ISSUES AND THEMES
IN
ANTHROPOLOGY

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ISBN 81 - 85799 - 49 - 0

First Edition : 2004

Published by Kamal Kishore for **PALAKA PRAKASHAN,**
3930/18, Kanhaiya Nagar, Tri Nagar, Delhi-110 035. INDIA
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Laser Typeset at *Neekaashi Graphics*, Delhi,
printed at *New Gyan Offset*, Delhi.

HUMAN BIOLOGICAL DIVERSITY IN EARLY HOLOCENE INDIA : A COMPARISON OF TOOTH SIZE AND DENTAL MORPHOLOGY AMONG INHABITANTS OF THE INDUS AND THE GANGA PLAINS

JOHN R. LUKACS

THE Indo-Gangetic Plains of northern India provide two clusters of human settlement in the early Holocene: Neolithic Mehrgarh (Baluchistan, Pakistan) in the greater Indus Valley and the Mesolithic Lake Culture Complex (Uttar Pradesh, India) in the middle Ganga Plain. The dental morphometrics of Lake Culture Complex sites (Damdama, Mahadaha, and Sarai Nahar Rai) in the middle Ganga Valley are described and compared with pene-contemporary samples from Mehrgarh. This comparative analysis of dental morphology and odontometry represents an extension of prior studies of site-specific and regional trends in dental wear and paleopathology.

This study was conducted to address broad questions of population affinity (dental morphology) and biological adaptation (tooth size). Do these early settlements in the Indus and Ganga

Valleys represent separate distinctive genetically isolated population groups? or might they represent one large north Indian breeding population? In dental dimensions and tooth size apportionment, how similar or distinct are the Mehrgarh and the Mesolithic Lake Culture samples?

Standardized protocols for classification of dental morphology (Turner *et al.*, 1991) and measurement of crown dimensions (Kieser, 1990) were followed. Extreme dental wear limits the size of dental samples for the Ganga Valley sites. While the frequency of most morphological traits of the dentition are similar in the Mehrgarh Neolithic and Mesolithic Lake Culture samples, several traits are significantly different (5 cusped mandibular M3, Y groove mandibular M3, and entoconulid mandibular M3). In a comparison of dental morphology with five prehistoric South Asian skeletal samples 9 of 21 (42.9%) traits differ significantly among groups and yielded a closer linkage between Neolithic Mehrgarh and Lake Culture sites than previous studies based on smaller sample sizes. Overall tooth size at Mehrgarh (1262 mm2) is significantly smaller than the composite value for Lake Culture sites (1383 mm2), and may reflect increased reliance on agriculture and more refined food processing methods.

INTRODUCTION

This essay on the bioarchaeology of Mesolithic people of ancient India honors Professor D.K. Bhattacharya on the occasion of his retirement. Appropriately, we share an interest in bio-cultural interaction in Indian prehistory and Prof. Bhattacharya has made substantive theoretical and empirical contributions to the understanding of Mesolithic archaeology in India. In the Dharani Sen Memorial Lecture to the Indian Anthropological Society, for example, he (Bhattacharya 1992) applied Binford's stress model of cultural transformation to the Indian Mesolithic and advanced the idea that the biological model known as punctuated equilibrium, rather than its alternative phyletic gradualism (Eldredge and Gould 1972), could explain the cultural stasis of the Mesolithic period in India. More recently, Prof. Bhattacharya (1999, 2002) advocated the view that insights derived from ethnoarchaeological research, on the Bihror in particular, are directly relevant to gaining a better idea of the social and economic processes of adaptation in Mesolithic cultures. The role of inter-group economic exchange and the impact of symbiotic relations between hunter-gatherers and settled groups is especially relevant in the South Asian context, since biological as well as cultural consequences have been documented (Bhattacharya 2002; Lukacs 1990, 2002).

The Indo-Gangetic Plains of northern India provide two clusters of human settlement in early to middle Holocene times. Neolithic Mehrgarh (MR3; Baluchistan, Pakistan) is located in the Kachhi Plain of the greater Indus Valley (Jarrige and Meadow, 1980), and the Mesolithic Lake Culture Complex (MLC; Uttar Pradesh, India) is situated in the middle of the Ganga Plain, north of Allahabad (Sharma 1973). These sites have yielded human skeletal remains in abundance and provide a unique opportunity to evaluate issues of human biological variation in the Indo-Gangetic Plain during the early / middle Holocene.

