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A Cranial Nonmetric Trait Investigation of Chalcolithic-Bronze Age Era Interactions across the Iranian Plateau: Methodological Protocols and Interaction Scenarios

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Abstract: A battery of 32 cranial nonmetric traits were assessed among 436 adult individuals recovered from nine Chalcolithic and Bronze Age archaeological contexts from the western, northern and southeastern peripheries of the Iranian Plateau. Three archaeologically based theoretical models of interactions across the plateau—the Neolithic food prodfuction, the Namazga expansion, and Bronze Age interregional interaction—were evaluated with four analytical models. In the first model all 32 traits were included. In the second model only those traits that differ across all nine samples at $\alpha < 0.05$ were retained. In the third model only those that met the alpha threshold with Bonferroni's adjustment for multiple comparisons were included. In the fourth model, samples found not to differ from one another with the first three models were pooled and only those traits that met Holm's (1979) nested rejective modification of Bonferroni's adjustment were employed. Retained traits were assessed with correspondence analysis, neighbour-joining cluster analysis, and multidimensional scaling. Results indicate that the fourth method yielded the most robust and non-volatile patterns of intersample affinities. None of the three reconstructions were supported in their entirety by the pattern of biodistance affinities obtained from cranial nonmetric trait frequencies. However, the biodistance patterns are most congruent with those expected with a population expansion across the Iranian Plateau during Neolithic era fueled by food production and animal husbandry that resulted in a pattern of interregional biological affinities dominated by long-standing bouts of in situ continuity. Some support is found for an overlay on this general pattern laid down in the Neolithic due to population growth and dispersal during the subsequent Namazga expansion, especially in southern Central Asia. In contrast, no support is provided forsignificant impacts due to Bronze Age interregional interactionps.

Keywords: Biodistance, Spread of Agriculture, Gene Flow, Genetic Drift, Indus Valley, Interregional Trade

Introduction

Cranial Nonmetric Trait Variation and Biological Distance Analysis

Nonmetric cranial traits have been used for many years to examine evolutionary relationships between populations defined at various levels (cf. Berry, A.C. and Berry, R.J., 1967; Berry, R.J., 1963; Brothwell, 1958; Green and Suchey, 1976; Halgrimsson *et al.*, 2004; Hanihara *et al.*, 2004; Hanken and Hall, 1993; Hauser and De Stefano, 1989; Ishida and Dodo, 1993; Lane and Sublett, 1972; Laughlin and Jørgensen, 1956; Pardoe, 1991; Saunders, 1989; Sjøvold, 1973; Sutter and Mertz, 2004). These traits are known to develop during the growth and development of an individual, particularly in the embryological and early postnatal phases (Berry and Seable, 1963; Cheverud and Buikstra, 1981a; Pucciarelli, 1974; Richtsmeier and McGrath, 1986; Barnes, 1994; Lieberman *et al,* 2000b). These traits do not follow a simple Mendelian pattern of inheritance but instead conform to what Grüneberg (1951, 1952, 1963, 1965) described as a quasi-continuous pattern of inheritance involving an array of multiple genes with small additive effects. Consequently, such traits are expressed either as present/absent, or when present to varying degrees of expression (Harris, 1977; Scott, 1973).

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During the 1970s and '80s cranial nonmetric traits were favoured in biodistance studies because, unlike metric variables, nonmetric traits were maintained to be independent of age (Erdene, 2008; Movsesian, 2013; Movsesian and Vagner-Sapukhina, 2021) and sex (Erdene, 2008; Movsesian, 2013; Movsesian and Vagner-Sapukhina, 2021), were largely independent of one another (Erdene, 2008; Hanihara, Ishida, and Dodo, 2003; Movsesian, 2013; Nakashima *et al.*, 2010), were only minimally affected by environmental factors (but see Carson, 2006), and — because of their ease in scoring — were held to be less subject to intra- and interoberver error (Berry, A.C. and Berry, R.J., 1967). However, subsequent research has revealed that cranial nonmetric traits share similar developmental patterns with metric variation of the cranium, both generally and locally (Cheverud *et al.*, 1979; Corruccini, 1974, 1976; Prowse and Lovell, 1995). Other researchers have reported significant differences in trait frequencies between males and females of the same ethnic group (Berry, A.C., 1975; Corruccini, 1974; Herrera, Hanihara, and Godde, 2014; Finnegan, 1972; Jantz, 1970; Khudaverdyan, 2012; Mouri, 1976, 1988; Perizonius, 1979; Sublett, 1967; Tagaya, 2020; Vecchi, 1968), but others have not (Ossenberg, 1976, 1977). Likewise, some researchers have reported the presence of age effects (Akbori, 1933; Buikstra, 1972; Carpenter, 1976; Corruccini, 1974; Khudaverdyan, 2012), but others have either found no such age effects (Perizonius, 1979), that age effects are largely confined to infancy and early adulthood (Ossenberg, 1969, 1970; but see Barnes, 1994; Del Papa and Perez, 2007; Kongisberg *et al.*, 1993; Lieberman *et al.*, 2000a,b), or that such effects tend to be highly erratic across samples (Corruccini, 1974).

Nevertheless, despite the liability of such traits to be affected by environmental and maternal factors (Carpenter, 1976; Cheverud, 1979; Cheverud and Buikstra, 1981a,b; Corruccini, 1974; Dahinten and Pucciarelli, 1983; Deol and Truslove, 1957; Jantz, 1970; Ossenberg, 1970; Rightmire, 1972; Searle, 1954; Self and Leamy, 1978; Suchey, 1975; Trinkaus, 1978; Wilkinson, 1971), a majority of studies have confirmed that these traits are marked by rather high heritability values (Berry, A.C., 1975; Berry, A.C. and Berry, R.J., 1967; Cheverud and Buikstra, 1981a,b; Erdene, 2008; Hertzog, 1968; Lane, 1977; Movsesian, 2005; Pietrusewsky and Douglas, 1993; Richtsmeier and McGrath, 1986; Saunders, 1989; Saunders and Popovich, 1978; Selby *et al.*, 1955; Sjøvold, 1973; Torgerson, 1951a,b; but see Carson, 2006). Indeed, heritability values — especially for hyperostotic traits — were found by Cheverud and Buikstra (1982) to be significantly higher (median h^2= 0.722) in a sample of free-ranging macaques than those for metric variables (median h^2= 0.294; but see Corruccini, 1976), although the same cannot be asserted for foraminal traits (median h^2= 0.343).

Estimates of population distances with such biodistance measures as Smith's mean measure of divergence (MMD) statistic assume that individual traits are uncorrelated (Grewal, 1962; Berry, R.J., 1963; Sjøvold, 1973, 1977). Although there appears to be some relationship between cranial size and nonmetric trait variation (Gruneberg, 1952; Corruccini, 1976; Richtsmeier *et al.*, 1984). Dodo, Noi, and Kondo (1998) found in their examination of craniometric and nonmetric variation among 1,835 crania from 18 Ainu and Ryukyuan samples that average tetrachoric correlations among cranial nonmetric traits (0.068) were far lower than the average correlations among 18 metric variables (0.235).

Ever since publication of Berry and Berry's (1967) seminal paper on cranial nonmetric variation among human populations the relative value of metric versus nonmetric variables for biodistance analysis have been the subject of much debate. Jantz (1970) reviewed metric- and nonmetric comparative studies and correlated discrete and metrical distances. He found concordance to range between r= -0.48 to r= 0.66, leading him to conclude that there is only a 'vague relation' between these two systems of biological variation. Jantz interpreted the metrical distances as more genetically meaningful and a similar conclusion has been reached by others working on a wide array of recent human populations (Carpenter, 1976; El-Najjar, 1974; Rightmire, 1972; Zegura, 1975) . In contrast, a similar review by Corruccini (1974) yielded very different results. He found the correlation between metric (d2) and nonmetric (Θ2) distances to be r= 0.777. This signals a high degree of concordance between the two systems of variation and hence Corruccini (1974, 1976) concluded that there is no basis to judge one type of data over the other as more reflective of genetic differences between populations. Indeed, in recent years cranial nonmetric traits have been advocated as reflecting patterns among human populations similar to those obtained through other avenues of biological variation, including molecular genetic analyses, locally (Spence, 1974; Spence *et al.*, 2005; Velasco 2018), regionally (Beekman and Christensen, 2003; Herrera *et al.*, 2014; Movesesian, 2013; Movsesian and Bakholdi, 2017; Nikita *et al.*, 2012) and worldwide (Hanihara *et al.*, 2012).

Prehistoric Interactions across the Iranian Plateau

It has been known for some time that post-Pleistocene population interactions in the eastern Mediterranean, southern Central Asia, and the Indus Valley featured contacts across the Iranian Plateau. Initially, Amiet (1977, 1988) maintained that such interactions involved a primarily west to east vector of contact from Elam in southwestern Iran across an array of local polities scattered on and alongside the Iranian Plateau in the wake of the collapse of Uruk (Algaze, 1993). In another formulation, Sarianidi (1999) called for two waves of dispersion of Indo-Aryan-speaking populations from the Syro-Anatolian region. He envisioned the first as spreading across northern Iran and terminating in Margiana, Bactria, and perhaps Xinjiang, while the second dispersed across southern Iran to Khorassan and Pakistani Baluchistan. In yet another formulation, Renfrew (1989) suggested that initial interactions across the Iranian Plateau came about with a wave-of-advance dispersal of Indo-Aryan-speaking populations who brought crop cultivation and animal husbandry to the Iranian Plateau.

Neolithic Food Production

Evidence for food production and establishment of early farming villages at Djeitun was discovered in southern Turkmenistan in the early 1990s (Harris, 1997a, b; Harris and Godsen, 1996; Masson & Harris, 1994). Here, remains of six-row barley (*Hordeum sativum*), einkorn (*Triticum monoccum*), emmer (*T. dicoccum*) and possibly bread wheat (*T. aestivum*) were recovered from levels dated between 6380-5770 cal BCE (Harris, 2010; Harris *et al.*, 1993). Sites of the food-producing Djeitun culture encompass the latter half of the 7th and the entirety of the 6th millennia BCE (Dolukhanov, 1986; Korobkova and Masson, 1978) and are found in an area of some 400 km^2 extending from the northern slopes of the Kopet Dagh foothills (the piedmont) to the Gorgan Plain adjacent to the Caspian Sea in the west and to the Turkmeno-Khorassan Mountains in the east (Kohl, 1984; Masson and Sarianidi, 1972). Site locations in terminal deltaic fans suggest that food production was based on dry farming — a parlous undertaking in this ecological setting (Bonora and Vidale, 2013; Harris and Gosden, 1996; Hiebert, 2002; Sarianidi, 1992; but see Usitsina, 2016).

Subsequent cultural development during the Chalcolithic (*i.e.,* Aeneolithic) era (*c.* 4500-2800 BCE; Bonora and Vidale, 2013) is maintained to have been a largely indigenous affair with common overarching themes across the Kopet Dagh foothill piedmont of southern Turkmenistan coupled with subregional distinctiveness in the western, central and eastern portions of the piedmont as populations gradually spread eastward (Hiebert, 1994; Khlopin, 1963, 1964, 1974; Kohl, 1984, 1992; Masson 1992a; Tosi, 1983), culminating in the first settlement of a desert oasis environment (the Geoksyur oasis) — a settlement made possible through the development of intensive irrigation works during the Middle to Late Chalcolithic (Gupta, 1979; Khlopin, 1964; Lisitsina, 1969, 1978; Masson, 1992a; Tosi, 1973-74).

The Namazga Expansion

Other researchers, while recognising the importance of the shift from food collection to food production during the Neolithic, assert that these early influences were overshadowed by later developments during the Chalcolithic, for it is during the era between the Late Chalcolithic through the Middle Bronze Age (*c.* 3000 – 2200 BCE: Kohl, 1992) that regional styles of the central, east and western zones of the Kopet Dagh foothill plain arose (Hiebert, 1994, 166; Kohl, 1992, 183). While the Early Chalcolithic (NMG I: *c.* 4500-4000 BCE: Kohl, 1992) largely attests to a continuance of the long-standing local village lifeway established during the preceding Iranian-inspired Neolithic Djeitun and Early Chalcolithic Anau I cultures (Hiebert, 2002; Kohl, 1984, 1992; Masson and Sarianidi, 1972), the subsequent Middle Chalcolithic period (NMG II: *c.* 4000-3500 BCE: Kohl , 1992) is marked by considerable change. These include a fundamental change in community and domestic architecture, evidence of increasing social differences (*i.e.*, social stratification), increasing regional differences in ceramic wares, and a great expansion of the newly colonized desert-adapted settlements within the Geoksyur oasis (Khlopin, 1964; Lisitsina, 1969; Masson, 1992a).

According to Tosi (1973-74), initial colonization of the Tedjen River delta occurred during the final portion of the Early Chalcolithic (*c.* 4250 – 4000 BCE: Kohl, 1992). This appears to have been a gradual, expansionist process rather than a migratory shift stimulated by the acquisition of the technical knowledge required to colonize a river delta with a medium flow-rate. Initially Late Namazga II wares are found at sites within the Tedjen delta but later Namzga III wares are found, not only throughout the delta, but also further afield at Sarazm in the upper Zeravshan valley, in Khorassan, and even with the Period I occupation at Shahr-I Sokhta in Seistan (Biscione, 1973; Lyonnet and Dubova, 2020; Muftin and Lamberg-Karlovsky, 2020). In fact, Namaza III wares have been found at Mundigak in the Helmand Valley and at Quetta along the western margin of the Indus Valley (Biscione and Vahdati, 2020; Kohl and Lyonnet, 2008; Lyonnet and Dubova, 2020).

Recognizing the common geographic pattern of the Namazga expansion of the third millennium and the subsequent expansion of the Bactrian-Margiana Archaeological Complex (BMAC) a 1,000 years later, several authorities have suggested the development of the latter is ultimate consequence of a long multiregional, multicultural congeries (Jarrige, C. *et al.*, 1995; Jarrige, 1994; Mutin, 2013, 2020; Mutin & Lamberg-Karlovsky, 2020). Consequently, the Namazga expansion encompassing a geographic area between southern Central Asia, the western margin of the Indus Valley, and southeastern Iran served as the 'formative area' for the later BMAC (Biscione and Vahdati, 2020; but see Mutin and Lamberg-Karlovsky, 2020). Therefore, it is to the Namazga expansion of the third millennium that the crucial population conacts were forged that shaped interactions across the Iranian Plateau during the later Bronze Age.

Bronze Age Interregional Interaction

The initial signs of interregional interaction during the Namazga expansion of the third millennium only intensify during the course of the subsequent millennium. Indeed, Jarrige and Hassan (1989) argue that interregional contacts across the Indo-Iranian borderlands are clearly evident by the end of the fourth millennium BCE thereby establishing the foundation for the dramatic intensification of such contacts during the late third and early second millennia BCE .

It is during the late Middle Bronze Age that urban centers of the foothill zone are structurally differentiated from surrounding secondary villages (Kircho, 1980) and these urban centers grew to larger sizes than ever before. It has been suggested that these cities exceeded their carrying capacities resulting in an 'urban crisis' (Biscione, 1977; Masson, 1992b) in which 'we can suggest that, given a crisis in food production in the foothill sites, the long-known richness of the desert oases would seem very attractive, people from the foothill sites would then invest the energy necessary to clear the land and settle there. There may be a correlation between the depopulation of the urban foothill sites of the Kopet Dagh at the end of Namazga V and the origins of widespread occupation in Bactria' (Hiebert 1994, 172). It may be that as the Tedjen delta itself became populated, the quest for raw matereials may have taken the Namazgans ever further afield in their quest for resources (Hiebert, 1994; Mutin and Lamberg-Karlovsky, 2020).

Recognising the continuity between the earlier Namazga expansion and the later expansion of the BMAC, Biscione and Vahdati (2020) maintain that the formative area for the characteristic objects of the BMAC are to be found in Khorasan, south of the traditional "core area" encompassing the oases of Bactria and Margiana (Lyonnet and Dubova, 2020). Many explanations have been proposed for the widespread distribution of Bronze Age oasis settlements in Margiana and Bactria. These include migrations from the Iranian Plateau (Sarianidi, 1987), evolution from the Baluchistan tradition (Jarrige, 1991), nomadic incursions (Alyekshin, 1980), migration from the southern foothill zone (Biscione 1977; Hiebert, 1994, 2002; Hiebert and Lamberg-Karlovsky, 1992; Jarrige, 1994; Parpola, 1988, 1993a, 1995), and continuous growth from a local population in the oasis areas (Udemuradov, 1988). Regardless of origin, initial occupation of Margiana appears to have occurred simultaneously over a large area and the myriad similarities in the ceramics, small finds, and architecture have suggested to many authorities that the cultural traditions of the colonists remained very close to the foothill culture during the initial phase of colonisation in Margiana, but perhaps less so for the intial phase of occupation of the Bactrian oases further east (Francfort, 1984; Gözelt, 1995; Salvatori, 1995, 2000, 2008).

Thus, according to most researchers the origins of BMAC were largely local (Anthony, 2007; Francfort, 2005; Hiebert, 1994; Kohl and Lyonnet, 2008; Lamberg-Karlovsky, 2002, 2012; Salvatori, 2016; Vidale, 2017) during a period of interregional interaction between 3000 – 2500/2200 BCE (Francfort, 2005; Hiebert, 1994; P'yankova, 1994), while the materials recovered from sites in Seistan and other southern regions represent a subsequent diffusion from the BMAC homeland (Lamberg-Karlovsky, 2012; Mutin and Lamberg-Karlovsky, 2020). Salvatori (2000) concurs with this scenario, but suggests that after initial exuberance the period after 1900 BCE witnesses a marked decline in interregional trade (Salvatori, 2016; see also Biscione and Vahdati, 2020) and it may be the the polarity of expansion shifted from north to south to south to north (Mutin and Lamberg-Karlovsky, 2020).

There has been considerable disagreement over the factors behind the rapid dispersal of BMAC artefacts across a broad area of the Iranian Plateau and adjacent Indo-Iranian borderlands. BMAC presence ranges from coexistence with objects of the local cultural tradition to the presence of just a few luxury goods (Biscione and Vahdati, 2020). Possible explanations for the presence of nonlocal objects in the BMAC style include gifts, strategic marriages, and diplomatic exchanges (Lyonnet and Dubova, 2020). With regard to the latter, Jarrige (1991) suggested that the ornate bronze axes may have represented a shared prestige object used to legitimize political authority among the elite across a vast area. The fact that a large proportion of these exotic BMAC-type objects were obtained from funerary settings have suggested to many that trading was the most likely impetus behind the expansion of BMAC influence (Lyonnet and Dubova, 2020). Lapis lazuli was likely an important trade item, but trade in lapis long antedates the expansion of the BMAC (Francfort, 1981a; Tosi, 1973-1974). Another possibility is copper, but trade in copper also antedates the BMAC and appears to have been locally distributed (Lyonnet and Dubova, 2020). Far more likely is tin (Lyonnet, 2005; Kohl and Lyonnet, 2008; but see Kaniuth, 2007). Although there is disagreement as to when tin became important in alloying copper to make bronze, with Kaniuth (2006) and Tekekhova (1990) claiming it was little used during the first two period of the BMAC (Sapalli, Djarkutan), while Piggot (2018) believes it became important as early as the Late Chaclolithic at Khapuz Depe. Indeed, a number of authorities claim that the acquisition and distribution of tin to the Russo-Kazakh steppes to the north and to the Iranian Plateau and ultimately to Mesopotamia to the west was a major factor in in the rise and expansion of the BMAC (Anthony, 2007; Kohl and Lyonnet, 2008).

The nature of intereaction between BMAC populations and those of what Biscione and Vahdati (2020) term the 'influence area' are as yet unknown. Some have suggested that the emphasis upon trade resulted in movement of small populations of itinerant craftsmen rather than any large-scale population movement (Salvatori, 2010). Alternatively, they may have been dignitaries, raiders, or simply individuals seeking new lands and new opportunities (Mutin and Lamberg-Karlovsky, 2020). Several authorities have suggested that burials of individuals with BMAC artefacts are those of migrants from Margiana and Bactria. Indeed, as noted by Biscione and Vahdati (2020, p. 542), 'Isolated burials with grave goods mostly or fully BMAC/GKC indicate the presence of individuals originating from the core area who moved to other places for a variety of reasons (trade, specialized knowledge, and abilities needed abroad, etc.), as already stressed, for instance by Hiebert and Lamberg-Karlovsky (1992: 3, 6) or Thornton (2013: 195)'.

This reinforces the assertion from sites located in southeastern Iran that they cannot be considered a mere intrusion of BMAC-stype luxury goods, but represent a more significant presence (Mutin and Lamberg-Karlovsky, 2020). Likewise, Jarrige (1991) asserted that: the great number and nature of such BMAC artefacts relating to the Mehrgarh VIII/Dauda Damb cultural complex, evidence for a transitional phase at Nausharo in which Mehrgarh VIII ceramic components evolved from a previous Indus-related ceramic assemblage, while the permanent settlement at Sibri (Santoni, 1984) reflects a BMAC presence on the westeren periphery of the Indus Valley that included elites, craftsmen, and farmers who lived and interacted with the local indigenous population rather than unidirectional wholesale importation.

