phenomenon is currently under re-evaluation (Lukacs and Largaespada, 2006). In addition to sex differences in diet, differences in hormone levels associated with reproductive events over the female lifespan may have a more significant role to play in explaining sex differences in caries rates than previously believed.

Osteological evidence of nutritional and infectious diseases is absent. The absence of pathological skeletal lesions from cranial and postcranial remains strongly suggests that the people of Damdama were free from nutritional deficiency and infectious diseases that produce lesions in skeletal tissue. In particular, the absence of porotic hyperostosis and cribra orbitalia suggests the absence

of iron deficiency anemia, while the lack of periostitis is interpreted to indicate that infectious diseases were rare as well. In sum, the people of Damdama exhibit skeletal indicators of health commonly associated with mobile hunting and foraging societies. Trauma and markers of 'occupational' stress are rare. Bone fractures are uncommon suggesting that accidents, interpersonal violence, or intergroup conflict were not sufficiently common among the inhabitants of Damdama to be represented in their skeletal remains. Enthesial hypertrophy is evident in two main areas of the skeleton: the elbow (proximal ulna) and the leg (proximal tibia). These markers suggest repetitious use of the right forearm in throwing (spears, sling stone?) and habitual plantar flexion of the foot as in the propulsive phase of the human bipedal stride (distance walking possibly with loads) as typifies highly mobile people.

The people of Damdama were generally healthy and well adapted to their environment. Their skeletal pathology profile, pattern of trauma and activity markers, and tall stature are collectively consistent with a semi-nomadic foraging subsistence pattern and contrast dramatically with predictions for the expression of these variables among sedentary agriculturalists.

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