The dental morphology and odontometry of Lake Culture Complex sites (Damdama, Mahadaha, and Sarai Nahar Rai) in the middle Ganga Valley are described and compared with the pene-contemporary sample from Neolithic Mehrgarh. The dental pathology of these sites was previously analyzed to draw inferences regarding dietary and subsistence patterns (Lukacs and Pal 1993). While a preliminary comparison of tooth size was included in that study, the dental morphology and odontometry of an enlarged MLC sample is reported here for the first time. (See Map).

This study was conducted to address broad questions of population affinity (dental morphology) and biological adaptation (tooth size) between 9000 and 8000 yr BP in northern India. Located in different drainage basins and separated by 1500 km (Fig. 1), how similar or distinctive are the Neolithic people of Mehrgarh and the Mesolithic foragers of the Ganga Plain? Do these early settlements in the Indus and Ganga Valleys represent separate distinctive, genetically isolated, populations? Or might they represent samples from one large north Indian breeding population? In dental dimensions and tooth size apportionment, how similar or distinct are the Mehrgarh and the Mesolithic Lake Culture samples? Can inter-group variation in odontometry or size apportionment be correlated with cultural patterns of subsistence or food preparation? These are the questions that motivated the study, but before directly answering them the sites in question must be placed in context of prior archaeological and anthropological research.

Archaeological Context

The site of Damdama is located in the middle Ganga Plain, 72 km NNE of the modern city of Allahadad (lat. 26E10' N; long. 82E10' E). Sister-sites are located nearby: Mahadaha - 5 km SSE and Sarai Nahar Rai - 40 km SW of Damdama. MLC 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 that consist of faunal remains, stone and bone tools, and abundant human burials.

The antiquity of MLC sites is problematic for several reasons, but recent AMS 14C dates derived from human bone samples suggest an early Holocene antiquity (8865 and 8640 B.P.; Lukacs *et al.* 1996).

The Mehrgarh site complex is situated in the Kachhi Plain on flat alluvium, 15 m above the active Bolan River (lat. 29E 28' N; long. 67E 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 B.P., and continues through early Chalcolithic MR2, 6500 B.P.), to late Chacolithic (MR1, 4500 B.P.; Jarrige and Lechavellier1980).

Cemeteries are similarly located within the living area at both sites, though the depth of burial features at Mehrgarh (MR3; 11.0 m) is substantially greater than the depth of deposition at MLC sites: Damdama (DDM; 1.50 m), Mahadaha (MDH; 0.60 m), Sarai Nahar Rai (SNR; 0.06).

Burials exhibit significant differences in structural features, position of the deceased, and funerary accouterments. 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 decomposition of joints (Lechevallier and Quivron 1981, 1985; Sellier 1990, 1992). A general description of Mesolithic Lake Culture settlements (Pal 1986, 1994) and burials by Pal (1992) note the close association of hearths, artifacts, and burials at DDM and MDH. Site-specific burial descriptions, line drawings and photographs are available for SNR (Sharma 1973) and MDH (Pal 1985). Particular attention has been given to variation in the orientation and position the 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 Mehrgarh and among the Lake Culture complex. Representative burials from Neolithic Mehrgarh (MR 3 - 153) and Mesolithic Damdama (DDM - 38) are provided in Figure 2. Note the absence of structural features and burial goods in the MLC burial from Damdama.

Table 1. Comparison of Burial Features in early Holocene Indus and Ganga Iraves.

Burial Feature	*Neolithic Mehrgarh-Indus* (MR 3)	*Mesolithic Lake Culture -Ganga* (DDM, MDH, SNR)
Structures	mud brick wall	ovoid pit
Orientation of body	west-east	west-east
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 & cores	few : body ornaments (antler, bone) lithics fauna
Example	MR 3 - 153 (Fig. 2a)	DDM - 38 (Fig. 2b)

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 MLC sites.

Bioarchaeological Foundations : The Context of Research

This study of dental morphometric 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; Lukacs and Hemphill 1991), dental wear patterns (Lukacs and Pastor 1988, 1990), as well as diverse aspects 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 1991, 1996).

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 & Pal 1993) confirm a phenotypic pattern similar to that described for SNR and MDH. More recently, the analysis of human remains from Damdama have focused on aspects of skeletal pathology and subsistence patterns (Lukacs and Pal 2004) 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 the foundation of prior research and comprise the first inter-regional comparison of dental morphometric variation between pene-contemporaneous early Holocene populations of the greater Indus Valley and middle Ganga Plains.