Materials and Methods

Materials

This research is based on examination of the cranial remains of 436 individuals (205 males, 209 females, 22 of unknown sex) recovered from sites located about the western, northern, and eastern periphery of the Iranian Plateau (Fig. 1). These sites range in antiquity from the mid-4th millennium BCE to the mid-2nd millennium BCE (Table 1). The greatest number of individuals (n= 169) were recovered from the site of Tepe Hissar located in northwestern Iran, followed by BMAC era individuals (n= 142) recovered from the site of Djarkutan located in the North Bactrian Oasis of southern Uzbekistan. The fewest individuals were recovered from the Middle Bronze Age Namazga V period occupation of Altyn depe, an urban center located in the Kopet Dagh foothill plain of southern Turkmenistan (n= 17) and from Cemetery R37 located at the Indus Valley urban center of Harappa (n= 20).

Methods

A total of 32 nonmetric traits were selected for study from those considered by Berry and Berry (1967), Brothwell (1972), Buikstra (1976), Hauser and De Stefano (1989) and Ossenberg (1969). Traits occurring in the sagittal plane were scored with the individual as the operational taxonomic unit (OTU). Contrary to the practice of some researchers who consider the OTU for bilateral traits to be the side (cf., Green *et al.*, 1979; Hallgrimsson *et al.*, 2004; Mouri, 1988; Ossenberg, 1981), bilateral traits were scored in a manner analogous to the 'individual count' method described for dental morphology trait frequencies by Turner and Scott (1977). In such cases, in which an individual exhibited asymmetry in the expression of a specific trait, the greatest expression (*i.e.*, 'positive') was used. This procedure assumes that a single genotype controls nonmetric traits on both sides of the cranium (Brasili and Gualdi-Russo, 1989; Brasili *et al.*, 1999; McGrath *et al.* 1984). When asymmetry exists, the side exhibiting the maximum expression (in this case a 'positive' expression) is assumed to be closest to the true underlying genotype for that trait. In contrast, the side in which the trait is not present is interpreted as having its phenotypic expression compromised by environmental factors resulting in varying amounts of fluctuating asymmetry . This procedure also serves to maximize sample sizes, for in cases where a specific trait is observable on one side, but not the other, the observable side is considered the maximum expression for the trait.

Cranial nonmetric traits for Altyn depe, Geoksyur, Harappa and Tepe Hissar were scored by BEH, while nonmetric traits for the samples from Djarkutan (DJR, KUZ, MOL, BUS) and Sapalli tepe were scored by AFC. Observer

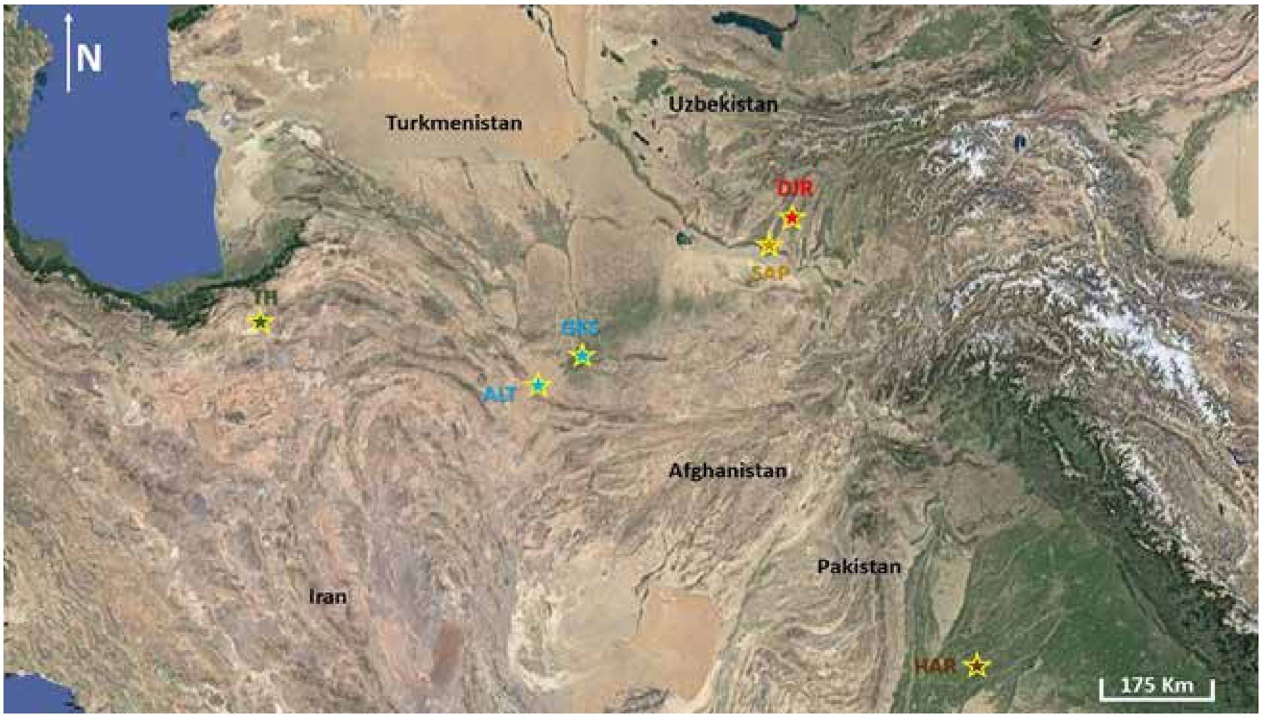

Figure 1. Map of Sampling Localities. Note: Bustan (BUS), Djarkutan (DJR), Kuzali (KUZ), and Molali (MOL), represent temporally successive phases of occupation at the site of Djarkutan (DJR).

Table 1. Samples Considered in the Study by Sex.

Sample	Abb.	Antiquity[1]	Females	Males	Unknown
Altyn depe	ALT	2500 – 2200 BC	5	10	2
Bustan[2]	BUS	1500 – 1300 BC	6	6	0
Djarkutan	DJR	2000 – 1800 BC	33	14	1
Geoksyur	GKS	3200 – 2800 BC	29	12	0
Harappa R37	HAR	2500 – 2000 BC	10	10	0
Kuzali	KUZ	1800 – 1650 BC	25	12	0
Molali	MOL	1650 – 1500 BC	25	20	0
Sapalli Tepe	SAP	2200 – 2000 BC	21	14	12
Tepe Hissar	TH	3300 – 1700 BC	75	87	7
TOTAL			205	209	22

1. Dates for the various sites are from Bonora and Vidale (2013), Dyson and Lawn (1989), Hiebert (1994), Hurst and Lawn (1984), Kenoyer (1998), and Kohl (1984, 1992).

2. Bustan, Djarkutan, Kuzali, Molali represent different temporal phases of occupation at the site of Djarkutan. In the multi-step phase of this study these samples are pooled and designated as BMAC.

repeatability was assessed by means of Cohen's (1960) kappa. As logistical concerns rendered rescoring of the Bactrian materials impossible, intraobsever repeatability assessment was based on rescoring of 30 Tepe Hissar crania selected at random originally assessed by BEH in July 1995 and rescored in July 2009 and a rescoring of a Mississippian series from Tennessee by AFC in October 1994 and again in May 1995. These same crania were scored by Hemphill in April 1998 to assess the level of interobserver reliability.

Most researchers who use nonmetric variations of the bony skeleton, including the cranium, assess a battery of traits defined by previous researchers (e.g., Anderson, 1962, 1963; Berry A.C. and Berry, R.J. 1967; Brothwell, 1958; Buikstra and Ubelaker, 1994; Hauser and de Stefano, 1989; Ossenberg, 1969) often in their entirety (e.g., González Jose *et al.*, 2001; Movsesian and Bakholdina, 2017; Ricault and Waelkens, 2008), as a truncated battery of traits that has yielded useful results within a specific geographic or historical context (e.g., Carson, 2006; del Papa and Perez, 2007; Dodo *et al.*, 1998; Dodo and Ishida, 1990; Hanihara *et al.*, 2012; Nikita *et al.*, 2012; Ossenberg, 1977), or in a modified form for forensic purposes (Burns, 1999; Byers, 2001; Hefner, 2009; Rhine, 1990). However, some researchers have focused on traits that previous studies have identified as being predominantly under genetic control (Prowse and Lovell, 1995; Sjøvold, 1984; Stefan and Chapman, 2003).

Following Sutter and Mertz (2004; see also Sutter, 1997, 2000a,b), traits found to be invariable or traits found to be completely absent or completely fixed (100% frequency) in all samples were eliminated from further consideration after initial modeling (*i.e.*, single-step Model 1, see below). This resulted in the elimination of a single trait (Bregmatic Bone: BB). Determination of sex was based on standard techniques. These assignations were checked by examining morphological features of the cranium and, where possible, the post-cranial skeleton by the first author using the standards of Bass (1987), Brothwell (1972), and Buikstra and Ubelaker (1994).

Of additional concern when choosing which traits to include in a comparative study based on biodistances are influences due to inter-trait correlations, environmental factors, advancing age at death, and the sex of the deceased. As noted in the Introduction, inter-trait correlations have been found by most researchers to be low and unlikely to cause much influence on patterns of biological affinity (Cheverud and Buikstra, 1981b; Corruccini, 1974; Dodo *et al.*, 1998; Hanihara, 2008; Hertzog, 1968). The same is also true of advancing age (Brasili and Gualdi-Russo, 1989; Brasili *et al.*, 1999; Carson, 2006) and — except in unusual circumstances — environmental factors as well (see Harris *et al.*, 2001).

In contrast, debate continues over the extent and nature of sexual influence over the expression of cranial nonmetric traits. Some researchers insist that sex-based effects necessitate that sexes be considered separately (cf. Axelson and Hedegaard, 1985; Berry, A.C., 1975; Brasili-Gualandi and Gualdi-Russo, 1989; Brasili *et al.*, 1999; Carson, 2006; Cesnys, 1982; Corruccini, 1974; Czarnetzki, 1972; Donlon, 2000; Milne *et al.*, 1983; Muller, 1977; Ossenberg, 1976; Sciulli, 1990; Woo, 1950), while others maintain that pooling of the sexes does not introduce bias in biodistance analysis (cf. Berry, A.C. and Berry, R.J., 1967; Cossedu *et al.*, 1979; Maxia *et al.*, 1974; Movsesian and Bakholdina, 2017; Nikita *et al.*, 2012; Sutter and Mertz, 2004; Vecchi, 1968). In light of this on-going debate, trait frequencies were compared between females and males with Pearson's chi-square. Only those traits that did not show a consistent pattern of sex-based differences in expression were pooled for additional analyses.

Sutter and Mertz (2004) recommend further winnowing of traits by selecting only those traits that yield significant contingency $\chi 2$ values (see Rothhammer *et al.*, 1984). However, this procedure only informs whether a significant difference occurs among all of the samples contrasted, but provides no insight into the covariance among traits and hence there is no control for multicollinearity within a battery of such variables. An alternative approach is to retain those traits that yield at least one statistically significant pairwise difference at $\alpha < 0.05$ (Harris and Sjøvold, 2004; Nikita *et al.*, 2012). However, this approach also does not deal with multicollinearity and because the same battery of traits is contrasted across multiple pairwise contrasts, one runs into the problem of artificially inflating type I errors. One way to reduce type I errors is to lower the alpha value to render the likelihood of accepting a difference as significant when in fact it is not increasingly remote. This can be accomplished two ways. The first is to simply choose a more stringent alpha value, say $\alpha < 0.01$ rather than $\alpha < 0.05$. The most popular approach is Bonferroni's adjustment (1935, 1936) in which the desired alpha value is divided by the number of multiple comparisons. However, Bonferroni's adjustment is well-known to be overly severe (Glickman *et al.*, 2014). Yet, such a procedure, which reduces type I statistical errors, leads to a concomitant increase in the likelihood of committing a type II statistical error and as such does nothing to increase the statistical power of such comparisons (Kim, 2015). A second strategy to identify the optimum number of variables to be included in multiple comparisons is to conduct those comparisons in hierarchically nested steps and then invoke Holm's (1979) less stringent modification of the Bonferroni adjustment for assessment of biodistances among members of sequentually nested sets of samples. This approach controls for the inflationary effect of multiple comparisons on type I errors with minimal reduction in statistical power.

This research utilises a series of sex- and adult age-pooled comparisons based upon multiple criteria. The first three models are single-step procedures in which: 1) All variables are included, 2) Only those variables in which at least one pairwise contrast yields a statistically significant contrast with $\alpha < 0.05$, and 3) Only those variables in which alpha values fall below an overly conservative Bonferroni adjusted 0.05 value with 36 comparisons ($\alpha<0.0536= 0.001389$). The fourth comparison pools those samples that consistently yield few significant differences among them, both by individual trait, as reflected by Pearson's chi-square , and across multiple variables as reflected by Smith's mean measure of divergence distances (Grewal, 1962; Sjøvold, 1973).The remaining samples are then contrasted with Holm's (1979) nested modification of Bonferroni's adjustment, which reduces sequentially in reverse order the number of degrees of freedom as each pairwise contrast is identified at an adjusted alpha value of <0.05.

The batteries of traits yielded by these trait 'winnowing' procedures were then subjected to correspondence analysis. Correspondence analysis is a useful version of principal components analyses that is especially well-suited for examining the relationships between nominal variables (Bølviken *et al.*, 1982; Hill, 1974), as is the case when suites of trait frequencies are used to distinguish unique assemblages of crania from temporally and geographically specific localities. Correspondence analysis was used to plot trait patterns, sample patterns, and the interplay between the patterning of trait frequencies and samples. Multivariate biodistances were computed with Smith's mean measure of divergence statistic (MMD). All distances greater than 2.0 were interpreted as statistically significant (Dodo and Ishida, 1990; Donlon, 2000; Prowse and Lovell, 1995; Ossenberg, 1977; Sjøvold, 1973, 1977). The zero-corrected triangular matrix of pairwise MMD distances was then submitted to neighbor-joining cluster analysis (Saitou and Nei, 1987) and to multidimensional scaling with Guttman's (1968) coefficient of alienation. Goodness of fit of the multidimensionally-scaled models were based upon visual examination of Shepard diagrams, computation of the stress incurred in fitting the model, and the percentage of variance explained (Hartigen, 1975). A minimum-spanning tree (Hair *et al.*, 2009) was imposed on sample centroids to clarify patterns of affinities between samples.

The reconstruction of inter-sample affinities is evaluated in accordance with the following criteria. The best reconstruction will be marked by:

- The highest proportion of univariate (as identified by Pearson's chi-square) and multivariate significant differences (as identified by MMD distances) across OTUs without an undue reduction in statistical power (Lieberman and Cunningham, 2009; Nakagawa, 2004; Perneger, 1998).
- The greatest clarity in identification of

which variables yield common aggregated groups of samples and separate such aggregates from one another as identified by correspondence analysis (Bølviken *et al.*, 1982; Hill, 1974).

Results

Examination of intraobserver error for BEH and AFC with Cohen's kappa yielded uniformly high values. Hemphill's reassessments resulted in an average kappa value of 0.841 across all 32 traits. Highest repeatability was observed for metopism (MET) , ossicles in the coronal (CO) and lambdoidal sutures (LO), and for accessory bones at pterion (EPT) and lambda (OL) (k> 0.89), which reflects near-perfect agreement. Lowest values (k= 0.636 – 0.734) were observed for foramen ovale incomplete (FOI), condylar facet double (CFD), anterior alveolar palatine foramen (AAPF) and tympanic marginal foramen (TMF), which is indicative of substantial agreement (Cohen, 1960). Similar intraobserver reliability values were obtained by AFC, which ranged from perfect agreement for metopism (k= 1.0) to a low of 0.613 for the presence of the frontal foramen (FFOR). Assessment of inter-observer agreement yielded uniformly high values ranging from 0.97 for metopism to a low of 0.683 for mastoid foramen exsutural (MFX). Such values not only show high repeatability for each scorer, but also a degree of concordance between scorers that parallels or exceeds that obtained by other researchers (Gualdi-Russo *et al.*, 1999; Ishida and Dodo, 1990; Molto, 1979).

Frequencies of nonmetric traits by sample and by sex are provided in Table 2. Due to small effective sample sizes many of these traits are completely absent from these sex-segregated samples. A chi-square analysis of contrasts in trait frequencies between females and males obtained from the same archaeological context reveals few significant differences. Overall, 11 of 288 sex-based contrasts were significant (3.8%). The number of significant differences ranged from a high of two among the crania recovered from Harappa and Sapalli tepe to a low of zero among those recovered from Geoksyur. No pattern was observed among those traits found to differ significantly between females and males from the same site; in fact, only one variable, bifid hypoglossal canal (BHC), differed significantly in more than one sample (DJR, KUZ). Such results confirm previous work by others that sexes may be pooled by sample for comparative purposes (Berry A.C. and Berry, R.J., 1967; Corruccini, 1974; Perizonius, 1979; Vecchi, 1968). Trait frequencies for sex-pooled samples by site are provided in Table 3.

Single-step Model 1: All Traits

All 32 nonmetric traits are considered in the first single-step model (Table 4) even though one of the variables, an ossicle at bregma (Trait No. 5, Bregmatic Bone: BB), was found to be completely absent from the nine samples included in the study. With all 32 traits the average measure of divergence by trait is 3.002 (Table 5). The most influential trait is the presence of a tympanic marginal foramen (Trait no. 32: TMF), followed by the presence of a frontal foramen (Trait No. 16: FFOR) and ossicles in the lambdoidal suture (Trait No. 3: LO). A substantial number of traits (7/32= 21.9%) provide no differentiation between samples. In addition to the invariant ossicle at bregma (BB), these include metopism (Trait No. 6: MET), fronto-temporal articulation (Trait No. 9: FTA), an ossicle at asterion (Trait No. 11: AO), an auditory torus (Trait No. 12: AT), a double condylar facet (Trait No. 26: CFD), and an incomplete foramen ovale (Trait No. 29: FOI). Overall, some 36.28% of the pairwise contrasts (418/1152) yield significant differences (Table 6). These differences are not equally distributed across samples, for the Cemetery R37 sample from Harappa stands out as most unique with 90 significant pairwise differences, followed by Tepe Hissar with 67.

The first two coordinate dimensions of a correspondence analysis of the relationship between nonmetric trait frequencies and samples encompass 55.2% of the total variation. An examination of the plot for traits (Fig. 2a) identified by number (Table 4) shows that most traits occupy positions close to the origins for both dimensions. The close proximity of these points to one another indicates few differences in their ability to distinguish between samples. However, a few traits stand apart by occupying unique and more highly differentiated positions. These include foramen ovale incomplete (Trait No. 29: FOI) and fronto-temporal articulation (FTA: Trait No. 9) in the lower left of the plot and presence of a tympanic marginal foramen (TMF: Trait No. 32) on the right side. The presence of a maxillary torus (MXT: Trait No. 19) and precondylar tubercle (PTUB: Trait No. 27) in the upper right, absence of the zygofacial foramen (ZFFA: Trait No. 20) and an open foramen spinosum (FSO: Trait No. 30) in the lower center, and an ossicle at lambda (OL: Trait No. 2) and coronal suture (CO: Trait No. 7) on the near left side also exhibit heightened ability to distinguish between samples, albeit to a lesser degree.

A plot of samples (Fig. 2b) shows that most are located near to or immediately to the left of the origins of the first two coordinate dimensions. These include the BMAC era sample from Sapalli tepe (SAP) and the time successive BMAC era samples from Djarkutan (DJR, KUZ, MOL, BUS) along with the sample from Tepe Hissar (TH). Three samples stand apart. These include the sample from Cemetery R37 at Harappa (HAR) in the lower left and the two pre-BMAC Central Asian samples from southern Turkmenistan (ALT, GKS) on the right.

A biplot of traits and samples (Fig. 2c) shows little separation between five of the nine samples. HAR is found in the lower left. Its position is a consequence of relatively high prevalence for FOI (Trait 29: 6.3%), FTA (Trait 9: 4.2%), and ZFFA (Trait 20: 50.0%). The Bustan period sample

Table 2. Contrasts of Nonmetric Trait Frequencies within Samples by Sex.