DENTAL MORPHOLOGY

Morphological traits of the tooth crown were observed and classified according to standards of the Arizona State University (ASU) dental anthropology system (Turner *et al.* 1991). Homogeneity in the bio-cultural attributes of Mesolithic Lake Culture sites constitutes the basis for pooling dental morphological observations from Damdama (DDM), Mahadaha (MDH), and Sarai Nahar Rai (SNR) 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 MDH and SNR alone, were inadequate to accurately characterize 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 are presented in Figures 3a and 3b, 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 (UI2), and molar traits (hypocone, Carabelli's trait and metaconule), yet significant differences occur in only 2 traits: tuberculum dental (UI2) and the metaconule (UM2). 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 & C-7), while 5 cusped molars are more frequent at Mehrgarh (M1 & M3). Three lower molar traits are significantly different between groups: 5 cusped M3, Y groove M3, and the entoconulid (C-6, M3).

A comparison of dental trait frequencies at Meolithic Lake Culture (MLC) sites with Neolithic Mehrgarh (MR 3) and five key South Asian prehistoric samples is designed to reveal similarities and differences in trait expression. Morphological trait frequencies for all seven groups are presented in Table 2 (P = present; N = sample size; f = trait frequency). Chi-square test reveals that more than half (6/11) maxillary dental traits and 30% (3/10) mandibular traits compared are significantly different among groups. In order to facilitate inter-group comparison of trait expression, standardized frequencies (mean = 0, sd = 1) of selected traits are presented for six traits and seven samples (Figure 4). Arranged in approximate chronological order from left (earliest) to right (latest) these groups are :

MLC =	Mesolithic Lake Cultures (DDM, MDH, SNR; Ganga sample)
MR 3=	Neolithic Mehrgarh (Indus sample)
MR 2=	Chalcolithic Mehrgarh
HAR =	Harappa
INM =	Inamgaon
TMG =	Timargarha
SKH =	Sarai Khola

In maxillary incisor traits (Fig. 4, panel a), Ganga Lake Cultures and Neolithic Mehrgarh show strong positive deviations for UI1 shovelling, but express divergent deviations in marginal interruptions for UI2 : MLC negative and MR 3 positive. In upper molar morphology (Fig. 4, panel b), the Ganga and Indus samples share negative deviations for Carabelli's trait (UM1), though the Lake Culture sample is more strongly negative than the Indus sample. Expression of the metaconule (UM2) is strongly divergent as well, with moderate negative values for MLC and a highly positive deviation for Neolithic Mehrgarh period. Lower molar traits (Fig 4, panel c) display different patterns as well, with 5 cusped LM2 exhibiting a strong positive deviation in the Ganga sample and a modest negative deviation in the Indus sample, however both groups express moderately positive deviation for the Y occlusal groove pattern in LM2.

Overall the MLC 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 (C-5). Examples of mandibular dental traits include low levels of incisor shoveling and the distal canine accessory ridge, molarized P4, and the presence of Y-groove and five-cusped M2.

The relationship among South Asian prehistoric skeletal samples was preliminarily assessed using Ward's minimum variance cluster analysis with standardized trait frequencies as input. The results are presented in Figure 5 and are in close agreement with previous studies (Lukacs 1986) documenting affinity between neolithic Mehrgarh (MR 3) and Inamgaon (INM), a Chalcolithic site in peninsular west India. Yet this new analysis contrasts with prior results (Lukacs and Hemphill 1991) in revealing a closer linkage between Mesolithic Ganga Plain sites (DDM, MDH, SNR) and the cluster comprised of neolithic Mehrgarh and Inamgaon.

ODONTOMETRICS

Mesiodistal and buccolingual crown dimensions were measured according to guidelines set forth by Buikstra and Ubelaker (1994) and by Kieser (1990). The following analysis employs the composite variable of crown area and derived variables including anterior, post-canine, and total crown area in comparing tooth size variation at Mesolithic Damdama and Neolithic Mehrgarh. Based on the overall impression of increased sedentism, greater progress toward domestication, and more complex material culture at Neolithic Mehrgarh, the hypothesis under consideration here is that people of the Mesolithic Lake Cultures should display larger dental crown areas than Neolithic inhabitants of Mehrgarh.

Table 3 presents mean crown areas for maxillary and mandibular teeth at Mehrgarh and Damdama, together with results of t-tests. These data are presented graphically in Figure 6, in which bar height indicates crown area and the error bar signifies one standard deviation. All comparisons reveal significantly larger tooth crown areas at Damdama than at Mehrgarh, with the only exception being third molars. The largest differences are evident in maxillary and mandibular canine teeth, and in mandibular P4 and M2. Total crown area at Damdama (1383.0 mm^2) is 121.0 mm^2 greater than the total crown area at Neolithic Mehrgarh (1262.0 mm^2). This overall difference is difficult to evaluate statistically, since it is a sum of individual tooth crown areas and has no associated indicator of variance. However, an experimental analysis conducted by Brace on complete dental arcades of Australian aboriginals, revealed that inter-group differences in crown area of approximately 50 mm^2 were regarded as significant $\alpha = 0.05$, and differences of ≥ 100 mm^2 were likely to have significance $\alpha = 0.01$ (Brace 1980). According to these guidelines, tooth size among Mesolithic inhabitants of the Ganga Plain is significantly greater than tooth size among Neolithic people of Mehrgarh.

Two additional perspectives on variation in tooth size among prehistoric South Asians are presented here : a) one based on standardized deviations of composite crown areas; and b) the second plots total crown area against time. Crown areas were summed separately for anterior (I1, I2 & C) and post-canine teeth (P3, P4, M1, M2 & M3) and for all teeth, then standardized deviations (mean = 0, std=1) for each composite variable were plotted in the vertical bar chart for seven prehistoric South Asian skeletal series. The results are presented in Figure 7a (maxillary teeth) and Figure 7b (mandibular teeth). Sites are arranged in approximate chronological sequence from left (older) to right (younger), a sequence that is associated with changes in material culture from semi-nomadic mesolithic cultures (Damdama, DDM and Mahadaha MDH), through early agriculturalists (Neolithic and Chalcolithic Mehrgarh, MR 3 and MR 2), to later urban or more sedentary agricultural groups (Harappa, HAR; Timargarha, TMG; and Sarai Khola, SKH). Deviations above the zero line represent relatively large toothed groups while those below the zero line signify small toothed groups. The dashed line indicates the overall trend toward reduced tooth size through time, a change associated with an increasingly efficient technology of food preparation and changes in subsistence, including greater reliance on agricultural produce.

The final characterization of dental reduction in South Asian prehistory is based on a plot of total crown area against antiquity in radiocarbon years B.P. (Figure 8). In this scatter plot, time in years before present is scaled on the x axis, and summed (total) tooth crown size, in millimeters squared is scaled on the y axis. The least squares regression line (solid line) and 95% confidence limits (dashed curved lines) are included. The Mesolithic Lake Culture sites in this scatter plot (Damdama and Mahadaha) appear above the regression line, suggesting somewhat larger total crown areas for their antiquity than Neolithic Mehrgarh, whose summed crown area falls well below the regression line, and on the line indicating the lower 95% confidence limit. Collectively, Figures 6 through 8, demonstrate from slightly different perspectives the large tooth size of Mesolithic foragers of the Ganga Plain, the comparatively smaller tooth size of the Neolithic inhabitants of Mehrgarh, and the association between time, technology, subsistence and dental reduction in South Asian prehistory.

CONCLUSIONS

This comparative analysis of morphometric variation in the dentition of early Holocene inhabitants of the Ganga and Indus Valleys yields new insight into population relationships and adaptive aspects of dental variation in South Asian prehistory. Significant findings derived from this study include :

1) More similarities than differences in dental morphology. Neolithic Mehrgarh and Mesolithic Lake Culture (MLC) sites of the Ganga Plain exhibit more similarities than differences in dental trait frequencies. Nevertheless, some differences in anterior and posterior dental traits are sufficiently important to imply a moderate degree of biological distance between groups. The enlarged dental sample from Damdama permits statistical comparisons that reveal affinities between MLC sites of the Ganga Plain and a cluster comprised of Neolithic Mehrgarh and Inamgaon.

2) Lake Culture Complex sites display significantly larger teeth than the Neolithic Mehrgarh sample. The Mesolithic foragers of the Ganga Plain clearly display significantly larger teeth throughout the dental arcade. The differences in tooth crown area between Mehrgarh and Damdama are great and appear consistent with inter-site differences in material culture, food processing technology and subsistence patterns.