	Altyn depe								Bustan							
	Females			Males					Females			Males				
Trait	p^1	n^2	Freq.	p	n	Freq.	χ^2	Prob.	p	n	Freq.	p	n	Freq.	χ^2	Prob.
HNL	1	3	0.333	2	8	0.250	0.076	0.782	4	6	0.667	3	5	0.600	0.052	0.819
OL	0	3	0.000	0	5	0.000	0.000	1.000	0	5	0.000	2	4	0.500	3.214	0.073
LO	3	6	0.500	6	7	0.857	0.476	0.490	2	2	1.000	3	3	1.000	0.000	1.000
PFOR	4	6	0.667	6	7	0.857	0.629	0.428	3	5	0.600	1	4	0.250	1.102	0.294
BB	0	4	0.000	0	8	0.000	0.000	1.000	0	6	0.000	0	5	0.000	0.000	1.000
MET	0	4	0.000	1	10	0.100	0.431	0.512	1	6	0.167	0	6	0.000	1.091	0.296
CO	0	2	0.000	0	3	0.000	0.000	1.000	1	3	0.333	1	3	0.333	0.000	1.000
EPT	0	2	0.000	1	4	0.250	0.600	0.439	0	3	0.000	1	4	0.250	0.875	0.350
FTA	0	3	0.000	0	3	0.000	0.000	1.000	0	5	0.000	0	6	0.000	0.000	1.000
PNB	1	4	0.250	0	8	0.000	2.182	0.140	0	6	0.000	0	5	0.000	0.000	1.000
AO	0	3	0.000	1	8	0.125	0.412	0.521	1	4	0.250	1	4	0.250	0.000	1.000
AT	0	4	0.000	0	8	0.000	0.000	1.000	0	6	0.000	0	6	0.000	0.000	1.000
MFX	2	3	0.667	5	7	0.714	0.023	0.880	2	5	0.400	0	4	0.000	2.057	0.151
MFA	1	3	0.333	1	7	0.143	0.476	0.490	1	5	0.200	3	4	0.750	2.723	0.099
SFC	3	4	0.750	3	9	0.333	1.935	0.164	0	6	0.000	4	5	0.800	7.543	**0.006**
FFOR	2	4	0.500	3	9	0.333	0.325	0.569	4	4	1.000	4	4	1.000	0.000	1.000
ALPF	2	3	0.667	4	7	0.571	0.079	0.778	3	4	0.750	2	2	1.000	0.000	1.000
PTOR	1	4	0.250	0	8	0.000	2.182	0.140	2	5	0.400	0	5	0.000	2.500	0.114
MXT	0	5	0.000	0	9	0.000	0.000	1.000	0	6	0.000	0	5	0.000	0.000	1.000
ZFFA	0	5	0.000	3	10	0.300	1.875	0.171	2	5	0.400	1	4	0.250	0.225	0.635
AIOF	0	3	0.000	1	8	0.125	0.412	0.521	0	4	0.000	1	3	0.333	1.556	0.212
IOS	2	4	0.500	5	8	0.625	0.171	0.679	2	3	0.667	3	4	0.750	0.058	0.809
NFOR	3	3	0.500	3	4	0.750	0.875	0.350	3	3	1.000	2	3	0.667	1.200	0.273
AAPF	0	4	0.000	7	8	0.875	8.400	**0.004**	3	5	0.600	1	3	0.333	0.533	0.465
FH	1	3	0.333	2	7	0.286	0.023	0.880	0	6	0.000	0	6	0.000	0.000	1.000
CFD	0	2	0.000	0	6	0.000	0.000	1.000	0	6	0.000	0	3	0.000	0.000	1.000
PTUB	0	2	0.000	1	3	0.333	0.833	0.361	1	6	0.167	0	4	0.000	0.741	0.389
BHC	0	2	0.000	0	5	0.000	0.000	1.000	1	6	0.167	0	4	0.000	0.741	0.389
FOI	0	5	0.000	0	3	0.000	0.000	1.000	0	6	0.000	0	6	0.000	0.000	1.000
FSO	3	4	0.750	2	4	0.500	0.533	0.465	4	5	0.800	1	5	0.200	3.600	0.058
PFOSS	1	2	0.500	0	3	0.000	1.875	0.171	0	6	0.000	1	4	0.250	1.667	0.197
TMF	3	4	0.750	6	7	0.857	0.196	0.658	0	5	0.000	0	4	0.000	0.000	1.000

Table 2. Continued…

					Djarkutan									Geoksyur		
		Females			Males					Females			Males			
Trait	p	n	Freq.	p	n	Freq.	χ^2	Prob.	p	n	Freq.	p	n	Freq.	χ^2	Prob.
HNL	11	29	0.379	7	14	0.500	0.565	0.452	3	9	0.333	6	25	0.240	0.296	0.586
OL	1	28	0.036	0	13	0.000	0.476	0.490	1	9	0.111	2	23	0.087	0.044	0.833
LO	6	13	0.462	3	6	0.500	0.024	0.876	9	10	0.900	16	23	0.696	1.585	0.208
PFOR	12	26	0.462	9	13	0.692	1.857	0.173	8	10	0.800	24	27	0.889	0.493	0.482
BB	0	25	0.000	0	14	0.000	0.000	1.000	0	11	0.000	0	25	0.000	0.000	1.000
MET	2	32	0.063	0	14	0.000	0.915	0.339	1	11	0.091	0	28	0.000	2.612	0.106
CO	1	23	0.043	4	14	0.286	4.369	**0.037**	1	7	0.143	1	19	0.053	0.586	0.444
EPT	4	28	0.143	1	13	0.077	0.360	0.548	1	6	0.167	2	24	0.083	0.370	0.543
FTA	1	33	0.030	0	14	0.000	0.433	0.510	0	6	0.000	0	21	0.000	0.000	1.000
PNB	2	29	0.069	2	14	0.143	0.611	0.434	2	10	0.200	1	24	0.042	2.200	0.138
AO	1	22	0.045	0	13	0.000	0.608	0.435	0	10	0.000	3	24	0.125	1.371	0.242
AT	0	31	0.000	0	14	0.000	0.000	1.000	0	10	0.000	1	25	0.040	0.412	0.521
MFX	9	27	0.333	7	14	0.500	1.076	0.300	5	9	0.556	16	23	0.696	0.563	0.453
MFA	15	28	0.536	5	14	0.357	1.193	0.275	4	9	0.444	6	23	0.261	1.015	0.314
SFC	16	33	0.485	6	14	0.429	0.125	0.724	5	12	0.417	14	26	0.538	0.487	0.485
FFOR	18	30	0.600	9	14	0.643	0.074	0.786	7	12	0.583	21	26	0.808	2.131	0.144
ALPF	9	21	0.429	8	13	0.615	1.121	0.290	5	10	0.500	8	20	0.400	0.271	0.602
PTOR	3	27	0.111	2	14	0.143	0.087	0.768	1	9	0.111	2	20	0.100	0.008	0.928
MXT	0	31	0.000	0	14	0.000	0.000	1.000	0	10	0.000	2	23	0.087	0.926	0.336
ZFFA	8	26	0.308	6	14	0.429	0.584	0.445	1	11	0.091	9	25	0.360	2.757	0.097
AIOF	7	20	0.350	4	13	0.308	0.063	0.801	0	10	0.000	3	24	0.125	1.371	0.242
IOS	12	26	0.462	7	14	0.500	0.054	0.816	3	10	0.300	8	24	0.333	0.036	0.850
NFOR	21	27	0.778	12	14	0.857	0.370	0.543	6	6	1.000	19	21	0.905	0.617	0.432
AAPF	17	22	0.773	5	11	0.455	3.341	0.068	10	11	0.909	16	20	0.800	0.624	0.429
FH	6	30	0.200	1	14	0.071	1.179	0.277	1	10	0.100	5	24	0.208	0.570	0.450
CFD	1	30	0.033	0	14	0.000	0.478	0.490	0	7	0.000	1	18	0.056	0.405	0.524
PTUB	3	32	0.094	1	14	0.071	0.061	0.805	1	5	0.200	4	16	0.250	0.053	0.819
BHC	5	32	0.156	6	14	0.429	3.970	**0.046**	0	6	0.000	3	17	0.176	1.218	0.270
FOI	1	29	0.034	0	14	0.000	0.494	0.482	0	8	0.000	0	18	0.000	0.000	1.000
FSO	12	25	0.480	3	13	0.231	2.224	0.136	3	7	0.429	5	16	0.313	0.289	0.591
PFOSS	5	30	0.167	5	14	0.357	1.972	0.160	1	5	0.200	2	16	0.125	0.175	0.676
TMF	6	22	0.273	2	10	0.200	0.194	0.660	7	10	0.700	17	24	0.708	0.002	0.961

Table 2. Continued…

					Harappa									Kuzali		
		Females			Males					Females			Males			
Trait	p	n	Freq.	p	n	Freq.	χ^2	Prob.	p	n	Freq.	p	n	Freq.	χ^2	Prob.
HNL	1	25	0.040	5	9	0.556	12.103	**0.001**	2	8	0.250	4	9	0.444	0.701	0.402
OL	1	10	0.010	0	4	0.000	0.431	0.512	2	9	0.222	2	6	0.333	0.227	0.634
LO	2	23	0.087	0	10	0.000	0.926	0.336	7	9	0.778	5	6	0.833	0.069	0.792
PFOR	6	23	0.261	2	8	0.250	0.004	0.952	7	9	0.778	5	8	0.625	0.476	0.490
BB	0	10	0.000	0	8	0.000	0.000	1.000	0	6	0.000	0	9	0.000	0.000	1.000
MET	0	11	0.000	0	10	0.000	0.000	1.000	0	8	0.000	1	10	0.100	0.847	0.357
CO	0	17	0.000	0	12	0.000	0.000	1.000	2	7	0.286	2	5	0.400	0.171	0.679
EPT	0	15	0.000	0	10	0.000	0.000	1.000	1	7	0.143	1	10	0.100	0.073	0.787
FTA	1	16	0.063	0	6	0.000	0.393	0.531	0	10	0.000	1	10	0.100	1.053	0.305
PNB	1	22	0.045	0	11	0.000	0.516	0.473	3	9	0.333	2	9	0.222	0.277	0.599
AO	3	21	0.143	0	11	0.000	1.734	0.188	0	7	0.000	1	8	0.125	0.938	0.333
AT	0	18	0.000	0	11	0.000	0.000	1.000	1	9	0.111	0	10	0.000	1.173	0.279
MFX	6	21	0.286	0	6	0.000	2.204	0.138	1	9	0.111	4	10	0.400	2.039	0.153
MFA	3	21	0.143	1	6	0.167	0.021	0.885	4	9	0.444	3	10	0.300	0.425	0.515
SFC	2	19	0.105	3	12	0.250	1.139	0.286	4	10	0.400	5	10	0.500	0.202	0.653
FFOR	4	20	0.200	2	11	0.182	0.015	0.902	6	10	0.600	5	9	0.556	0.038	0.845
ALPF	5	12	0.417	2	10	0.200	1.180	0.277	5	8	0.625	2	6	0.333	1.167	0.280
PTOR	0	10	0.000	0	8	0.000	0.000	1.000	1	10	0.100	1	9	0.111	0.006	0.937
MXT	0	19	0.000	0	16	0.000	0.000	1.000	0	10	0.000	0	9	0.000	0.000	1.000
ZFFA	8	17	0.471	6	10	0.600	0.422	0.516	3	10	0.300	4	10	0.400	0.220	0.639
AIOF	0	12	0.000	0	12	0.000	0.000	1.000	3	9	0.333	2	7	0.286	0.042	0.838
IOS	2	17	0.118	0	12	0.000	1.516	0.218	3	9	0.333	3	9	0.333	0.000	1.000
NFOR	5	9	0.556	5	9	0.556	0.000	1.000	9	10	0.900	7	8	0.875	0.028	0.867
AAPF	0	16	0.000	1	13	0.077	1.275	0.259	4	7	0.571	5	9	0.556	0.004	0.949
FH	0	18	0.000	0	12	0.000	0.000	1.000	3	10	0.300	2	9	0.222	0.148	0.701
CFD	0	10	0.000	0	6	0.000	0.000	1.000	1	8	0.125	0	8	0.000	1.067	0.302
PTUB	0	20	0.000	1	9	0.111	2.302	0.129	0	9	0.000	1	9	0.111	1.059	0.303
BHC	1	19	0.053	0	11	0.000	0.599	0.439	0	10	0.000	3	9	0.333	3.958	**0.047**
FOI	0	19	0.000	2	10	0.200	4.801	**0.043**	0	9	0.000	0	10	0.000	0.000	1.000
FSO	6	15	0.400	3	7	0.429	0.016	0.899	3	10	0.300	2	10	0.200	0.267	0.606
PFOSS	1	12	0.083	0	6	0.000	0.529	0.467	1	9	0.111	2	10	0.200	0.281	0.596
TMF	0	20	0.000	0	15	0.000	0.000	1.000	1	9	0.111	1	8	0.125	0.008	0.929

Table 2. Continued…

	Molali								Sapalli Tepe							
	Females			Males					Females			Males				
Trait	p	n	Freq.	p	n	Freq.	χ^2	Prob.	p	n	Freq.	p	n	Freq.	χ^2	Prob.
HNL	9	24	0.375	7	13	0.538	0.918	0.338	10	14	0.710	7	9	0.780	0.115	0.735
OL	3	18	0.167	0	11	0.000	2.045	0.153	1	13	0.080	0	10	0.000	0.804	0.370
LO	11	15	0.733	7	10	0.700	0.033	0.856	5	11	0.450	4	7	0.570	0.234	0.629
PFOR	11	21	0.524	9	13	0.692	0.41	0.332	12	15	0.800	9	11	0.820	0.014	0.907
BB	0	22	0.000	0	14	0.000	0.000	1.000	0	19	0.000	0	12	0.000	0.000	1.000
MET	4	25	0.160	0	19	0.000	3.344	0.067	1	19	0.050	1	13	0.080	0.078	0.780
CO	4	17	0.235	3	16	0.188	0.113	0.737	0	8	0.000	0	9	0.000	0.000	1.000
EPT	6	19	0.316	2	17	0.118	2.038	0.153	0	9	0.000	1	7	0.140	1.371	0.242
FTA	0	25	0.000	1	19	0.053	1.346	0.246	0	12	0.000	0	9	0.000	0.000	1.000
PNB	2	22	0.091	1	19	0.053	0.220	0.639	1	12	0.080	1	12	0.080	0.000	1.000
AO	2	20	0.100	1	14	0.071	0.084	0.773	3	12	0.250	1	11	0.090	1.011	0.315
AT	0	24	0.000	0	20	0.000	0.000	1.000	0	20	0.000	1	13	0.080	1.587	0.208
MFX	8	21	0.381	7	19	0.368	0.007	0.935	3	14	0.210	9	10	0.900	10.971	**0.001**
MFA	10	22	0.455	7	20	0.350	0.475	0.491	6	15	0.400	0	11	0.000	5.720	**0.017**
SFC	12	25	0.480	7	20	0.350	0.770	0.380	9	18	0.500	4	13	0.310	1.146	0.284
FFOR	15	24	0.625	14	19	0.737	0.604	0.437	19	19	1.000	12	12	1.000	0.000	1.000
ALPF	6	17	0.353	9	14	0.643	2.584	0.108	15	15	0.730	7	11	0.640	0.280	0.597
PTOR	2	23	0.087	1	18	0.056	0.147	0.702	1	12	0.080	0	11	0.000	0.958	0.328
MXT	0	23	0.000	0	11	0.000	0.000	1.000	0	16	0.000	0	11	0.000	0.000	1.000
ZFFA	8	24	0.333	6	17	0.353	0.017	0.896	7	17	0.410	4	13	0.310	0.344	0.558
AIOF	4	19	0.211	3	14	0.214	0.001	0.979	6	12	0.500	3	10	0.300	0.903	0.342
IOS	8	21	0.381	9	16	0.563	1.205	0.272	4	12	0.333	4	11	0.360	0.023	0.879
NFOR	17	22	0.773	15	15	1.000	3.942	**0.047**	9	10	0.900	5	6	0.830	0.152	0.696
AAPF	10	20	0.500	10	16	0.625	0.562	0.453	12	16	0.750	8	13	0.620	0.607	0.436
FH	2	24	0.083	3	20	0.150	0.481	0.488	4	17	0.240	4	11	0.360	0.539	0.463
CFD	0	22	.0000	1	20	0.050	1.127	0.288	0	15	0.000	1	11	0.090	1.418	0.234
PTUB	1	22	0.045	0	19	0.000	0.885	0.347	2	15	0.130	0	10	0.000	1.449	0.229
BHC	6	24	0.250	4	20	0.200	0.155	0.694	1	16	0.060	2	12	0.170	0.778	0.378
FOI	1	24	0.042	0	18	0.000	0.768	0.381	0	15	0.000	0	9	0.000	0.000	1.000
FSO	9	22	0.409	7	19	0.368	0.071	0.790	5	15	0.333	0	9	0.000	3.789	0.052
PFOSS	2	22	0.091	3	19	0.158	0.427	0.513	7	14	0.500	3	11	0.270	1.326	0.250
TMF	2	23	0.087	0	16	0.000	1.467	0.226	0	17	0.000	0	12	0.000	0.000	1.000

Table 2. Continued…

	Tepe Hissar							
	Females			Males				
Trait	p	n	Freq.	p	n	Freq.	χ^2	Prob.
HNL	26	63	0.413	41	72	0.569	3.302	0.069
OL	3	63	0.048	16	72	0.222	8.470	**0.004**
LO	37	63	0.587	40	69	0.580	0.008	0.930
PFOR	54	63	0.857	64	73	0.877	0.113	0.737
BB	0	64	0.000	0	73	0.000	0.000	1.000
MET	1	66	0.015	2	73	0.027	0.246	0.620
CO	16	62	0.258	20	69	0.290	0.166	0.684
EPT	19	57	0.333	16	69	0.232	1.601	0.206
FTA	1	59	0.017	0	69	0.000	1.179	0.278
PNB	12	62	0.194	13	72	0.181	0.037	0.847
AO	8	63	0.127	11	72	0.153	0.185	0.667
AT	1	62	0.016	4	72	0.056	1.442	0.230
MFX	40	63	0.635	50	72	0.694	0.536	0.464
MFA	22	63	0.349	15	72	0.694	3.351	0.067
SFC	29	64	0.453	32	72	0.451	0.001	0.977
FFOR	56	66	0.848	67	72	0.931	2.394	0.122
ALPF	43	65	0.662	59	80	0.738	0.992	0.319
PTOR	15	65	0.231	21	81	0.259	0.158	0.691
MXT	12	68	0.176	14	82	0.171	0.009	0.926
ZFFA	21	66	0.318	17	84	0.202	2.620	0.106
AIOF	8	63	0.127	12	80	0.150	0.155	0.694
IOS	34	63	0.540	31	77	0.403	2.618	0.106
NFOR	43	45	0.956	62	63	0.984	0.793	0.373
AAPF	36	63	0.571	47	83	0.566	0.004	0.950
FH	15	60	0.250	19	70	0.271	0.077	0.782
CFD	1	52	0.0191	1	56	0.018	0.003	0.958
PTUB	10	53	0.189	18	60	0.300	1.871	0.171
BHC	8	55	0.145	18	62	0.290	3.539	0.060
FOI	2	59	0.034	1	67	0.015	0.486	0.486
FSO	13	58	0.224	21	69	0.304	1.034	0.309
PFOSS	9	54	0.167	14	60	0.233	0.784	0.376
TMF	12	58	0.207	11	68	0.162	0.427	0.513

1. Number of individuals in which the trait is present.
2. Number of individuals in which the trait could be assessed.

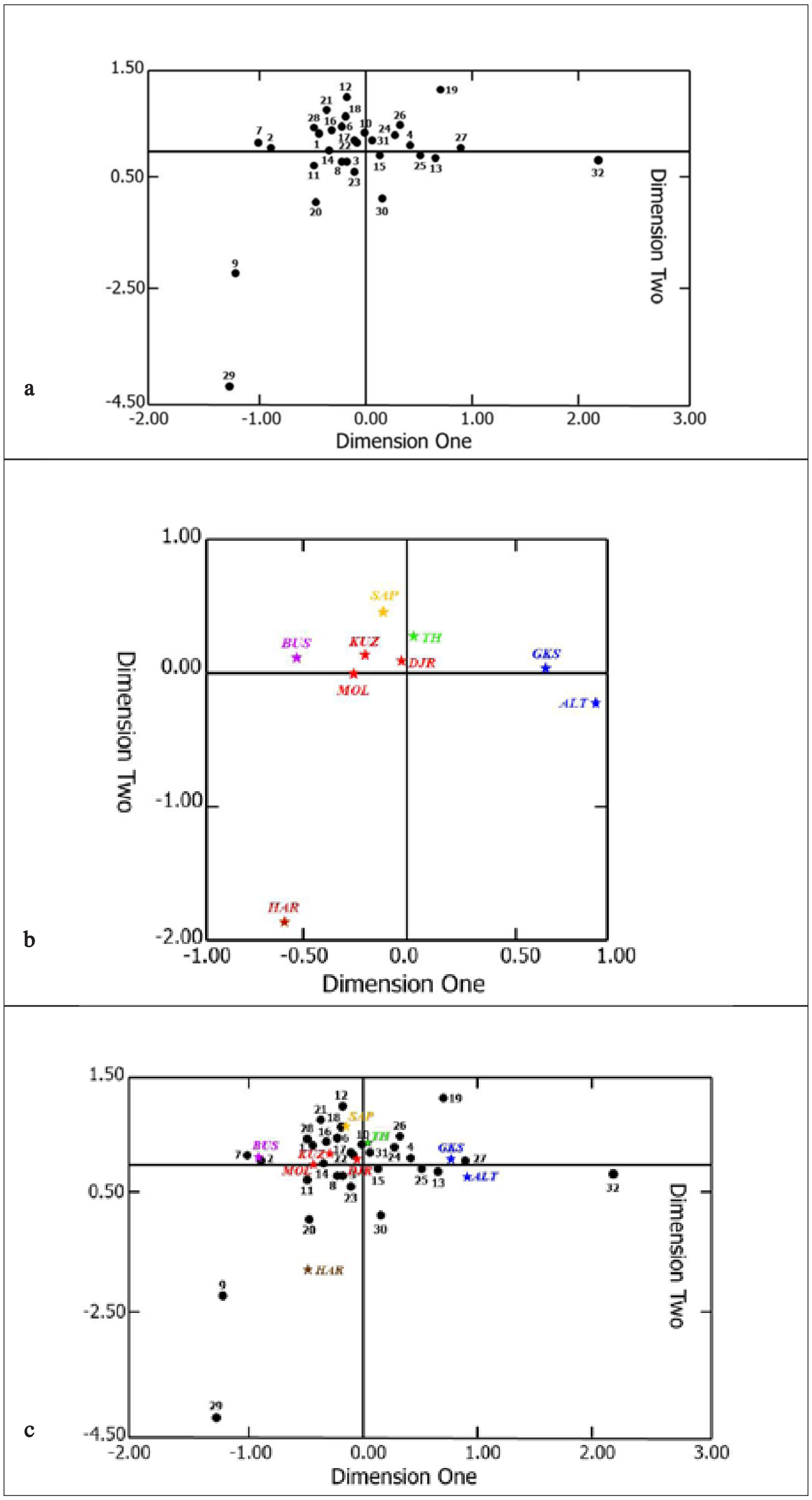

Figure 2a-c. Correspondence analysis based upon all 32 cranial nonmetric traits among nine samples: a) plot of traits (circles), b) plot of samples (stars), and c) biplot of traits (circles) and samples (stars). Trait numbers are from Table 4, sample abbreviations are from Table 1.

stands to the left of the main sample aggregate and this separation is largely the consequence of relatively high frequencies of OL (22.2%) and CO (33.3%), which would also account for the more proximal position of the Kuzali and Molali phase samples that immediately antedate it. However, it does not explain the separation between BUS and TH, the latter of which is also characterized by relatively high frequencies of OL (13.9%) and CO (27.1%). Present on the right side of the biplot, the samples from GKS and ALT also stand apart from the main aggregate, but in this case the separation is driven by the presence of an exsutural mastoid foramen (Trait 13: MFX: 63.9 – 70.0%), precondylar tubercles (Trait No. 27: PTUB: 20.0 – 21.7%), and especially a tympanic marginal foramen (Trait No. 32: TMF: 68.4 – 81.8%). These traits describe accurately the separation of these two pre-BMAC samples from HAR as well as from all of the BMAC samples. However, these trait differences fail to explain the separation between ALT and GKS from TH, which is also characterized by identically high prevalence of MFX (66.4%) and PTUB (25.4%).

The matrix of MMD values is presented in Table 7. Distances are below the diagonal and standard deviations are above. Distances greater than two times the standard deviation, signaling a significant pairwise separation of samples, are indicated in bold. Negative MMD distances have been set to zero. The average MMD distance across all 36 pairwise comparisons is 0.0661. Of the 36 pairwise contrasts, one-fourth (9) provide no separation between sample pairs and the majority (6/9= 66.7%) occur between the temporally successive samples from Djarkutan. Eleven (30.6%) pairwise contrasts provide non-statistically significant separations between sample pairs, while the remaining 16 contrasts (44.4%) are statistically significant. As with the univariate contrasts, multivariate significant differences are not randomly distributed, but primarily involve separation HAR (100% significant), TH (75% significant) and GKS (50% significant).

Neighbour-joining cluster analysis (Fig. 3a) identifies the Cemetery R37 sample from Harappa (HAR) as the most unique. This highly divergent sample links to the temporally successive BMAC samples from Djarkutan via DJR, then MOL, and then KUZ. The latest of the BMAC period samples (BUS) is identified as possessing closer affinities to the earliest BMAC sample (SAP) and to the sample from Tepe Hissar (TH) than to the temporally antecedent BMAC samples from Djarkutan. In contrast, the two pre-BMAC samples from southern Turkmenistan (ALT, GKS) are identified as possessing closest affinities to one another with secondary affinities to the BMAC Kuzali period sample (KUZ) from Djarkutan.

Multidimensional scaling with Guttman's coefficient of alienation into three dimensions was accomplished in three iterations. The stress incurred in fitting the individual points was 0.020 with the final configuration capturing 99.94% of the variance between points. The resulting plot (Fig. 3b) shows a wide separation of samples. HAR is isolated on the left side of the array, SAP is isolated in the right foreground, ALT occupies a position in the right background opposite SAP, while TH and GKS occupy opposite positions with high and low scores along the third dimension, respectively. At first glance there appears to be an atomization of affinities across the samples. However, closer inspection reveals relatively close affinities among the four time successive BMAC era samples from Djarkutan in the right center of the array. What is notable is that the four members of this temporal series each share unique affinities with samples from other sites such that KUZ is aligned with ALT and GKS, BUS with TH, MOL with SAP, and KUZ with HAR.

Model 2: α< 0.05 for at Least One Pairwise Difference

Following the recommendation of Harris and Sjøvold (2004), Model 2 includes all variables in which at least one pairwise difference is statistically significant at α< 0.05. This criterion resulted in the elimination of five traits: BB, FTA, AT, CFD, and FOI (Table 4). The average measure of divergence by trait for the remaining 27 traits is 3.017 (Table 5). As with the first model, the most influential trait is TMF, followed by FFOR, LO and the presence of the parietal foramen (Trait No. 4: PFOR). Two traits, metopism (MET) and ossicle at asterion (AO), vary across samples but this variation does not contribute to the overall separation of samples. Overall, some 418 of 972 (43%) contrasts by variable and by sample pair are statistically significant (Table 6). As with the previous model, these statistically significant differences were not equally distributed across samples. Overall, fewer significant differences were found between the time successive BMAC samples from Djarkutan ($\overline{X}$= 0.5) than among the remaining samples ($\overline{X}$= 2.67), with the number of significant contrasts between sample pairs being greatest for HAR (n= 88) and TH (n= 67).

The first two coordinate dimensions of a correspondence analysis of the relationship between nonmetric trait frequencies and samples for those traits that yield at least one statistically significant contrast at $\alpha < 0.05$ encompass a much greater proportion of the total variance (72.8%) than observed for single-step Model 1. This is largely due to the elimination of the five non-discriminating variables, for the plot of traits yields a very similar distribution to that seen with the previous model, with most traits occupying positions close to the origins for both dimensions (Fig. 4a). As before, the close proximity of these points indicates few differences in their ability to distinguish between samples. The same few traits stand apart by occupying unique and more highly weighted positions, however elimination of the non-discriminating traits results in FOI (Trait 29) and FTA (Trait 9) being no longer separated from the main cloud of points near the origins, while ZFFA (Trait 20) and FSO (Trait 30) are more strongly separated than before. In addition, OL (Trait 2), CO (Trait 7) and asterionic ossicle (AO: Trait 11) stand apart in the lower left, albeit to a lesser degree.

Not surprisingly, the plot of samples is very similar to that obtained for all 32 traits (Fig. 4b). The only difference is that BUS and TH are less separated from the three earlier time successive BMAC era samples from Djarkutan and the same is true for SAP. Once again, HAR occupies an isolated position in the lower left, while the two pre-BMAC samples from ALT and GKS are separated on the right side.

The biplot of traits and samples (Fig. 4c) shows little separation between five of the nine samples. HAR stands apart by possessing relatively high prevalence of ZFFA (50%) but is not unique among samples for FSO. The two pre-BMAC samples from ALT and GKS are distinguished by relatively high prevalence of MFX (64-70%: Trait 13), PTUB (20 – 22%: Trait 27), and especially TMF (68 – 82%: Trait 32). As noted for Model 1, such differences describe accurately the separation of ALT and GKS from HAR as well as all the BMAC samples. However, these differences fail to explain the separation of ALT and GKS from TH, the latter of which is

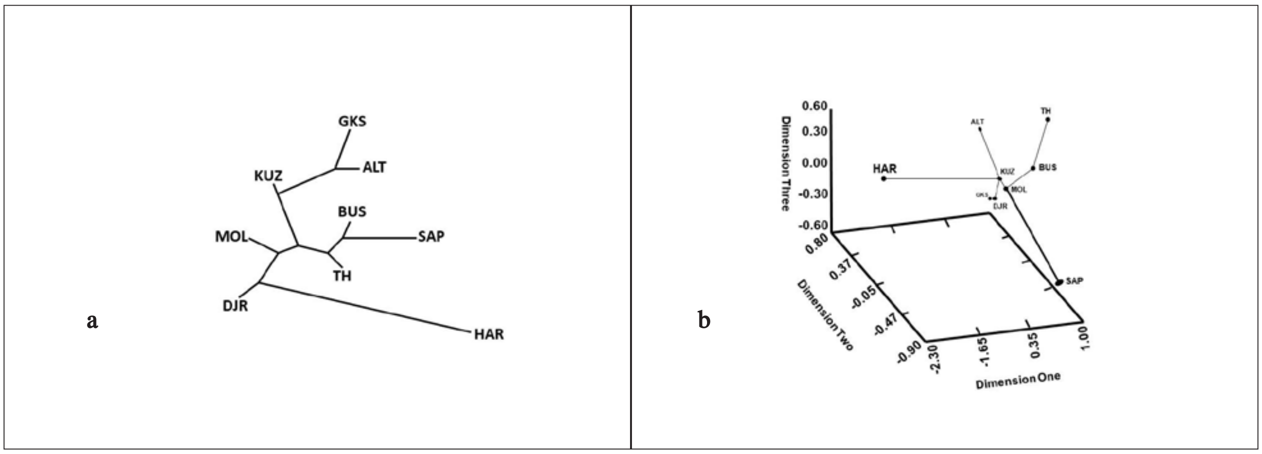

Figure 3. a) Neighbor-joining cluster analysis and b) multidimensional scaled scatterplot with Guttman's coefficient of alienation into three dimensions with all 32 traits considered (Single-Step Model 1). Sample abbreviations from Table 4.

Table 3. Nonmetric Trait Frequencies by Sample with Sexes Pooled.

Sample	Trait	p[1]	n[2]	Freq.	Sample	Trait	p	n	Freq.	Sample	Trait	p	n	Freq.
ALT	HNL	3	11	0.273	BUS	HNL	7	11	0.636	DJR	HNL	18	43	0.419
ALT	OL	0	8	0.000	BUS	OL	2	9	0.222	DJR	OL	1	41	0.024
ALT	LO	9	10	0.900	BUS	LO	5	5	1.000	DJR	LO	9	19	0.474
ALT	PFOR	10	11	0.909	BUS	PFOR	4	9	0.444	DJR	PFOR	21	39	0.538
ALT	BB	0	12	0.000	BUS	BB	0	11	0.000	DJR	BB	0	39	0.000
ALT	MET	1	14	0.071	BUS	MET	1	12	0.083	DJR	MET	2	46	0.043
ALT	CO	0	5	0.000	BUS	CO	2	6	0.333	DJR	CO	5	37	0.135
ALT	EPT	1	6	0.167	BUS	EPT	1	7	0.143	DJR	EPT	5	41	0.122
ALT	FTA	0	6	0.000	BUS	FTA	0	11	0.000	DJR	FTA	1	47	0.021
ALT	PNB	1	12	0.083	BUS	PNB	0	11	0.000	DJR	PNB	4	43	0.093
ALT	AO	1	11	0.091	BUS	AO	2	8	0.250	DJR	AO	1	35	0.029
ALT	AT	0	12	0.000	BUS	AT	0	12	0.000	DJR	AT	0	45	0.000
ALT	MFX	7	10	0.700	BUS	MFX	2	9	0.222	DJR	MFX	16	41	0.390
ALT	MFA	2	10	0.200	BUS	MFA	4	9	0.444	DJR	MFA	20	42	0.476
ALT	SFC	6	13	0.462	BUS	SFC	4	11	0.364	DJR	SFC	22	47	0.468
ALT	FFOR	5	13	0.385	BUS	FFOR	8	8	1.000	DJR	FFOR	27	44	0.614
ALT	ALPF	6	10	0.600	BUS	ALPF	5	6	0.833	DJR	ALPF	17	34	0.500
ALT	PTOR	1	12	0.083	BUS	PTOR	2	10	0.200	DJR	PTOR	5	41	0.122
ALT	MXT	0	14	0.000	BUS	MXT	0	11	0.000	DJR	MXT	0	45	0.000
ALT	ZFFA	3	15	0.200	BUS	ZFFA	3	9	0.333	DJR	ZFFA	14	40	0.350
ALT	AIOF	1	11	0.091	BUS	AIOF	1	7	0.143	DJR	AIOF	11	33	0.333
ALT	IOS	7	12	0.583	BUS	IOS	5	7	0.714	DJR	IOS	19	40	0.475
ALT	NFOR	6	7	0.857	BUS	NFOR	5	6	0.833	DJR	NFOR	33	41	0.805
ALT	AAPF	7	12	0.583	BUS	AAPF	4	8	0.500	DJR	AAPF	22	33	0.667
ALT	FH	3	10	0.300	BUS	FH	0	12	0.000	DJR	FH	7	44	0.159
ALT	CFD	0	8	0.000	BUS	CFD	0	9	0.000	DJR	CFD	1	44	0.023
ALT	PTUB	1	5	0.200	BUS	PTUB	1	10	0.100	DJR	PTUB	4	46	0.087
ALT	BHC	0	7	0.000	BUS	BHC	1	10	0.100	DJR	BHC	11	46	0.239
ALT	FOI	0	8	0.000	BUS	FOI	0	12	0.000	DJR	FOI	1	43	0.023
ALT	FSO	5	8	0.625	BUS	FSO	5	10	0.500	DJR	FSO	15	38	0.395
ALT	PFOSS	1	5	0.200	BUS	PFOSS	1	10	0.100	DJR	PFOSS	10	44	0.227
ALT	TMF	9	11	0.818	BUS	TMF	0	9	0.000	DJR	TMF	8	32	0.250

Table 3. Continued…

Sample	Trait	p	n	Freq.	Sample	Trait	p	n	Freq.	Sample	Trait	p	n	Freq.
GKS	HNL	11	38	0.289	HAR	HNL	6	40	.0150	KUZ	HNL	6	17	0.353
GKS	OL	4	36	0.111	HAR	OL	1	16	0.063	KUZ	OL	4	15	0.139
GKS	LO	28	37	0.757	HAR	LO	4	35	0.114	KUZ	LO	12	15	0.590
GKS	PFOR	33	40	0.825	HAR	PFOR	8	37	0.216	KUZ	PFOR	12	17	0.870
GKS	BB	0	39	0.000	HAR	BB	0	18	0.000	KUZ	BB	0	15	0.000
GKS	MET	1	42	0.024	HAR	MET	0	21	0.000	KUZ	MET	1	18	0.021
GKS	CO	2	29	0.069	HAR	CO	2	31	0.065	KUZ	CO	4	12	0.271
GKS	EPT	3	34	0.088	HAR	EPT	2	27	0.074	KUZ	EPT	2	17	0.276
GKS	FTA	0	31	0.000	HAR	FTA	1	24	0.042	KUZ	FTA	1	20	0.008
GKS	PNB	3	37	0.081	HAR	PNB	1	37	0.027	KUZ	PNB	5	18	0.184
GKS	AO	3	38	0.079	HAR	AO	3	37	0.081	KUZ	AO	1	15	0.139
GKS	AT	1	39	0.026	HAR	AT	0	36	0.000	KUZ	AT	1	19	0.036
GKS	MFX	23	36	0.639	HAR	MFX	6	32	0.188	KUZ	MFX	5	19	0.664
GKS	MFA	11	36	0.306	HAR	MFA	4	31	0.129	KUZ	MFA	7	19	0.270
GKS	SFC	22	42	0.524	HAR	SFC	6	35	0.171	KUZ	SFC	9	20	0.449
GKS	FFOR	30	42	0.714	HAR	FFOR	6	35	0.171	KUZ	FFOR	11	19	0.872
GKS	ALPF	15	33	0.455	HAR	ALPF	7	23	0.304	KUZ	ALPF	7	14	0.713
GKS	PTOR	3	33	0.091	HAR	PTOR	0	18	0.000	KUZ	PTOR	2	19	0.258
GKS	MXT	2	37	0.054	HAR	MXT	0	35	0.000	KUZ	MXT	0	19	0.179
GKS	ZFFA	12	40	0.300	HAR	ZFFA	14	28	0.500	KUZ	ZFFA	7	20	0.260
GKS	AIOF	4	38	0.105	HAR	AIOF	0	24	0.000	KUZ	AIOF	5	16	0.135
GKS	IOS	12	38	0.316	HAR	IOS	2	29	0.069	KUZ	IOS	6	18	0.458
GKS	NFOR	27	29	0.931	HAR	NFOR	12	20	0.600	KUZ	NFOR	16	18	0.972
GKS	AAPF	28	35	0.800	HAR	AAPF	1	31	0.032	KUZ	AAPF	9	16	0.559
GKS	FH	7	38	0.184	HAR	FH	3	33	0.091	KUZ	FH	9	19	0.256
GKS	CFD	2	28	0.071	HAR	CFD	0	16	0.000	KUZ	CFD	1	16	0.019
GKS	PTUB	5	23	0.217	HAR	PTUB	1	35	0.029	KUZ	PTUB	1	18	0.254
GKS	BHC	3	25	0.120	HAR	BHC	1	34	0.029	KUZ	BHC	3	19	0.229
GKS	FOI	0	29	0.000	HAR	FOI	2	32	0.063	KUZ	FOI	0	19	0.023
GKS	FSO	10	26	0.400	HAR	FSO	9	24	0.375	KUZ	FSO	5	20	0.264
GKS	PFOSS	3	23	0.130	HAR	PFOSS	1	21	0.048	KUZ	PFOSS	3	19	0.209
GKS	TMF	26	38	0.684	HAR	TMF	0	35	0.000	KUZ	TMF	2	17	0.180

Table 3. Continued…

Sample	Trait	p	n	Freq.	Sample	Trait	p	n	Freq.	Sample	Trait	p	n	Freq.
MOL	HNL	16	37	0.432	SAP	HNL	23	31	0.742	TH	HNL	67	137	0.489
MOL	OL	3	29	0.103	SAP	OL	2	31	0.065	TH	OL	19	137	0.139
MOL	LO	18	25	0.720	SAP	LO	14	25	0.560	TH	LO	79	134	0.590
MOL	PFOR	20	34	0.588	SAP	PFOR	28	35	0.800	TH	PFOR	120	138	0.870
MOL	BB	0	36	0.000	SAP	BB	0	41	0.000	TH	BB	0	138	0.000
MOL	MET	4	44	0.091	SAP	MET	3	45	0.067	TH	MET	3	141	0.021
MOL	CO	7	33	0.212	SAP	CO	0	23	0.000	TH	CO	36	133	0.271
MOL	EPT	8	36	0.222	SAP	EPT	2	22	0.091	TH	EPT	35	127	0.276
MOL	FTA	1	44	0.023	SAP	FTA	0	28	0.000	TH	FTA	1	128	0.008
MOL	PNB	3	41	0.073	SAP	PNB	2	33	0.061	TH	PNB	25	136	0.184
MOL	AO	3	34	0.088	SAP	AO	4	30	0.133	TH	AO	19	137	0.139
MOL	AT	0	44	0.000	SAP	AT	1	44	0.023	TH	AT	5	137	0.036
MOL	MFX	15	40	0.375	SAP	MFX	16	33	0.485	TH	MFX	91	137	0.664
MOL	MFA	17	42	0.405	SAP	MFA	9	36	0.250	TH	MFA	37	137	0.270
MOL	SFC	19	45	0.422	SAP	SFC	16	40	0.400	TH	SFC	61	136	0.449
MOL	FFOR	29	43	0.674	SAP	FFOR	40	40	1.000	TH	FFOR	123	141	0.872
MOL	ALPF	15	31	0.484	SAP	ALPF	15	31	0.484	TH	ALPF	107	150	0.713
MOL	PTOR	3	41	0.073	SAP	PTOR	2	33	0.061	TH	PTOR	39	151	0.258
MOL	MXT	0	42	0.000	SAP	MXT	0	38	0.000	TH	MXT	28	156	0.179
MOL	ZFFA	14	41	0.341	SAP	ZFFA	13	40	0.325	TH	ZFFA	40	154	0.260
MOL	AIOF	7	33	0.212	SAP	AIOF	11	31	0.355	TH	AIOF	20	148	0.135
MOL	IOS	17	37	0.459	SAP	IOS	12	31	0.387	TH	IOS	66	144	0.458
MOL	NFOR	32	37	0.865	SAP	NFOR	18	22	0.818	TH	NFOR	106	109	0.972
MOL	AAPF	20	36	0.556	SAP	AAPF	27	39	0.692	TH	AAPF	85	152	0.559
MOL	FH	5	44	0.114	SAP	FH	10	38	0.263	TH	FH	34	133	0.256
MOL	CFD	1	42	0.024	SAP	CFD	1	33	0.030	TH	CFD	2	108	0.019
MOL	PTUB	1	41	0.024	SAP	PTUB	2	32	0.063	TH	PTUB	29	114	0.254
MOL	BHC	10	44	0.227	SAP	BHC	5	36	0.139	TH	BHC	27	118	0.229
MOL	FOI	1	42	0.024	SAP	FOI	0	32	0.000	TH	FOI	3	128	0.023
MOL	FSO	16	41	0.390	SAP	FSO	6	32	0.188	TH	FSO	34	129	0.264
MOL	PFOSS	5	41	0.122	SAP	PFOSS	11	31	0.355	TH	PFOSS	24	115	0.209
MOL	TMF	2	39	0.051	SAP	TMF	0	37	0.000	TH	TMF	23	128	0.180

1. Number of individuals in which the trait is present.
2. Number of individuals in which the trait could be assessed.

also characterized by relatively high prevalence (66.4%) of MFX and PTUB (25.4%). BUS is set apart from the main aggregate of samples to a lesser degree than HAR, ALT or GKS and this separation is largely driven by relatively high prevalence of OL (22.2%), CO (33.3%) and AO (25.0%). Yet, as noted for the separation of ALT and GKS from the other samples, high prevalence of OL fails to account for the separation of BUS from KUZ (26.7%), while high prevalence of CO fails to differentiate BUS from KUZ (33.3%) or TH (27.1%).

The matrix of multivariate MMD scores is presented in Table 8. The average MMD across all 36 pairwise comparisons is 0.0909. Of the 36 pairwise contrasts, six (16.7%) provide no separation between sample pairs and all but one (5/6= 83.3%) occur between the four time successive BMAC era samples from Djarkutan. Like the first model, another 12 (33.4%) pairwise contrasts provide separations between sample pairs, but the distances separating them are not statistically significant. The remaining 18 contrasts (50.0%) provide statistically significant separations between sample pairs. Significant differences are not randomly distributed across sample pairs and, as with the first model, primarily involve separation of HAR (all eight significant). However, in a reversal from the previous model, GKS with six significant pairwise differences (75%) is identified as more unique relative to the other samples than TH (five of eight: 62.5% significant).