Table 2. Dental Morphology Trait Frequencies - Prehistoric South Asia.

Antiquity (yrs BP)		Mesolithic Lake Culture 8700			Neolithic Mehrgarh 8000			Chalcolithic Mehrgarh 6500			Haarappa 4500			Inamgaon 3350-2650			Timargarha 3000			Sarai Khola 2000		
Dental Trait	Tooth	P	N	f	P	N	f	P	N	f	P	N	f	P	N	f	P	N	f	P	N	f
Shovel-shape	UI1	20	23	0.870	25	28	0.893	21	25	0.840	10	18	0.556	22	24	0.917	7	7	0.143	3	9	0.333
	UI2	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
Tuberculum	UI1	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
dentale	UI2	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	UI1	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
Groove	UI2	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	2	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	1	0.000	2	13	0.154
Carabelis Trait	UM1	2	20	0.100	7	27	0.259	11	18	0.611	4	9	0.444	13	40	0.325	9	1	0.500	2	9	0.222
Metaconule	UM1	3	16	0.188	7	28	0.250	5	19	0.263	6	13	0.462	6	41	0.146	4	1	0.211	3	9	0.333
(C-5)	UM2	3	23	0.130	10	25	0.400	6	18	0.333	4	16	0.250	3	20	0.150	0	1	0.000	2	14	0.143
Cusp Number	LM1	14	20	0.700	39	43	0.907	20	23	0.870	17	20	0.850	32	39	0.821	19	2	0760	9	15	0.600
	LM2	6	26	0.231	3	49	0.061	2	24	0.083	0	33	0.000	4	24	0.167	3	1	0.176	1	15	0.067
Y-Groove	LM1	17	17	1.000	23	25	0.920	15	21	0.714	15	17	0.882	32	35	0.914	12	1	0.706	5	7	0.714
Pattern	LM2	9	24	0.375	12	37	0.324	6	22	0.273	3	31	0.097	7	24	0.292	3	1	0.167	5	14	0.357
Entoconulid	LM1	1	17	0.059	3	37	0.081	5	23	0.217	1	20	0.050	4	37	0.108	0	2	0.000	1	14	0.071
(C-6)	LM2	1	25	0.040	0	44	0.000	1	23	0.043	0	28	0.000	0	24	0.000	1	1	0.056	0	15	0.000
Metaconulid	LM1	3	23	0.130	4	40	0.100	3	25	0.120	1	22	0.045	2	36	0.056	2	2	0.083	1	15	0.067
(C-7)	LM2	1	32	0.031	0	43	0.000	0	24	0.000	0	28	0.000	1	25	0.040	2	2	0.100	0	15	0.000

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

Table 3. Tooth Crown Areas Compared : Mesolithic Damdama Vs Neolithic Mehrgarh.

	Damdama (Ganga Plain, MLC)			Statistical Result			Neolithic Mehrgarh (MR3)		
Tooth	mean	n	StDev	diff	t	p	mean	n	StDev
UI1	71.4	15	7.8	7.8	3.497	0.001	63.6	28	6.5
UI2	52.6	11	4.2	4.8	3.077	0.004	47.8	30	4.5
UC	75.0	17	7.6	10.0	5.582	<0.001	65.0	34	5.1
UP3	77.1	19	7.1	9.1	4.894	<0.001	68.0	35	6.2
UP4	70.2	21	8.0	5.0	2.498	0.016	65.2	31	6.4
UM1	136.3	17	13.5	9.6	2.832	0.007	126.7	38	10.7
UM2	125.8	23	10.9	8.1	3.088	0.030	117.7	37	9.2
UM3	109.2	24	18.7	4.5	0.922	0.361	104.7	29	16.8
max total	717.6	--	--	58.9	--	--	658.7	--	--
LI1	37.6	8	2.3	4.4	3.564	0.001	33.2	23	3.2
LI2	43.8	7	3.3	4.5	3.309	0.002	39.3	28	3.2
LC	63.5	15	8.1	10.8	5.220	<0.001	52.7	36	6.1
LP3	66.3	16	7.7	9.8	5.053	<0.001	56.5	37	5.9
LP4	71.3	16	10.1	10.6	4.534	<0.001	60.7	39	6.8
LM1	136.2	11	13.7	7.3	2.027	0.048	128.9	37	9.4
LM2	129.1	20	12.9	14.8	4.586	<0.001	114.3	40	11.2
LM3	117.6	22	17.5	-0.1	-0.024	0.981	117.7	36	13.7
mand total	665.4	--	--	62.1	--	--	603.3	--	--
total	1383.0	--	--	121.0	--	--	1262.0	--	--