As was the case with the first model, neighbor-joining cluster analysis (Fig. 5a) identifies HAR as the most unique sample. However, when alpha is set at <0.05 this highly divergent sample links to the temporally successive BMAC era samples from Djarkutan via MOL, *then* DJR, and then KUZ. The Kuzali period sample stands at the nexus of two clades. The first may be described as an indigenous clade of north Bactrians that includes the earliest (SAP) and latest (BUS) of the Bronze Age samples from this region. The second links TH with the two pre-BMAC era (ALT, GKS) that occupy a rather isolated position with close affinities to one another and only very distant links to the other samples via TH. Indeed, ALT and GKS stand out as most divergent from HAR.

Multidimensional scaling with Guttman's coefficient of alienation into three dimensions was accomplished in two iterations. The stress incurred in fitting the individual points was 0.006 and the totality of the variance between points was captured by the configuration. The resulting plot (Fig. 5b) is virtually identical to that yielded by Model 1. That is, there is a wide separation of samples in which HAR is isolated on the left side of the array, the early BMAC sample from SAP is isolated in the right foreground, ALT occupies a position in the right background opposite to SAP, while TH and GKS occupy opposite positions with high and low scores along the third dimension, respectively. The only difference concerns the placement of the Djarkutan period sample (DJR). Instead of joining the sample from GKS on a separate vector from the other temporally successive samples from Djarkutan (as in single-step Model 1), this sample now provides the link to the earliest BMAC sample from SAP. This difference minimizes phenetic space separating SAP from the Djarkutan samples.

Model 3: $\alpha < 0.05$ with Bonferroni's Adjustment for Multiple Comparisons

Model 3 takes the most conservative approach for the inclusion of variables. In this case, for a variable to be retained it must have an associated p-value less than that recommended for $\alpha < 0.05$ with Bonferroni's adjustment for multiple comparisons. With nine samples there are 36 possible pairwise contrasts, therefore the Bonferroni adjusted alpha value is far lower than 0.05 at 0.00139 ($\alpha B < 0.0536 = 0.00139$). Hence, only those variables whose associated p-value is less than 0.00139 across all samples were retained. This resulted in the elimination of 15 traits in addition to the five traits eliminated as a consequence of the strictures of Model 2. As a result, Model 3 involves inter-sample contrasts based on a battery of 12 nonmetric traits (Table 4). The average measure of divergence by trait is 2.605 (Table 5). As with the previous models, the most influential trait is TMF, followed by FFOR, LO and PFOR. Unlike Model 2, all of the retained traits contribute to the overall separation of samples. Overall, some

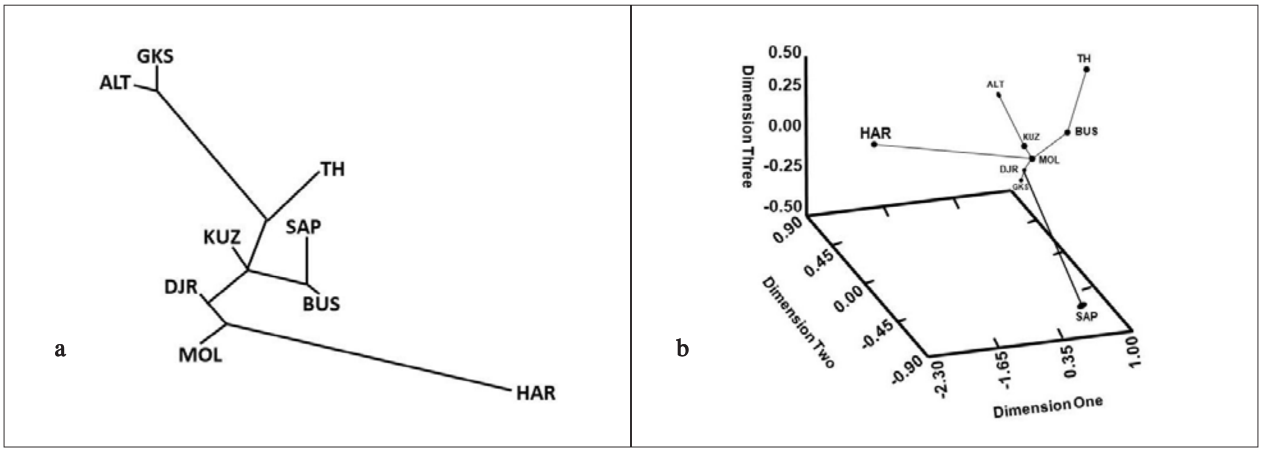

Figure 5. a) Neighbor-joining cluster analysis and b) multidimensional scaled scatterplot with Guttman's coefficient of alienation into three dimensions with 27 traits considered (Single-Step Model 2). Sample abbreviations from Table 4.

Table 4. Chi-square Analysis of Trait differences across all Samples and Nonmetric Traits included after Elimination Criteria Imposed by the Four Models.

Trait Name	No.	Abb.	X^2	p	Model 1 All Traits	Model 2 α< 0.05[1]	Model 3 α_B< 0.05[2]	Model 4 α_{BH}< 0.05[3]
Highest Nuchal Line	1	HNL	34.310	0.000	+	+	+	+
Ossicle at Lambda ("Inca Bone")	2	OL	11.245	0.188	+	+		
Lambdoidal Ossicle	3	LO	49.266	0.000	+	+	+	+
Parietal (Obelionic) Foramen	4	PFOR	80.468	0.000	+	+	+	+
Bregmatic Bone	5	BB	0.000	1.000	+			
Metopism	6	MET	6.860	0.552	+	+		
Coronal Ossicle	7	CO	20.794	0.008	+	+		+
Epipteric Bone	8	EPT	13.641	0.092	+	+		+
Fronto-Temporal Articulation	9	FTA	4.683	0.791	+			
Parietal Notch Bone	10	PNB	16.679	0.034	+	+		
Asterionic Ossicle	11	AO	14.104	0.079	+	+		
Auditory Torus	12	AT	5.870	0.662	+			
Mastoid Foramen Ex-sutural	13	MFX	43.491	0.000	+	+	+	+
Mastoid Foramen Absent	14	MFA	15.252	0.054	+	+		+
Supraorbital Foramen Complete	15	SFC	11.146	0.194	+	+		+
Frontal Foramen	16	FFOR	100.715	0.000	+	+	+	+
Accessory Lesser Palatine Foramen	17	ALPF	26.950	0.001	+	+	+	+
Palatine Torus	18	PTOR	21.094	0.007	+	+		+
Maxillary Torus	19	MXT	40.517	0.000	+	+	+	+
Zygofacial Foramen Absent	20	ZFFA	8.293	0.405	+	+		
Accessory Infraorbital Foramen	21	AIOF	24.158	0.002	+	+		+
Infraorbital Suture	22	IOS	22.095	0.005	+	+		+
Nasal Foramen	23	NFOR	27.755	0.001	+	+	+	+
Anterior Alveolar Palatine Foramen	24	AAPF	49.287	0.000	+	+	+	+
Foramen of Huschke	25	FH	12.752	0.121	+	+		
Condylar Facet Double	26	CFD	2.359	0.968	+			
Precondylar Tubercle	27	PTUB	26.287	0.001	+	+	+	+
Bifid Hypoglossal Canal	28	BHC	11.659	0.167	+	+	+	
Foramen Ovale Incomplete	29	FOI	4.943	0.764	+			
Foramen Spinosum Open	30	FSO	12.198	0.143	+	+		
Pharyngeal Fossa	31	PFOSS	10.986	0.203	+	+		
Tympanic Marginal Foramen	32	TMF	108.320	0.000	+	+	+	+
TOTAL					32	27	12	18

1. For $\alpha<0.05$, a trait was considered valid if any pairwise contrast yielded a difference in which $p< 0.05$.
2. For $\alpha_B<0.05$, a trait was considered valid if $\alpha<0.05$ after Bonferroni adjustment for multiple comparisons.
3. For $\alpha_{BH}<0.05$, a trait was considered valid if $\alpha<0.05$ after a Holm's (1979) nested modification of Bonferroni adjustment for multiple comparisons, controlling for multicollinearity and unique vectors of sample segregation.

124 of 336 (36.90%) contrasts by variable and by sample pair are statistically significant (Table 6). Once again, statistically significant differences are not equally distributed across samples; however, with this model only slightly less than half rather than less than one-fifth of significant differences on average occur between the time successive BMAC era samples from Djarkutan ($\bar{X}$= 8.25) than among the remaining samples ($\bar{X}$= 19.00), with the greatest number of significant differences occurring for HAR (n= 37), with far fewer for TH (n= 21) and SAP (n= 14).

The first two coordinate dimensions of a correspondence analysis of the relationship between nonmetric trait frequencies and samples for those traits that yield a significant difference at Bonferroni adjusted $\alpha< 0.05$ across all nine samples encompasses 75.4% of the total variation. The plot for traits (Fig. 6a) shows a broadly similar distribution to that observed for the first two models with most traits aggregating near the origins for the first two coordinate dimensions . Apart from a few traits (LO, PFOR, AAPF), the remainder show an enhanced ability to distinguish

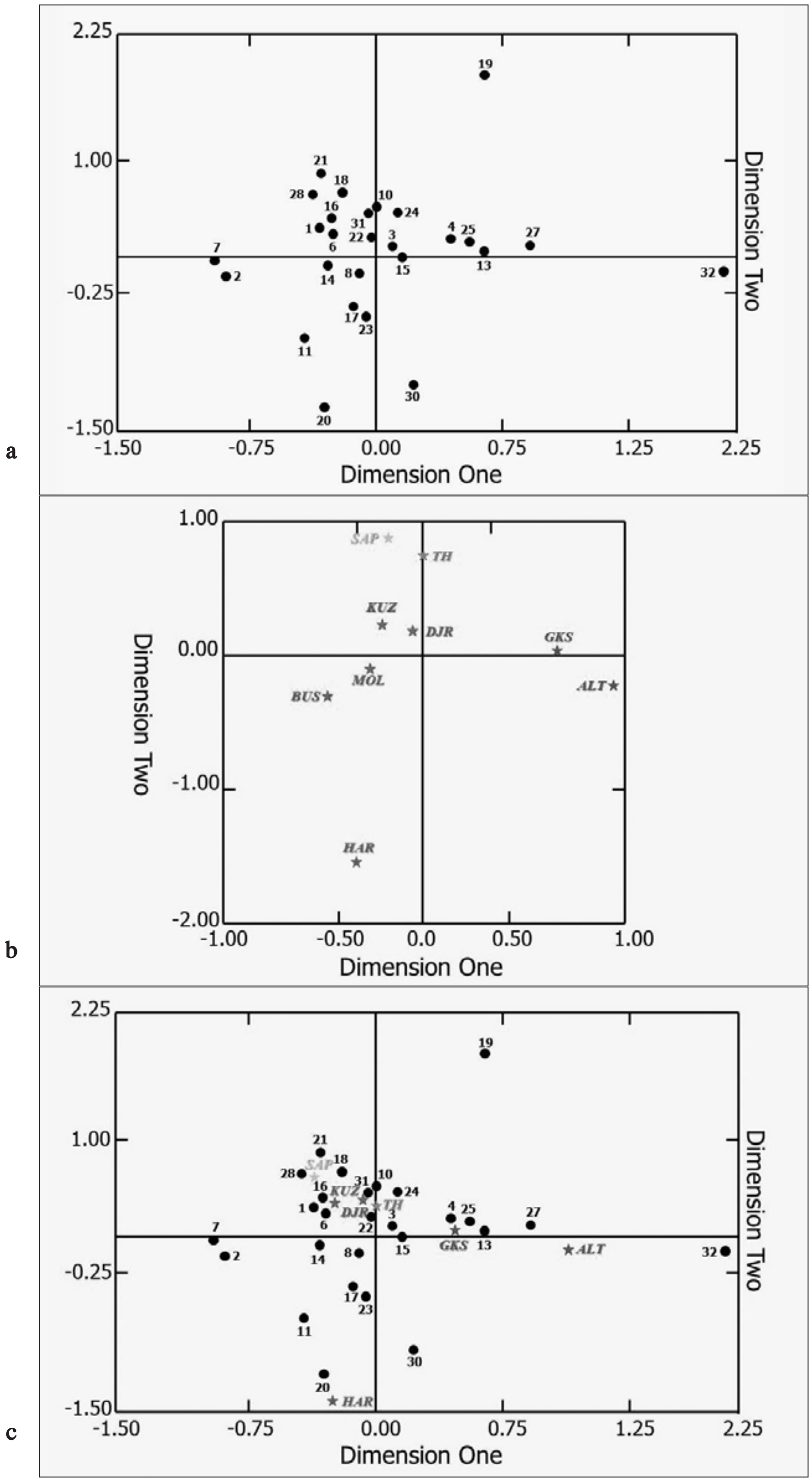

Figure 4. Correspondence analysis based upon the 27 cranial nonmetric traits remaining after elimination of the five traits failing to meet Harris and Sjøvøld's (2004) threshold of at least one pairwise contrast being significant with $\alpha < 0.05$ among nine samples: a) plot of traits (circles), b) plot of samples (stars), and c) biplot of traits (circles) and samples (stars). Trait numbers are from Table 4, sample abbreviations are from Table 1.

Table 5. Contribution of each Trait to the Total Measure of Divergence across Groups by Model.

		Model 1 (All Traits)			Model 2 ($\alpha < 0.05$)			Model 3 ($\alpha_B < 0.05$)		
No.	Abb.	MD[1]	MD/TMD[2]	Rank[3]	MD[1]	MD/TMD[2]	Ranking[3]	MD[1]	MD/TMD[2]	Ranking[3]
1	HNL	0.1984	6.6089	7	0.1993	6.6056	7	0.2148	8.2435	7
2	OL	0.01335	0.4510	20	0.0142	0.4723	20			
3	LO	0.3403	11.3366	3	0.3426	11.3543	3	0.3502	13.4412	3
4	PFOR	0.2867	9.5507	4	0.2881	9.5507	4	0.2961	11.3658	4
5	BB	0.0000	0.0000							
6	MET	0.0000	0.0000		0.0000	0.0000				
7	CO	0.0536	1.7853	12	0.0551	1.8278	10			
8	EPT	0.0038	0.1274	23	0.0038	0.1274	23			
9	FTA	0.0000	0.0000							
10	PNB	0.0225	0.7512	16	0.0238	0.7894	14			
11	AO	0.0000	0.0000		0.0000	0.0000				
12	AT	0.0000	0.0000							
13	MFX	0.2283	7.6073	5	0.2327	7.7144	5	0.2423	9.3026	5
14	MFA	0.0604	2.0125	10	0.0490	1.6243	12			
15	SFC	0.0237	0.7884	14	0.0238	0.7884	15			
16	FFOR	0.5157	17.1811	2	0.5233	17.3458	2	0.5462	20.9678	2
17	ALPF	0.0796	2.6508	9	0.0800	2.6508	9	0.0888	3.4084	8
18	PTOR	0.0099	0.3308	21	0.0100	0.3308	21			
19	MXT	0.0093	0.3092	22	0.0093	0.3092	22	0.0127	0.4859	11
20	ZFFA	0.0031	0.1047	24	0.0032	0.1047	24			
21	AIOF	0.0542	1.8057	11	0.0545	1.8057	11			
22	IOS	0.1585	5.2820	8	0.1594	5.2820	8			
23	NFOR	0.0227	0.7578	15	0.0229	0.7578	16	0.0250	0.9604	9
24	AAPF	0.2278	7.5883	6	0.2289	7.5883	6	0.2334	8.9593	6
25	FH	0.0161	0.5373	19	0.0162	0.5373	19			
26	CFD	0.0000	0.0000							
27	PTUB	0.0195	0.6495	17	0.0196	0.6495	17	0.0236	0.9040	10
28	BHC	0.0027	0.0894	25	0.0027	0.0894	25	0.0028	0.1071	12
29	FOI	0.0000	0.0000							
30	FSO	0.0437	1.4551	13	0.0439	1.4551	13			
31	PFOSS	0.0161	0.5377	18	0.0162	0.5377	18			
32	TMF	0.5914	19.7015	1	0.5944	19.7015	1	0.5693	21.8540	1
	Σ(MD)=	3.0016			3.0169			2.6051		

		Model 4 ($\alpha_{BH} < 0.05$)		
No.	Abb.	MD[1]	MD/TMD[2]	Rank[3]
1	HNL	0.1827	6.4926	7
2	OL			
3	LO	0.3514	12.4877	3
4	PFOR	0.2882	10.2442	4
5	BB			
6	MET			
7	CO	0.0438	1.5553	10
8	EPT	0.0069	0.2469	18
9	FTA			
10	PNB			
11	AO			
12	AT			
13	MFX	0.1836	6.5244	6
14	MFA	0.0355	1.2610	12
15	SFC	0.0262	0.9301	14
16	FFOR	0.4529	16.0979	2
17	ALPF	0.0891	3.1662	9
18	PTOR	0.0122	0.4351	16
19	MXT	0.0098	0.3467	17
20	ZFFA			
21	AIOF	0.0429	1.5230	11
22	IOS	0.1666	5.9195	8
23	NFOR	0.0096	0.9601	13
24	AAPF	0.2525	8.9753	5
25	FH			
26	CFD			
27	PTUB	0.0181	0.6434	15
28	BHC			
29	FOI			
30	FSO			
31	PFOSS			
32	TMF	0.6244	22.1906	1
	Σ(MD)=	2.8137		

1. MD= Measure of divergence defined as $[(\theta_1 - \theta_2)^2 - (1/N_1 + 1/N_2)]$, $\theta = \sin^{-1}(1-2p)$.
2. Total measure of divergence (TMD)= Σ(MD). MD/TMD expressed as a percentage.
3. Only those variables that contribute to the measure of divergence (>0) receive ranks

between samples. Two traits, MXT in the upper center and TMF in the center right, are the most divergent. The remaining traits fall into three distinct groups. The first (PFOR, MFX, PTUB) is found in the upper right, the second (LO, AAPF) is found in the lower center, while the third (HNL: highest nuchal line: Trait 1, FFOR, AAPF, and NFOR: nasal foramen: Trait 23) is found in the center left.

The plot of samples (Fig. 6b) shares some differences and similarities from that seen in the previous models. In dramatic contrast to Models 1 and 2, HAR does *not* stand apart from all other samples. Instead, HAR occupies a semi-isolated position in the upper left of the array intermediate between TH and the BMAC samples from Sapalli tepe and Djarkutan. An inspection of Figure 6c in conjunction with Table 3 reveals that this positioning of HAR is the consequence of low prevalence of PFOR (21.6%), MFX (18.8%) and especially TMF (81.8%) relative to all other samples. It is the sample from Tepe Hissar (TH), found in the upper center of the array that occupies the most isolated position relative to the other samples. This isolation is driven by MXT, which has a prevalence of 17.9%, and is completely absent from all other samples, except GKS where it occurs with a frequency of 5.4%. All three models identify the two pre-BMAC samples (ALT, GKS) as peripheral to the other samples due to the relatively high prevalence of PTUB (except for TH) and TMF. Perhaps what is most unique is the clear association of all BMAC era samples to one another in the lower right. Neither the earliest (SAP) nor the latest (BUS) stands apart, while the most centrally located — with near-equidistant affinities to all other BMAC era samples — is the Molali phase sample (MOL). An inspection of Figure 6c in tandem with Table 3 indicates that the aggregation of BMAC era samples in the lower left is due to relatively higher prevalence of HNL (35.3 – 74.2%), except for TH (48.9%),high prevalence of FFOR (47.4 – 100.0%), except for GKS (71.4%) and TH (87.2%), and by relatively low prevalence for NFOR (80.5 – 89.9%), again with exceptions for GKS (93.1%) and TH (97.2%).

The matrix of MMD scores is presented in Table 9. The average MMD across all 36 pairwise

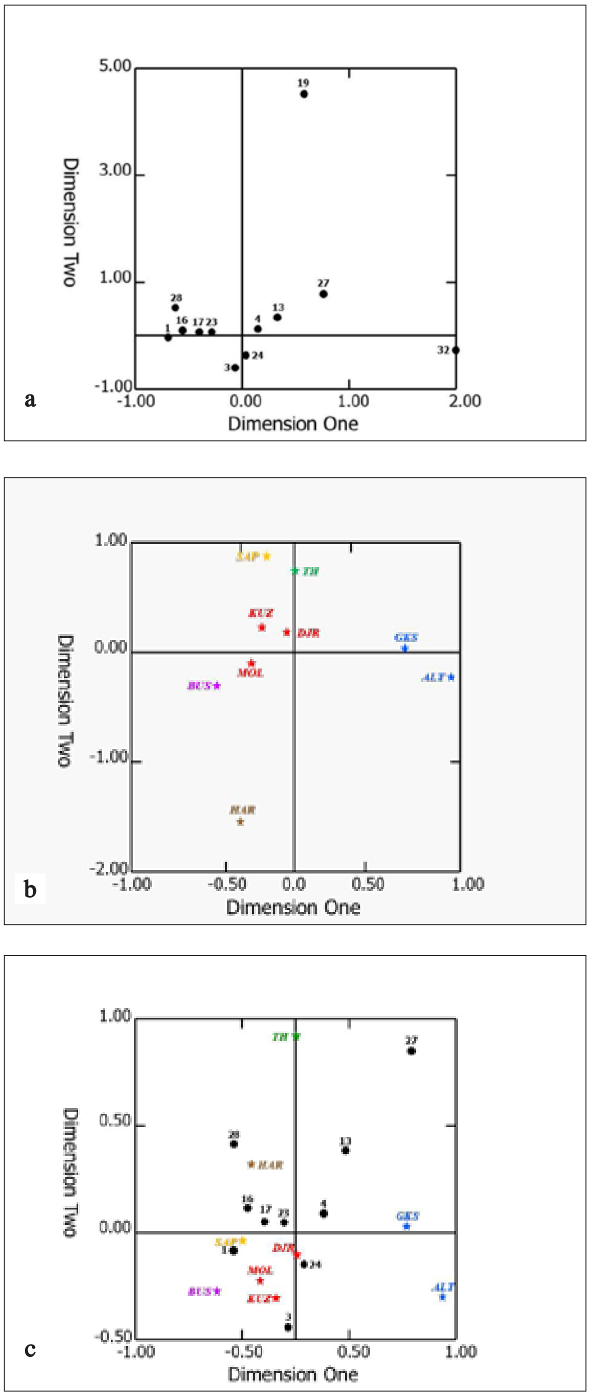

Figure 6. Correspondence analysis of 12 cranial nonmetric traits among nine samples after elimination of traits based on $\alpha > 0.05$ after Bonferroni adjustment for multiple comparisons (n= 36 comparisons): a) plot of traits (circles), b) plot of samples (stars), and c) plot of traits (circles) and samples stars). Maxillary torus (MXT: Trait No. 19) and tympanic marginal foramen (TMF: Trait No. 32) eliminated from plot of traits and samples to enhance patterning among remaining traits and samples. Sample abbreviations are from Table 1, trait numbers are from Table 4.

comparisons is 0.0764. As with Model 2, of the 36 pairwise contrasts, six (16.7%) provide no separation between sample pairs and all but one of these non-separations (ALT-GKS) occur between the temporally successive samples from Djarkutan. Another three (8.3%) provide non-significant separations between sample pairs, while the remaining 28 contrasts (77.8%) are statistically significant. As observed with the previous models, significant differences are non-randomly distributed across sample pairs. The relevant criterion is whether the contrast occurs between the time successive BMAC era samples from Djarkutan (DJR, KUZ, MOL, BUS) or between samples obtained from other sites. Among the former not a single contrast is statistically significant, but among the latter all eight contrasts separate HAR from all other samples. For TH, SAP, and GKS seven of the eight contrasts are significant. The only exceptions are between the BUS sample for TH and SAP and between ALT and GKS. Six contrasts separate ALT from the other samples; the two exceptions being GKS and KUZ.

Neighbor-joining cluster analysis (Fig. 7a) yields an array very similar to that obtained with the two previous models. Located in the lower

Table 6. Chi-square Analysis of trait differences across all Nine Samples and Nonmetric Traits after Elimination Criteria Imposed by the First Three Models.

	Altyn depe			Bustan			Djarkutan			Geoksyur			Harappa		
Trait No.	All Traits	α< 0.05	α_B< 0.05	All Traits	α< 0.05	α_B< 0.05	All Traits	α< 0.05	α_B< 0.05	All Traits	α< 0.05	α_B< 0.05	All Traits	α< 0.05	α_B< 0.05
1	1	1	1	2	2	1	2	2	0	3	3	1	5	5	3
2	0	0	---	1	1	---	3	3	---	0	0	---	0	0	---
3	2	2	2	2	2	1	4	4	0	2	2	1	8	8	7
4	4	4	2	4	4	1	5	5	1	4	4	1	7	7	6
5	0	---	---	0	---	---	0	---	---	0	---	---	0	---	---
6	0	0	---	0	0	---	0	0	---	0	0	---	0	0	---
7	0	0	---	1	1	---	0	0	---	2	2	---	2	2	---
8	0	0	---	0	0	---	1	1	---	1	1	---	1	1	---
9	0	---	---	0	---	---	0	---	---	0	---	---	0	---	---
10	0	0	---	0	0	---	0	0	---	0	0	---	2	2	---
11	0	0	---	1	1	---	1	1	---	0	1	---	0	0	---
12	0	---	---	0	---	---	0	---	---	0	---	---	0	---	---
13	3	3	1	3	3	0	2	2	0	5	5	1	4	4	2
14	0	0	---	1	1	---	2	2	---	0	0	---	4	4	---
15	1	1	---	0	0	---	1	1	---	2	2	---	6	6	---
16	4	4	3	4	4	1	4	4	3	4	4	2	7	7	6
17	0	0	0	1	1	0	1	1	0	2	2	0	3	3	1
18	0	0	---	1	1	---	1	1	---	0	0	---	2	2	---
19	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0
20	0	0	---	0	0	---	0	0	---	0	0	---	1	1	---
21	0	0	---	0	0	---	3	3	---	3	3	---	4	4	---
22	1	1	---	1	1	---	1	1	---	1	1	---	8	8	---
23	0	0	0	0	0	0	1	1	1	1	1	0	4	4	1
24	1	1	1	2	2	1	1	1	1	5	5	1	8	8	8
25	1	1	---	4	4	---	1	1	---	1	1	---	2	2	---
26	0	---	---	0	---	---	0	---	---	0	---	---	0	---	---
27	0	0	0	0	0	0	1	1	0	2	2	0	2	2	0
28	0	0	0	0	0	0	1	1	0	0	0	0	3	3	0
29	0	---	---	0	---	---	0	---	---	0	---	---	0	---	---
30	2	2	---	1	1	---	0	0	---	0	0	---	0	0	---
31	0	0	---	0	0	---	0	0	---	0	0	---	1	1	---
32	7	7	4	2	2	1	5	5	4	7	7	7	5	5	3
Total	27	27	14	31	31	7	42	42	10	45	45	14	90	90	37

Table 6. Continued…

	Kuzali			Molali			Sapalli Tepe			Tepe Hissar			TOTAL		
Trait No.	All Traits	α< 0.05	α_B< 0.05	All Traits	α< 0.05	α_B< 0.05	All Traits	α< 0.05	α_B< 0.05	All Traits	α< 0.05	α_B< 0.05	All Traits	α< 0.05	α_B< 0.05
1	1	1	0	2	2	0	7	7	2	3	3	1	26	26	8
2	1	1	---	0	0	0	0	0	0	1	1	0	6	6	0
3	1	1	1	1	1	1	1	1	1	1	1	1	22	22	7
4	1	1	0	4	4	2	3	3	1	4	4	4	36	36	8
5	0	---	---	0	---	0	0	---	0	0	---	0	0	---	0
6	0	0	---	1	1	0	0	0	0	1	1	0	2	2	0
7	3	3	---	1	1	0	4	4	0	3	3	0	16	16	0
8	0	0	---	0	0	0	0	0	0	3	3	0	6	6	0
9	0	---	---	0	---	0	0	---	0	0	---	0	0	---	0
10	4	4	---	1	1	0	1	1	0	2	2	0	10	10	0
11	0	0	---	0	0	0	0	0	0	0	0	0	2	2	0
12	0	---	---	0	---	0	0	---	0	0	---	0	0	---	0
13	2	2	1	2	2	1	1	1	0	4	4	3	26	26	4
14	1	1	---	1	1	1	0	0	0	1	1	0	10	10	0
15	1	1	---	1	1	0	1	1	0	1	1	0	14	14	0
16	3	3	3	3	3	2	7	7	6	6	6	4	42	42	30
17	0	0	0	1	1	0	2	2	0	4	4	1	14	14	2
18	0	0	---	1	1	0	1	1	0	4	4	0	10	10	0
19	0	0	0	1	1	0	1	1	0	4	4	0	8	8	0
20	0	0	---	0	0	0	0	0	0	1	1	0	2	2	0
21	2	2	---	1	1	0	3	3	1	2	2	0	18	18	2
22	1	1	---	1	1	1	1	1	0	1	1	1	16	16	10
23	1	1	0	2	2	0	1	1	0	4	4	2	14	14	4
24	2	2	1	2	2	1	1	1	1	2	2	1	24	24	16
25	6	6	---	2	2	0	1	1	0	4	4	0	22	22	0
26	0	---	---	0	---	0	0	---	0	0	---	0	0	---	0
27	0	0	0	2	2	1	1	1	0	4	4	1	12	12	1
28	0	0	0	1	1	0	0	0	0	1	1	0	6	6	0
29	0	---	---	0	---	0	0	---	0	0	---	0	0	---	0
30	0	0	---	0	0	0	2	2	0	1	1	0	6	6	0
31	0	0	---	1	1	0	2	2	0	0	0	0	4	4	0
32	4	4	2	4	4	2	5	5	3	5	5	2	44	44	32
Total	34	34	8	36	36	12	46	46	15	67	67	21	418	418	124

Table 7. Mean Measure of Divergence Distance Matrix across all Sample Pairs (Model 1)[1].

ALL TRAITS

Site	ALT	BUS	DJR	GKS	HAR	KUZ	MOL	SAP	TH
ALT	0	0.0542	0.0334	0.0347	0.0363	0.0410	0.0336	0.0349	0.0292
BUS	0.0198	0	0.0341	0.0349	0.0367	0.0417	0.0342	0.0353	0.0295
DJR	0.0013	0.0000	0	0.0137	0.0156	0.0205	0.0130	0.0140	0.0083
GKS	0.0000[2]	0.0565	0.0259	0	0.0167	0.0215	0.0139	0.0151	0.0093
HAR	**0.2446**	**0.2195**	**0.1524**	**0.2879**	0	0.0233	0.0158	0.0169	0.0112
KUZ	0.0000	0.0000	0.0000	0.0161	**0.1502**	0	0.0207	0.0218	0.0160
MOL	0.0180	0.0000	0.0000	**0.0421**	**0.1508**	0.0000	0	0.0142	0.0084
SAP	**0.0874**	0.0000	0.0190	**0.0758**	**0.2696**	0.0105	0.0136	0	0.0096
TH	**0.0244**	0.0004	**0.0496**	**0.0487**	**0.3077**	0.0155	**0.0348**	**0.0362**	0

1. Distances are below the diagonal, standard deviations are above, and bolded values represent significant pairwise differences (α< 0.05).
2. Off-diagonal negative MMD distances set to zero.

left, the sample from HAR is once again identified as unique, but unlike the previous two models, it appears no more unique than the dyad of pre-BMAC samples from ALT and GKS. As when all 32 traits were the basis of comparison (single-step Model 1), HAR connects to the other samples via the Djarkutan period (DJR) sample. This is followed by affinities to MOL and KUZ period samples. While this is similar to single-step Model 1, a key difference is that neither MOL nor KUZ serves as the nexus to other sample aggregates. Instead, all BMAC era samples, including the earliest (SAP) and the latest (BUS), are marked by closer affinities to one another than to non-BMAC samples. Finally, as with single-step Model 2, TH is identified as an intermediary between the BMAC samples from Sapalli tepe and Djarkutan and the pre-BMAC samples from ALT and GKS.

Multidimensional scaling (MDS) into three dimensions was accomplished in four iterations. The stress incurred was 0.011 and 99.99% of the variance between points was captured by the configuration. The resulting plot (Fig. 7b) shows many of the same features as those yielded by the other single-step models in the sense that there is a wide separation of samples. In this case, HAR is isolated on the right side of the array, the early BMAC sample from SAP is isolated in the left foreground, ALT occupies an isolated position in the upper left background opposite SAP, while TH and DJR occupy opposite positions with high and low scores along the third dimension, respectively. As was seen in single-step Models 1 and 2, the BMAC era samples from Djarkutan show fairly close affinities to one another. This is largely due to two important differences. First, with all three models TH occupies the distant position and BUS is identified as more proximate to the other BMAC era samples from Djarkutan. The second major difference concerns the two pre-BMAC samples. MDS plots based on single-step Models 1 and 2 show these two samples — ALT and GKS — as being quite divergent from one another, despite the fact that they are consistently placed together in both correspondence analysis and neighbor-joining plots. Figure 7b shows that these two sites occupy very similar positions along dimensions 1 and 2. It is only dimension 3 that separates them. If the minimum spanning tree linked these two samples together and then to KUZ via ALT or TH via ALT, this would be a pattern very similar to that seen in single-step Models 1 and 2.

Model 4: Multi-step Model 1 α< 0.05 with Holm's Adjustment for Multiple Comparisons

The multi-step model utilizes the results from single-step models to pool samples into more effective operational taxonomic units (OTUs) for further analysis based upon those samples that consistently yield the fewest significant

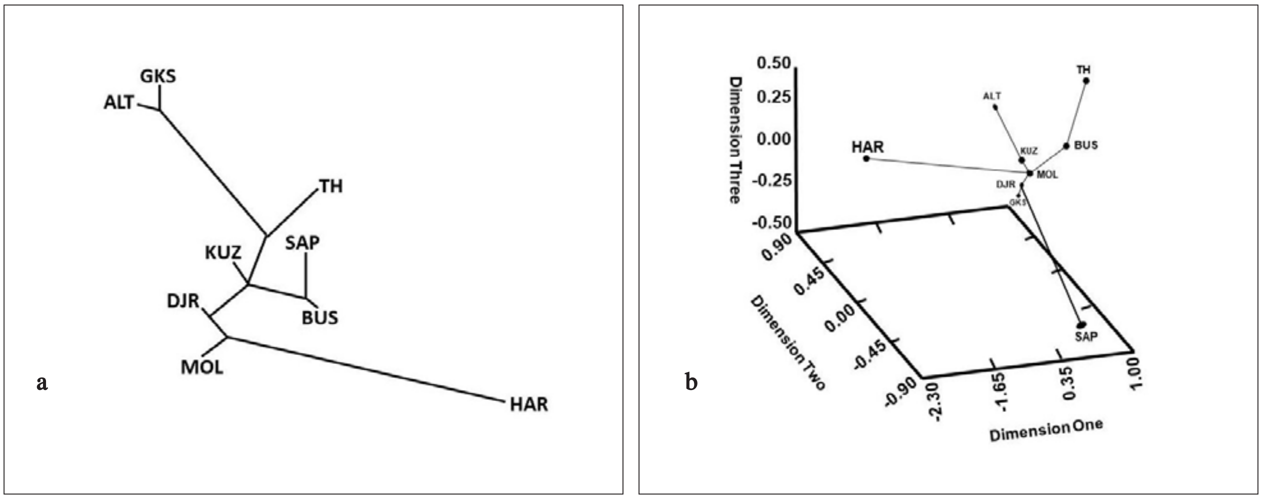

Figure 7. a) Neighbor-joining cluster analysis and b) multidimensional scaled scatterplot with Guttman's coefficient of alienation into three dimensions with 12 traits considered (Model 3). Sample abbreviations from Table 4.

differences among them, both by individual trait and across multiple variables as reflected by Smith's mean measure of divergence distances (Grewal, 1962; Sjøvold, 1973).The remaining samples are then contrasted with Holm's (1979) modification of Bonferroni's adjustment, which is a step-down procedure that sequentially ranks in reverse all of the observed p-values in order from smallest to largest. Each p-value is compared with the "Holmed" p-value threshold, which is $\alpha/(n - i + 1)$ in which n is the number of comparisons and i is the ranked comparison. Starting with the smallest p- value, these comparisons are conducted until the first non-rejection, such that with each comparison the number of comparisons is reduced sequentially and hence the p-value threshold increases relative to the unmodified alpha value, which in this case is 0.05

This procedure led to pooling of three of the four time successive BMAC era samples from Djarkutan (DJR, KUZ, MOL) into a single sample designated BMAC . This reduced the number of samples to seven and with seven samples there are 21 possible pairwise contrasts; therefore, the Holm-Bonferroni adjusted alpha value with no contrasts removed is 0.00238 ($\alpha B < 0.05 < 0.0521 = 0.00238$). Beginning with the smallest p-value after the first removal the Holm-Bonferroni adjusted threshold is now 0.00250, after the second removal it is 0.00263 and so on. This procedure resulted in the inclusion of 18 traits (Table 10), seven of which were not included in single-step Model 3 (CO, EPT, MFA, SFC, PTOR, AIOF, and IOS) and one (BHC) of which was eliminated. As with single-step Model 3, TMF, FFOR, LO and PFOR represent the four most influential traits in the multi-step model (Table 5). However, AAPF replaces MFX as the fifth most influential trait. The least influential traits are EPT, MXT, and PTOR each of which accounts for less than 0.5% of the total variation among samples.

The average measure of divergence by trait for the 18 trait battery is 2.814 (Table 5). Considered as a whole, 170 of 378 pairwise contrasts (44.97%) by variable are statistically significant (Table 11). HAR, with 53 significant pairwise differences by variable, is the most unique, followed by TH (n= 37) and the combined BMAC era sample from Djarkutan (n= 24). ALT and GKS, with 11 and 15 significant pairwise differences, are the least unique. The lack of uniqueness appears largely a consequence of their close affinities to one another as reflected by the fact that none of the 32 original traits differs significantly in frequency between them.

The first two coordinate dimensions of a correspondence analysis of the relationship between nonmetric trait frequencies and samples for those traits that yield a significant difference with a Holm-Bonferroni adjusted $\alpha < 0.05$ across

Table 8. Mean Measure of Divergence Distance Matrix across all Sample Pairs (Model 2).

α< 0.05

Site	ALT	BUS	DJR	GKS	HAR	KUZ	MOL	SAP	TH
ALT	0	0.0598	0.0363	0.0375	0.0389	0.0445	0.0365	0.0379	0.0316
BUS	0.0599	0	0.0382	0.0389	0.0406	0.0464	0.0383	0.0396	0.0331
DJR	0.0254	0.0183	0	0.0150	0.0167	0.0225	0.0144	0.0155	0.0091
GKS	0.0000	**0.0882**	**0.0398**	0	0.0177	0.0234	0.0152	0.0165	0.0101
HAR	**0.3178**	**0.2838**	**0.1922**	**0.3530**	0	0.0250	0.0169	0.0182	0.0118
KUZ	0.0189	0.0000	0.0000	0.0340	**0.1943**	0	0.0227	0.0239	0.0174
MOL	0.0454	0.0000	0.0000	**0.0592**	**0.1906**	0.0000	0	0.0157	0.0092
SAP	**0.1282**	0.0139	**0.0318**	**0.1004**	**0.3315**	0.0266	0.0256	0	0.0105
TH	0.0495	0.0176	**0.0641**	**0.0640**	**0.3730**	0.0282	**0.0468**	**0.0495**	0

1. Distances are below the diagonal, standard deviations are above, and bolded values represent significant pairwise differences (α< 0.05).

2. Off-diagonal negative MMD distances set to zero.

the seven remaining samples encompasses 69.9% of the total variation. The plot of traits (Fig. 8a) shows a broadly similar distribution to that observed for the single-step models with most traits aggregating near the origins of the first two coordinate dimensions. However, the greater dispersion of these points indicates an enhanced ability of these traits to distinguish between samples than was observed for the single-step models. This is especially the case for the coronal ossicle (7), the maxillary torus (19), and the presence of a tympanic marginal foramen (32) found in the upper left, upper right, and lower right of the plot, respectively. The plot of sites (Fig. 8b) shows the samples from HAR and TH to be separated from the other five samples with strongly positive scores for Dimension Two, while ALT and GKS are located near one another on the right side of the plot with positive scores for Dimension One. The broadly defined BMAC era samples (SAP, BMAC, BUS) are in the lower left with closest affinities to one another.

Examination of the biplot of traits and samples (Fig. 8c) indicates that TH is distinguished in the upper center of the array by high prevalence of PTOR (25.8%) and MXT (17.9%) relative to the other samples (PTOR: 0 – 10.8%, $\bar{X}$= 6.9%; MXT: 0 – 5.4%, $\bar{X}$= 1.1%). In contrast, HAR stands apart from all other samples, including TH, by possessing low prevalence of ALPF (30.4%) and NFOR (60%) relative to the other samples (ALPF: 45.5 – 71.3%, $\bar{X}$= 55.4%; NFOR: 81.8 – 97.2%, $\bar{X}$= 87.6%). The two pre-BMAC samples from ALT and GKS stand apart on the right side of the array with high prevalence of LO (75.7 – 90%, $\bar{X}$= 82.9%) and TMF (68.4 – 81.8%, $\bar{X}$= 75.1%) relative to the other samples (LO: 11.4 – 68.8%, $\bar{X}$= 48.8%; TMF: 0 – 18%, $\bar{X}$= 7.6%). BMAC samples, including SAP, stand apart in the lower left by possessing high prevalence of AIOF (27 – 35.5%, $\bar{X}$= 31.3%) relative to the other samples (0 – 13.5%, $\bar{X}$= 5.2%). The latest of these samples, BUS, stands apart from the others with high prevalence for the infraorbital suture (71.4%) relative to that observed among the other BMAC era samples (38.7 – 47.5%, $\bar{X}$= 44.5%).

The matrix of Smith's MMD scores is presented in Table 12. The average across all 21 pairwise comparisons is 0.1999. Broadly similar to the pattern seen with single-step Model 3, all but two (90.5%) of the pairwise contrasts yields a significant multivariate separation between sample pairs. Not surprisingly, given the univariate results above, the contrasts that yield no difference are those between ALT and GKS as well as that between the pooled BMAC sample and the BUS sample. Four pairwise contrasts (19.1%) yield non-significant differences and all

Table 9. Mean Measure of Divergence Distance Matrix across all Sample Pairs (Model 3)[1].