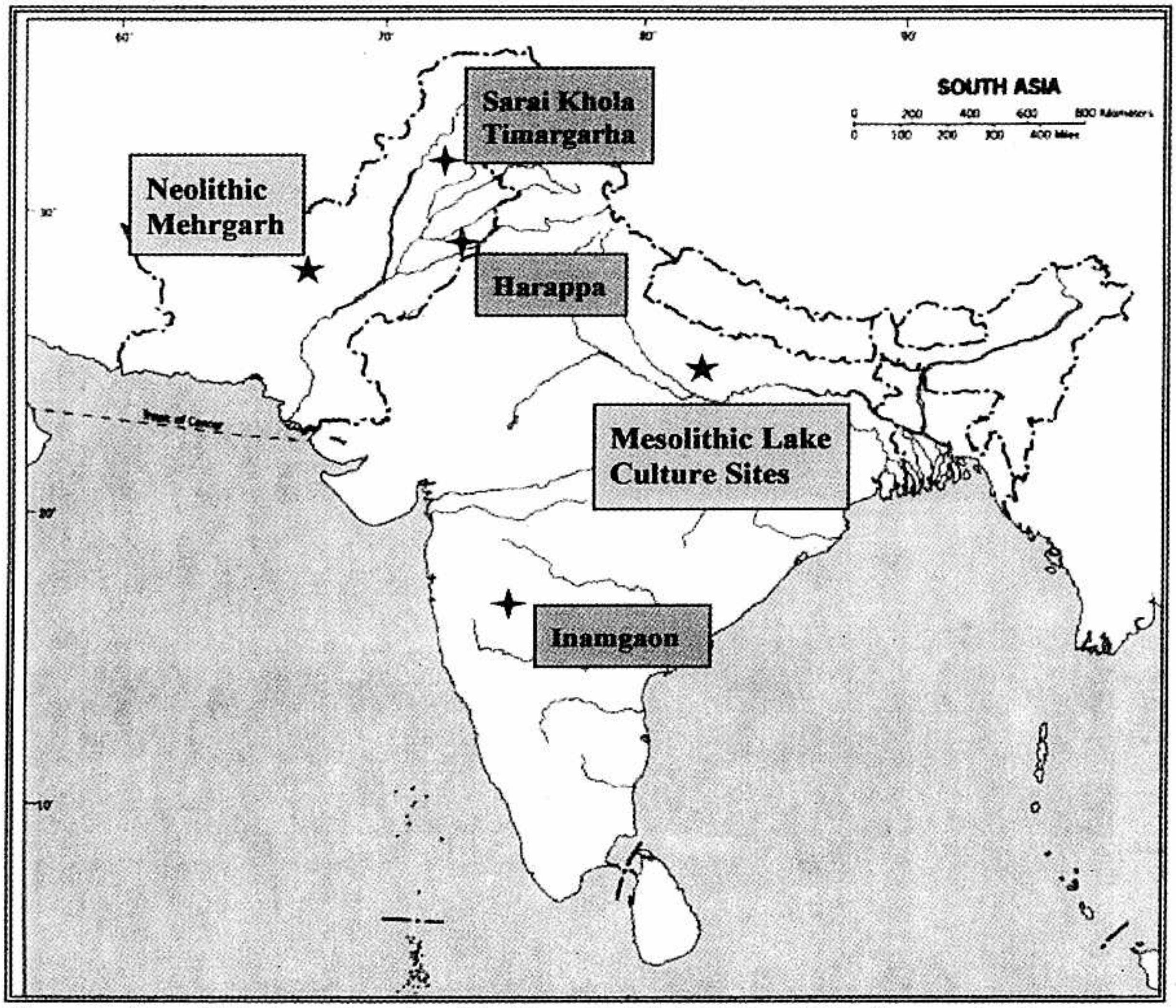

Figure 1. Map of Site Locations. (modified from DeBlij & Muller 2002. *Geography: Realms, Regions and Concepts.* New York: John Wiley and Sons.)

SITE LOCATION MAP