Bonferroni Adjusted (α< 0.05$_B$)

Site	ALT	BUS	DJR	GKS	HAR	KUZ	MOL	SAP	TH
ALT	0	0.0341	0.0202	0.0208	0.0209	0.0246	0.0202	0.0209	0.0174
BUS	**0.1018**	0	0.0227	0.0229	0.0233	0.0271	0.0226	0.0232	0.0196
DJR	**0.0520**	0.0183	0	0.0088	0.0091	0.0129	0.0085	0.0090	0.0054
GKS	0.0000[2]	**0.0881**	**0.0410**	0	0.0094	0.0383	0.0624	0.0874	0.0491
HAR	**0.2561**	**0.2042**	**0.1196**	**0.2924**	0	0.0135	0.0090	0.0096	0.0060
KUZ	0.0349	0.0000	0.0000	**0.0383**	**0.1323**	0	0.0129	0.0134	0.0098
MOL	**0.0729**	0.0000	0.0000	**0.0624**	**0.1374**	0.0000	0	0.0089	0.0053
SAP	**0.1307**	0.0032	**0.0312**	**0.0874**	**0.2490**	**0.0272**	**0.0184**	0	0.0059
TH	**0.0646**	0.0303	**0.0418**	**0.0491**	**0.2659**	**0.0335**	**0.0374**	**0.0272**	0

1. Distances are below the diagonal, standard deviations are above, and bolded values represent significant pairwise differences (α< 0.05).

2. Off-diagonal negative MMD distances set to zero.

involve BUS — a likely consequence of the small size of this sample.

Neighbor-joining cluster analysis (Fig. 9a) produces an array similar to that yielded by the single-step models. Once again HAR is identified as the most unique, connecting to the pooled BMAC sample at a very distant remove. The sample identified as bearing the shortest biodistance from the pooled BMAC sample from Djarkutan is the late BMAC era sample from BUS, followed by the early BMAC era sample from SAP. The sample from northeastern Iran (TH) is identified as possessing closer affinities to both SAP and the BMAC aggregate, than possessed by the two pre-BMAC samples from southern Turkmenistan (ALT, GKS), which occupy a rather isolated position in the upper left but share close affinities to one another.

Multidimensional scaling into three dimensions was accomplished in three iterations. The stress incurred in fitting the individual points was 0.001 and the totality of the variance between

Table 10. Chi-square Analysis of Trait differences across all Samples and Nonmetric Traits included after Elimination Criteria Imposed by Multi-step Model.

Trait					
Name	No.	Abb.	X^2	p	Model 4[1]
Highest Nuchal Line	1	HNL	35.455	0.000	+
Ossicle at Lambda (“Inca Bone”)	2	OL	5.095	0.532	
Lambdoidal Ossicle	3	LO	43.275	0.000	+
Parietal (Obelionic) Foramen	4	PFOR	83.917	0.000	+
Bregmatic Bone	5	BB	0.000	1.000	
Metopism	6	MET	5.096	0.532	
Coronal Ossicle	7	CO	18.640	0.005	+
Epipteric Bone	8	EPT	12.866	0.045	+
Fronto-Temporal Articulation	9	FTA	3.581	0.733	
Parietal Notch Bone	10	PNB	11.731	0.068	
Asterionic Ossicle	11	AO	11.203	0.082	
Auditory Torus	12	AT	3.744	0.711	
Mastoid Foramen Ex-sutural	13	MFX	42.592	0.000	+
Mastoid Foramen Absent	14	MFA	14.371	0.026	+
Supraorbital Foramen Complete	15	SFO	27.843	0.000	+
Frontal Foramen	16	FFOR	99.981	0.000	+
Accessory Lesser Palatine Foramen	17	ALPF	26.929	0.000	+
Palatine Torus	18	PTOR	20.726	0.002	+
Maxillary Torus	19	MXT	40.517	0.000	+
Zygofacial Foramen Absent	20	ZFFA	8.284	0.218	
Accessory Infraorbital Foramen	21	AIOF	22.339	0.001	+
Infraorbital Suture	22	IOS	20.991	0.002	+
Nasal Foramen	23	NFOR	26.653	0.000	+
Anterior Alveolar Palatine Foramen	24	AAPF	48.311	0.000	+
Foramen of Huschke	25	FH	9.175	0.164	
Condylar Facet Double	26	CFD	1.443	0.963	
Precondylar Tubercle	27	PTUB	25.580	0.000	+
Bifid Hypoglossal Canal	28	BHC	11.036	0.087	
Foramen Ovale Incomplete	29	FOI	4.514	0.607	
Foramen Spinosum Open	30	FSO	10.701	0.098	
Pharyngeal Fossa	31	PFOSS	9.435	0.151	
Tympanic Marginal Foramen	32	TMF	103.916	0.000	+
TOTAL					18

1. For $\alpha_{BH}<0.05$, a trait was considered valid if $\alpha<0.05$ after Holm-Bonferroni adjustment (Holm, 1979) for multiple comparisons.

points was captured by the configuration. The resulting plot (Fig. 9b) shows HAR as occupying a highly isolated position on the left side. The aggregated BMAC sample occupies the center of the array and shares closest affinities to the early BMAC era sample from SAP followed by the late BMAC era sample from BUS. TH occupies an isolated position in the upper right of the array while the two pre-BMAC era samples (GKS, ALT) occupy an isolated position in the lower right. Viewed in light of the results obtained from neighbor-joining cluster analysis, the MDS plot indicates that affinities between the two pre-BMAC samples are not especially close and it is the earlier sample from GKS that is identified as most unique while the later sample from ALT occupies a slightly closer position relative to the pooled BMAC sample from Djarkutan.

Discussion

Cranial Nonmetric Trait Selection and Model Efficacy

Biodistance studies, regardless of whether they are based on frequencies of cranial nonmetric traits or other modalities of biological variation, ultimately employ a series of pairwise comparisons to evaluate the degree of relatedness among the relevant operative taxonomic units (OTUs) (cf. Buikstra *et al.*, 1990; Dow and Cheverud, 1985; Erdene, 2008; Hens and Ross, 2017; Hanihara *et al.*, 2012; Meza-Peñloza *et al.*, 2021; Nikita *et al.*, 2012; Smouse *et al.*, 1986). A key issue surrounding multiple comparisons, when the same battery of variables is employed across a number of pairwise comparisons, is type I error in which researchers may incorrectly reject the null hypothesis because of number of recursive analyses involved across the experiments as a whole (Benjamini and Hochberg, 1995; Shaffer, 1995; Tukey, 1977).

Type I errors occur when the null hypothesis is rejected when, in fact, it is true. It is standard practice to accept an alpha level of <0.05 to distinguish statistically significant differences from those differences that are not significant statistically. Logically, when an alpha of <0.05 is used, one significant difference is expected to

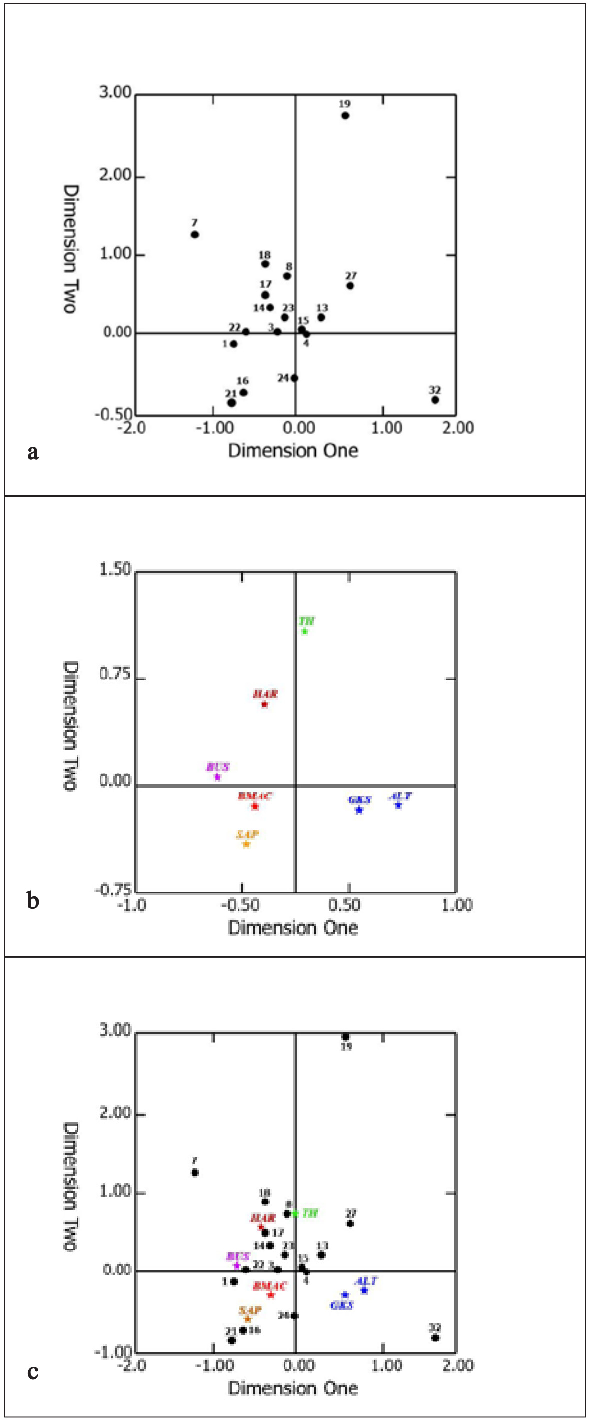

Figure 8. Correspondence analysis of 18 cranial nonmetric traits among six samples after pooling of time successive samples from Djarkutan into a single BMAC sample and elimination of traits based on $\alpha > 0.05$ after a multi-step Holm-Bonferroni adjustment for multiple comparisons (n= 15 comparisons): a) plot of traits (circles), b) plot of samples (stars), and c) plot of traits (circles) and samples stars). Sample abbreviations are from Table 1, trait numbers are from Table 4.

occur coincidentally for every 20 independent contrasts (Bland and Altman, 1995; Greenhalgh, 1997; Perneger, 1998; Sinclair *et al.*, 2013; Wilkinson, 1951; Williams, 1971). When more than one independent test is employed, the likelihood of finding a significant difference due merely to chance increases linearly as the number of tests increases (Tukey, 1977; Williams, 1971). To account for this, the usual procedure is to adjust the alpha level for each analysis to ensure the overall likelihood of obtaining a significant result remains at the stated alpha level (usually $\alpha < 0.05$). Many who advocate adjustments for multiple comparisons assert that control of type I error is crucial for avoiding spurious associations (Ahlbom, 1993; Bland and Atman, 1995; Perneger, 1998; Tukey, 1977; Zaykin *et al.*, 2002).

An array of methods for adjusting alpha levels to accommodate multiple comparisons has been formulated. Perhaps the best known is the Bonferroni (1935, 1936) correction. A Bonferroni correction adjusts the alpha level by taking the alpha value for each comparison as equal to the desired alpha level divided by the number of comparisons (Aickin and Gensler, 1996; Glickman *et al.*, 2014; Miller, 1981; Nakagawa, 2004; Perneger, 1998). While conceptually straightforward, the Bonferroni adjustment suffers from a number of problems. For brevity, only two will be mentioned here. First, the Bonferroni adjustment assumes that the experiment-wise error rate only applies to the hypothesis that the groups being compared in each pairwise contrast are identical *for all variables* considered. If any one of the *p*-values exceeds the universally Bonferroni adjusted *p*-value then the global null hypothesis is rejected. In such cases, one can say that two groups are not equal for all of the variables considered, but one cannot state which and how many variables differ (O'Keefe, 2003; Perneger, 1998; Schultz and Grimes, 2005) . In other words, the Bonferroni adjustment is testing the wrong hypothesis (Rothman, 1990; Savitz and Olshan, 1995; Thomas *et al.*, 1985), for researchers interested in biodistances are largely concerned whether the battery of predictor variables yields a significant difference between sample pairs, only secondarily are they concerned about which set of specific variables contribute to that difference . Indeed, most comparative analyses of cranial nonmetric trait prevalence across samples completely neglect assessment of which variables actually contribute to sample differences (cf. Dodo and Ishida, 1990; Fukumine *et al.*, 2006; Hanihara *et al.*, 2012; Meza-Peñaloza *et al.*, 2021; Movsesian and Vagner-Sapukhina, 2021). As a consequence, few pairwise contrasts

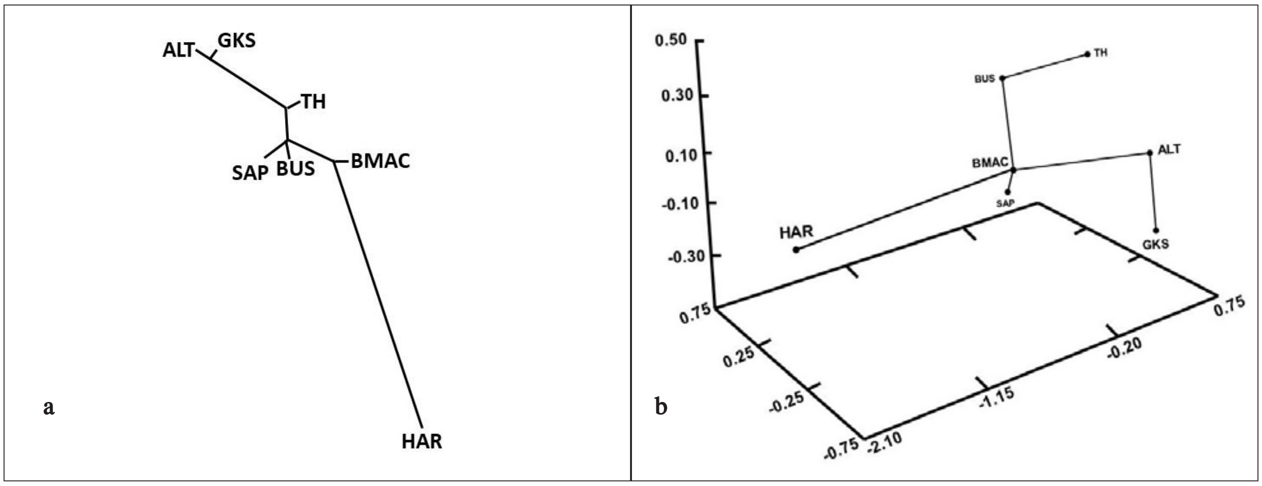

Figure 9. a) Neighbor-joining cluster analysis of Smith's mean measure of divergence distances and b) multidimensional scaled scatterplot with Guttman's coefficient of alienation into three dimensions among six samples after pooling of temporal period samples at Djarkutan into a single sample (BMAC) for those 18 traits yielding a significant difference ($\alpha < 0.05$) across all samples after a Holm-Bonferroni multi-step adjustment. Sample abbreviations are from Table 1.

Table 11. Number of Significant Trait differences by Sample and across all Six Samples included before and after Elimination Criteria.

	Altyn depe	BMAC	Bustan	Geoksyur	Harappa	Sapalli tepe	Tepe Hissar	Total
Trait No.	Multi-Step Model 4	Multi-Step Model 4	Multi-step Model 4	Multi-Step Model 4	Multi-Step Model 4	Multi-Step Model 4	Multi-Step Model 4	Multi-Step Model 4
1*	0	1	1	1	3	3	1	10
2	0	0	0	0	0	0	0	0
3*	1	1	1	1	6	1	1	12
4*	1	3	1	2	5	1	3	16
5	---	---	---	---	---	---	---	---
6	0	0	0	0	0	0	0	0
7	0	0	0	0	1	0	1	2
8	0	0	0	0	1	0	1	2
9	0	0	0	0	0	0	0	0
10	0	0	0	0	1	0	1	2
11	1	1	0	0	0	0	0	2
12	0	0	0	0	0	0	0	0
13*	1	2	0	2	3	0	2	10
14	0	1	0	0	1	0	0	2
15*	0	2	0	2	2	0	2	7
16*	2	3	1	2	5	4	3	20
17*	0	1	0	1	2	1	3	8
18*	0	1	0	0	1	0	2	4
19*	0	1	0	0	1	0	2	4
20	0	0	0	0	1	0	1	2
21*	0	2	0	0	2	2	2	8
22*	1	1	1	0	5	1	1	10
23*	0	1	0	0	1	1	3	6
24*	1	1	1	1	6	1	1	12
25	0	0	0	0	1	0	1	2
26	0	0	0	0	0	0	0	0
27*	0	1	0	0	1	0	2	4
28	0	0	0	0	1	0	1	2
29	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0
32*	5	2	2	5	3	2	3	22
Total	13	25	8	17	53	17	37	170

1. Asterisk indicates trait retained after imposition of elimination criteria noted in Table 10.

Table 12. Mean Measure of Divergence Distance Matrix between Sample Pairs under the Multi-step Model (Model 4)[1].

Site	ALT	BMAC	BUS	GKS	HAR	SAP	TH
ALT	0	0.0391	0.0757	0.0453	0.0467	0.0465	0.0383
BMAC	**0.0959**	0	0.0442	0.0150	0.0174	0.0160	0.0030
BUS	0.1423	0.0000	0	0.0502	0.0520	0.0515	0.0432
GKS	0.0000[2]	**0.1080**	**0.1713**	0	0.0209	0.0203	0.0120
HAR	**0.4948**	**0.3202**	0.4621	**0.5481**	0	0.0221	0.0139
SAP	**0.2109**	**0.0488**	0.0234	**0.1559**	**0.4836**	0	0.0132
TH	**0.0898**	**0.0910**	0.0326	**0.1027**	**0.5389**	**0.0782**	0

1. Distances are below the diagonal, standard deviations are above, and bolded values represent significant pairwise differences after multi-step Holm-Bonferroni adjustment. Sample abbreviations are from Table 1.

2. Off-diagonal negative MMD values set to zero.

are statistically significant and the patterning of relationships among samples is obscured by random statistical noise.

Procedures for simultaneous statistical inference have been developed that seek to control the maximum experiment-wise error rate (MEER) under any complete *or partial null hypothesis*. Such procedures that control the MEER are known as multiple level or as controlling experiment-wise error in a strong sense. As such, multiple level simultaneous statistical inference preserves the MEER — the probability of falsely rejecting at least one true null hypothesis (type I error) — regardless of which and how many of the other individual null hypotheses are true (Bender and Lange, 2001, pp. 333-4).

Second, in an effort to decrease the likelihood of committing a type I error, Bonferroni adjustments result in a concomitant increase in type II errors and hence, reduced statistical power (Jennions and Møller, 2003; Nakagawa, 2004; Perneger, 1998; Rothman, 1990). A type II error occurs when a researcher accepts a null hypothesis when in fact it is false. Type II errors are just as false as type I errors. Consequently, Bonferroni adjustments do not result in a more ‘cautious’ interpretation of results; they merely switch one type of statistical error for another (Lieberman and Cunningham, 2009). This situation is only exacerbated when experiment-wise error remains equally stringent when specific contrasts have been identified or eliminated as statistically significant (Holm, 1979; Rice, 1989).

Other adjustments to accommodate multiple comparisons have been offered in light of the identified shortcomings of the Bonferroni adjustment. The first is Holm’s (1979) sequentially rejective Bonferroni adjustment. As noted earlier, the Holm-Bonferroni adjustment is a step-down procedure that ranks all of the observed p-values in order from smallest to largest (Guo and Romano, 2007; Shaffer, 1995). Each pi is compared with the ‘Holmed’ p-value threshold $\alpha/(n - i + 1)$ in which n is the number of comparisons and i is the ranked comparison. Starting with the smallest p value, these comparisons are contrasted until the first non-rejection. Thus, with each comparison the number of comparisons is reduced sequentially and hence the p-value threshold increases relative to zero. This quality of sequential adjustment of multiple comparison p-values led Rice (1989) to adopt the Holm-Bonferroni adjustment because it controls for multiple comparisons with a markedly lesser decrease in statistical power (*i.e.*, liability of committing a type II error). As such, it operates in the same way that the Student-Newman-Keuls multiple-range test is more powerful than the Tukey test; ‘the rejection criteria are less stringent for all tests other than the test with the smallest p-value’ (Rice 1989, p. 224). While not ideal (see Hochberg, 1988), the Holm-Bonferroni adjustment was employed in the current study.

Two criteria were identified in the Introduction for assessment of different protocols for variable inclusion in models for computation of biodistances among the samples considered in the current study. These include: 1) The highest proportion of univariate and multivariate significant differences across samples without an undue reduction in statistical power, and 2) The greatest clarity in identification of which variables yield common sample aggregates and separate such aggregates from one another.

Greatest Proportion of Univariate and Multivariate Significant Differences without Undue Reduction in Power

Four models were employed to assess the ability to detect differences among samples based on the prevalence of cranial nonmetric traits. Three are single-step models and one is a multi-step model based upon the results obtained from the single-step models. The single-step models encompass 36 pairwise comparisons. Three assessments of significant differences in trait prevalence and two measures of statistical power may be employed to determine the relative efficacy of the models. Beginning with univariate assessments, single-step Model 1 in which all 32 traits provide the basis of comparison yields 418 significant differences out of the 1152 variable-based contrasts between sample pairs for a discernment rate of 36.3%. This rate improves to 43.0% (418/972) with the 27 traits retained with single-step Model 2 (in which a trait must possess an α value of < 0.05 across all nine samples). However, with single-step Model

3, in which traits are retained only if they meet the stringent inclusion conditions of the experiment-wise Bonferroni adjustment, performance declines with only 36.9% of contrasts between sample pairs (124/336) being statistically significant. This is an obvious consequence of the dramatic contraction of the critical region for acceptance of the null hypothesis thereby reducing statistical power due to the inflation of experiment-wise Type II errors.

The proportion of univariate significant contrasts between sample pairs exhibits a distinct pattern under all three single-step models. With Models 1 and 2 the average number of significantly different variables among sample pairs among the three time successive BMAC era samples from Djarkutan ($\bar{X}$= 0.5) is less than that occurring among the other samples ($\bar{X}$= 2.67) yielding a ratio of 0.19 to 1. With the more stringent Bonferroni adjusted alpha values Model 3 offers a nearly identical proportion (0.2 to 1) of significant differences on average between the time successive BMAC era samples from Djarkutan ($\bar{X}$= 0.48) than among the remaining samples ($\bar{X}$= 2.42). Such results suggest there is a threshold in the number of variables retained below which little to no improvement in the discernability among samples is obtained.

A similar pattern in univariate significant contrasts involves the fewer number of non-discriminatory traits and the prevalence of statistically significant pairwise contrasts overall. That is, the differential in the number of contrasts increases progressively as the criteria for variable retention becomes increasingly stringent and once again there is a decline under Model 3 with Bonferroni's adjustment. Model 1 in which all 32 traits are included is marked by seven non-discriminatory variables (21.9%) and only 418 of 1152 (36.3%) variable contrasts are significant across samples. With Model 2, in which five traits were eliminated due to a failure to reach a statistical threshold of $\alpha < 0.05$ across the nine samples considered yields two traits (metopism, asterionic ossicle) that do not contribute to separation among samples (Table 5). However, elimination of the five traits yields 418 of 972 (43.0%) pairwise contrasts statistically significant, an improvement of nearly 7%. With Model 3 only 12 traits meet the stringent alpha-threshold imposed by the Bonferroni adjustment across 36 multiple comparisons. Thus, all of the remaining traits differ significantly across samples, but there is a decline in the number of pairwise contrasts that differ significantly by varable across samples (36.9%). Once again, such results suggest there is a threshold in the number of traits considered below which the discriminatory power among samples is compromised.

The pattern of multivariate significant differences between sample pairs exhibits similarities to the pattern observed for univariate significant differences. Three patterns may be identified for multivariate differences. First, overall multivariate significant differences in MMD distances increase across single-step models with increasingly stringent criteria for variable inclusion. The proportion of significant distances ranges from a low of 44.4% of pairwise contrasts with single-step Model 1 to a high of 77.8% with single-step Model 3.

Second, a somewhat different pattern emerges for non-significant multivariate distances. These range from a high of 55.6% under single-step Model 1 to a low of 22.2% with single-step Model 3. Multi-step Model 1 yields six non-significant differences (28.6%) and these primarily involve ALT and KUZ. This is very different from the results obtained from either single-step Model 3 or multi-step Model 1 in which non-significant differences almost exclusively involve BUS. Such results suggest the more stringent Bonferroni and Holm criteria are less corrosive to the patterning of multivariate differences among samples than univariate differences.

The third pattern involves the ratio of the mean measure multivariate of significant differences to the standard deviation of that statistic. The mean MMD value obtained across all 36 pairwise contrasts with all traits considered (single-step Model 1) is 0.0661 and its ratio to its standard deviation is 2.755, reflecting the fact that while fewer than half of the contrasts are statisticaly significant, those that are, are markedly so. With elimination of the five traits that fail to meet the threshold of $\alpha < 0.05$ across the nine samples considered, the average MMD with single-step

Model 2 increases to 0.0904. When divided by its standard deviation it yields a ratio of 3.441 indicating that elimination of the non-significant variables (traits) increases the ability of the model to discern differences among samples. Single-step Model 3 involving the stringent Bonferroni adjustment yields an average MMD value that falls to 0.0763, which when divided by its standard deviation yields a ratio of 3.740. Such results indicate that despite the elimination of 15 variables relative to single-step Model 2, the power of discrimination nevertheless increases and inspection of Table 9 indicates that this heightened discriminatory ability involves separation of the time successive samples from Djarkutan from the pre-BMAC samples from ALT and GKS. Multi-step Model 1 involves pooling of three of the time successive BMAC era samples from Djarkutan (DJR, KUZ, MOL). Consequently the number of pairwise contrasts decreases from 36 to 21. An examination of the average MMD value of 0.1999 shows a marked elevation relative to any of the single-step models and this is further reflected by the ratio of the average MMD to its standard deviation, which yields a value of 6.113. While not directly comparable to the results obtained with the single-step models, such results suggest the multi-step model has far greater discriminatory power than any of the single-step models

Statistical power in the current discussion may be considered in two practical forms. The first is the ability for the selected variables to discriminate between samples. The second is the amount of stress incurred when attempting to fit the set of multivariate pairwise distances into a relatively few number of vectors with multidimensional scaling. With regard to the former, it is clear that both univariately and especially multivariately, the selected cranial nonmetric traits discriminate between samples well, especially when the traits are winnowed to those that differ most between samples.

Such results confirm that inclusion of non-contributing variables leads to statistical noise that compromises the ability of the model to depict the relationship between OTUs accurately (Blackard and Dean, 1999; Sousa *et al.*, 2007). The best performance was obtained when a multi-stage model was employed and when traits were winnowed with Holm's sequentially rejective modification of Bonferroni's adjustment. Examination of the stress incurred in fitting the diagonal matrix of MMD distances revealed that all models, both single- and multi-step, stress is extremely low and the percentage of variance explained approached or attained totality.

Together, the results obtained both univariately and multivariately confirm that winnowing of the cranial non-metric trait battery offers improvements in the ability to distinguish between these archaeologically derived cranial assemblages; however, univariate performance has a tendency to decline when trait retention is dependent upon meeting the strictures of the Bonferroni adjustment. As such, these results confirm assertions based on other datasets that the Bonferroni adjustment is too conservative (Bender and Lange, 2001; Rothman, 1990; Savitz and Olshan, 1995; Thomas *et al.*, 1985). Consequently, use of such an adjustment to curtail Type I statistical errors incurred with multiple comparisons decreases the ability to detect differences among samples, increases Type II statistical errors, thereby compromising the power of such formulations for detecting differences among nonmetric cranial asssemblages consistently (Jennions and Møller, 2003; Nakagawa, 2004; Perneger, 1998; Rothman, 1990).

Clarity in Identification of Which Variables Yield Common Sample Aggregates and Separate Such Aggregates from one another

With the first single-step model, in which all 32 traits were retained for analysis, the trait combinations contributing to the distinctiveness of only three of the nine samples were identified clearly. The most distinctive sample is HAR. The unique position of this sample in the lower left of the correspondence analysis plot (Figs. 2b, 2c) is due to relatively high frequencies of FTA (4.2%; Others: 0 – 2.1% [DJR, MOL]), FOI (6.3%; Others: 0 – 2.4% [MOL]), and ZFFA (50.0%; Others: 20.0 – 35%).The positioning of the two pre-BMAC samples from ALT and GKS on the right is the consequence of relatively high frequencies of PTUB (ALT: 20.0%, GKS: 21.7%; Others: 2.4 – 25.4% [TH]) and TMF (ALT: 81.8%, GKS: 68.4%; Others: 0 – 25%). None of the other samples exhibit a distinguishing set of trait frequencies that differentiate them from one another. Indeed, discernment among the remaining six samples is poor and inconsistent. Correspondence analysis (Fig. 2b) identifies six samples as an undifferentiated scatter near the origins of the first two dimensions. Neighbor-joining cluster analysis (Fig. 3a) identifies the uniqueness of HAR in the lower right and the two pre-BMAC samples (ALT, GKS) in the upper right, but the remaining samples form two aggregates that may be identified as 'core' BMAC era samples from Djarkutan on the left (DJR, KUZ, MOL) and BMAC iperipheral' samples (SAP, BUS) with TH on the right. MDS identifies the uniqueness of HAR on the left side of the three-dimensional scatterplot, but SAP is highly isolated in the right foreground, TH is isolated in the upper right, the two pre-BMAC samples are widely separated in the right background with GKS exhibiting unexpected close affinities to DJR. As such, single-step Model 1 yields obscure and volatile affinities among the majority of the samples considered.

The second single-single step model required that any trait in which at least one pairwise contrast is significant at $\alpha< 0.05$ level be retained. This criterion resulted in the elimination of five traits. The first two dimensions yielded by correspondence analysis captures 72.8% of the total variance. This increase illustrates the effect of statistical noise on multivariate analyses due to inclusion of non-contributing variables (Ferrer, 2007). HAR is once again identified as the most unique sample in the lower left of the array and the two pre-BMAC samples (ALT, GKS) are identified as unique based on the relative frequencies of PTUB and TMF. ALT occupies an increasingly isolated position on the right side of Figures 4b and 4c due to higher prevalence of the tympanic marginal foramen (ALT: 81.8%; GKS: 68.4%), but not GKS, which is found on the near-right side of Figure 4c occupying a position with closest affinities to TH. The affinities between GKS and TH — as well as the separation of the former from ALT — is due to three traits, PFOR, MFX, and FH all of which occur in frequencies among GKS crania similar to that observed in the TH sample. Remaining samples are divided between a 'core' BMAC group composed of the three-time successive samples from Djarkutan and two associated 'peripheral' samples, BUS to the lower left and SAP with a higher value for Dimension Two. Neighbor-joining cluster analysis (Fig. 5a) identifies HAR in the lower right as the most unique sample, but the two pre-BMAC samples in the upper left are also identified as unique. In this dendrogram TH lies peripheral to the two pre-BMAC samples, while the same 'core' BMAC era and 'peripheral' BMAC era samples may be identified in the center left and right, respectively. The three-dimensional scatterplot yielded by MDS (Fig. 5b) is identical to that described for single-step Model 1. Viewed as a whole, the performance of Model 2 offers little improvement in distinguishing samples over Model 1.

The third single-step model utilized a threshold for trait elimination based on alpha values set in accordance with Bonferroni's adjustment. This resulted in the elimination of 20 cranial nonmetric traits for a comparative trait battery of 12 variables. Correspondence analysis (Fig. 6a) identifies two traits as standing apart with high loadings: MXT in the upper center and TMF in the center-right. These loadings were so high that in order to show the dispersion of the sites and remaining traits the position of these two traits was not depicted in Figure 6c. The remaining traits fall into three aggregates: PTUB, MFX, and PTOR in the upper-right, LO and AAPF in the lower-center, and HNL, FFOR, ALPF, and NFOR in the center-left. Single-step Model 3, which accounts for 75.4% of the total variance, is quite successful in identifying the traits driving the unique positions of all nine samples. Once again, the distinctiveness of crania from TH in the upper center of the array is due to relatively high prevalence of MXT (17.9%), while the unique positions occupied by the two pre-BMAC samples from ALT and GKS are the consequence of relatively high prevalence of TMF (68.4 – 81.8%) and PTUB (20.0 – 21.7%). The location of the HAR sample in the near upper left is a consequence of its distinctiveness relative to the BMAC era samples driven by lower prevalence for HNL, LO, AIOF, and AAPF.

The improvement offered by single-step Model 3 is in the identification of traits that distinguish the BMAC era samples — including BUS — from one another. The DJR period sample occupies a position in the lower centre of Figure 6c immediately adjacent to that occupied by AAPF. As expected, DJR is distinguished from the other BMAC era samples by possessing the highest prevalence (66.7%) for this trait. The sample from SAP stands above and to the left of the DJR period sample very close to the position occupied by HNL. In contrast, the samples from KUZ and MOL occupy positions in the lower center closer to the position occupied by LO. Not surprisingly, SAP is distinguished from the other BMC era samples with the highest prevalence (74.2%) for HNL, while KUZ and MOL are distinguished by low prevalence of HNL (35.3%, 43.2%) coupled with high prevalence of LO (80.0%, 72.0%). BUS occupies a position in the lower left that is not closely associated with any of the 12 traits considered. Nevertheless, the position of BUS appears to be the consequence of relatively high prevalence of HNL (63.6%), which shifts it to the left away from DJR, KUZ and MOL, coupled with a ubiquitous prevalence of LO, which shifts the position of this sample downward away from SAP. The dendrogram obtained from neighbor-joining cluster analysis (Fig. 7a) is identical to that described for single-step Model 2, while the three-dimensional scatterplot obtained by MDS (Fig. 7b) reflects the close affinities among the "core" BMAC samples in the center of the array, with TH and HAR occupying highly isolated positions in the upper center and right side, respectively. However, SAP continues to occupy an isolated position in the left foreground, while the two pre-BMAC samples, while occupying isolation positions on the left side, exhibit no affinities to one another. Viewed overall single-step Model 3 offers the clearest association between sample locations in the correspondence analysis and the traits that led to those positions. The pattern of affinities identified in the dendrogram produced by neighbor-joining cluster analysis is congruent with those obtained from correspondence analysis, but the scatterplot obtained with MDS is plagued by two glaring inconsistencies: 1) the isolated position of SAP relative to other 'core' and 'peripheral' BMAC samples, and 2) the lack of affinities between the two pre-BMAC samples from ALT and GKS.

The fourth model utilised a multi-stage approach in which samples that consistently yield nonsignificant multivariate MMD distances were pooled together as an operational taxonomic unit (OTU) with alpha values set in accordance with Holm's (1979) sequentially rejective modification of Bonferroni's adjustment. This protocol resulted in a pooling of the three 'core' BMAC era samples from Djarkutan (DJR, KUZ, MOL) into a single BMAC sample. Use of Holm's modification resulted in a final trait battery of 18 variables.

Correspondence analysis (Fig. 8a) identifies four traits as driving the biodistances among the six samples. The maxillary torus (19) plots in the upper right and distinguishes TH from all other samples (Fig. 8c). The tympanic marginal foramen (32) and, to a lesser degree, the precondylar tubercle (Trait 27) plot on the right side (Fig. 8a) and separate the two pre-BMAC samples (ALT, GKS) from all others. Four traits plot in the lower left: HNL (1), FFOR (16), AIOF (21), and AAPF (24). These occur with relatively low frequency for HNL, high frequency for AIOF and moderate frequency for FFOR and AAPF in the combined BMAC sample and hence their placement in the lower left of the array (Fig. 8b). The two "peripheral" BMAC samples are distinguished by high prevalence of FFOR for BUS and HNL for SAP, which leads to their placement above and below the combined BMAC sample along Dimension Two. The dendrogram obtained with neighbor-joining cluster analysis (Fig. 9a) clearly distinguishes HAR in the lower right and the two pre-BMAC samples in the upper left from all other samples. TH is identified as occupying an isolated position along the vector toward the two pre-BMAC samples. SAP, BUS and the combined BMAC sample are found in the center of the array with closest affinities to one another. The three-dimensional scatterplot produced by MDS confirms the relationships identified by correspondence analysis and by neighbor-joiing cluster analysis. That is, HAR, TH and the two pre-BMAC samples are identified as distant outliers in the left, upper right, and lower right of the array, respectively. The combined BMAC sample is found in the center of the plot with closer affinities to the early sample from SAP than to the late sample from BUS.

The multi-step model with the pooled BMAC era samples from Djarkutan and with the nested Holm-modified Bonferroni adjustment provides the clearest and most robust identification of sample affinities and the cranial nonmetric traits that drive these differences. Single-step models 1 and 2 introduce too much noise into the multivariate delineation of sample affinities and this results not only in poor association of trait variation and intersample differences, but also excessive interanalytical volatility across the three modalities of analysis (correspondence analysis, neighbor-joining cluster analysis, multidimensional scaling of Smith's MMD values). Assessments based on Bonferroni-adjusted threshold values for multiple comparisons offers a substantial improvement in identifying which traits or combinations of traits contribute to intersample aggregations and disassociations. However, elimination of so many variables reduces the power of the model to such a degree that leads, not only to fewer statistically significant pairwise contrasts, but also to heightened interanalytical volatility. As such, the multi-step model with the Holm-Bonferroni adjustment for multiple comparisons represents the best approach for elucuidating meaningful and interanalytically robust patterns of biodistances among the samples considered here.

Chalcolithic-Bronze Age Era Contacts across the Iranian Plateau

Three periods have been identified as contributing to interregional interactions among Chalcolithic and Bronze Age populations scattered along the western, northern, and southeastern periphery of the Iranian Plateau. Each engenders different expectations concerning affinities among these populations. Here we evaluate which temporal dynamic appears most influential in light of the biodistance patterns obtained from assessment of cranial nonmetric trait frequencies.

Neolithic Food Production

Authorities who emphasize Neolithic era food production as shaping initial and subsequent interactions across the Iranian Plateau maintain that the development of agriculture and animal husbandry exerted two crucial influences on the human biography of this extensive region. The first was to render localities that were seen as inhospitable into site-specific localities of localized productivity (Berdiev, 1965; Kohl, 1992; Korobkova, 1975). The second was that the production of a regular supply of plant food and animal products, when coupled with a more sedentary lifestyle, likely led to an increase in fertility and population growth (Bellwood and Oxenham, 2008; Bentley *et al.*, 1993; Bocquet-Appel, 2002; Bocquet-Appel and Naji, 2006; Buikstra *et al.*, 1986; Eshed *et al.*, 2004; O'Brien, 1987).

These two factors are claimed to have resulted in a wave-of-advance expansion (Ammerman and Cavalli-Sforza, 1984; Renfrew, 1989) of Central Iranian farming populations of the Zagros Mountains (Braidwood, 1975; Masson, 1989), first to the north where this transition is manifested as the Djeitun Culture (Harris, 1997a,b; Masson and Harris, 1994) and then through the Kopet Dagh foothill plain across the northern margin of the Iranian Plateau (Hiebert, 2002; Kohl, 1984; Sarianidi, 1971). The development of irrigation technology (Lisitsina, 1969) near the beginning of the Middle Chalcolithic resulted in an initial dispersal into a true desert setting, first to the Geoksyur oasis (Khlopin, 1963, 1964) and then to the oases of Margiana (Masson, 1992a; Salvatori, 2008) and Bactria (Hiebert, 1994; but see Francfort, 1984, 1989). Subsequent dispersal introduced southern Central Asians to Iranian Seistan (Biscione, 1973; Tosi, 1973-74) and the Helmand Valley of Afghanistan (Casals, 1961), eventually reaching the the western periphery of the Indus Valley (Jarrige, 1991, 1994; Jarrige and Hassan, 1989; Santoni, 1984). As such, the population history of communities living adjacent to the Iranian Plateau ought to exhibit the following features:

- The original parental population ought to be traced to the Neolithic era inhabitants of the Zagros Mountains located at the western margin of the Iranian Plateau.

- Population differentiation ought to be a consequence of spatial and temporal autocorrelation (Konigsberg, 1990a,b; Malécot, 1969; Morton, 1977; Sokol and Wartenberg, 1983; Wright, 1943) such that populations closest in both space and temporality ought to be more similar to one another biologically than those separated by greater geographic and temporal differences.
- Because of long periods of *in situ* gene flow there should be greater homogeneity within regions than across the entire expanse encompassed by the dispersal of Neolithic farmers (Le Corre and Kremer, 1998; Wade and McCauley, 1988).
- Further, because of long-term within region population stability, temporally successive populations ought to vary from the original founding population along a unique vector in phenetic space such that the most recent members in each region ought to be the most divergent phenetically from series of other regions due to regionally-specific genetic drift (Austerlitz *et al.*, 1997; Kolbe *et al.*, 2012; Nei *et al.*, 1975; Neigel *et al.*, 1991; Wlasiuk *et al.*, 2003; but see Crispo and Hendry, 2005).

If it is true that the Chalcolithic-Bronze Age populations of the Iranian Plateau are the descendants of a human dispersal event from western Iran due to the advent of agricultural production and animal husbandry as has been maintained by Cappieri (1969, 1973), descendant populations ought to show increasing divergence from this ancestral population with increasing geographic and temporal distance. The degree of adherence of the patterning of phenetic affinities to the expectations of isolation-by-distance can be assessed with all three modalities of biological differentiation.

Plots of sample centroids yielded by correspondence analysis yield two different patterns. Those based on single-step models 1 and 2 as well as multi-step Model 1(Figs. 2b, 4b, 6b) show TH as occupying a position very near those occupied by 'core' and 'peripheral' BMAC era samples. In dramatic contrast, the plot obtained with single-step Model 3 shows TH occupying an isolated position in the upper center of the plot. Likewise, while the dendrograms based on single-step models identify HAR as the most divergent sample, those obtained with single-step Model 3 and multi-step Model 1 show HAR as occupying a position intermediate between TH on the one hand and the BMAC era samples on the other. However, all dendrograms produced by correspondence analysis, except that based on single-step Model 2, show the two pre-BMAC samples (GKS, ALT) as occupying an isolated position in direct contradiction of expectations of isolation by spatial and temporal distance.

Results obtained with neighbor-joining cluster analysis (Figs. 3a, 5a, 7a, 9a) are much more consistent and are in greater accord with the expectations of a diaspora of Neolithic era farmers and herders. As expected, HAR occupies a highly divergent position, while the pooled BMAC sample and the two 'peripheral' BMAC era samples all show close affinities to one another. Also, as expected, the two pre-BMAC samples from ALT and GKS show close affinities to one another while being distinguished from the later BMAC era samples. Two aspects of the dendrograms obtained with neighbor-joining cluster analysis stand at odds with a dispersal of Neolithic era farmers and herders. The first is the non-divergent position of TH from the 'peripheral' BMAC samples in the dendrogram based on single-step Model 1, while the second is absence of intra-regional genetic drift among the BMAC era samples.

The three-dimensional scatterplots obtained by MDS also yield two different patterns. Those based on single-step models 1 and 2 (Figs. 3b, 5b) show SAP as occupying an isolated position in the right foreground, no affinities between the two pre-BMAC samples, and unexpectedly close affinity between GKS and the DJR period sample from Djarkutan. The scatterplot based on single-step Model 3 (Fig. 7b) also shows SAP as occupying an isolated position and no affinities between the two pre-BMAC samples. However, TH is clearly divergent and there is no close affinity between the DJR period sample from Djarkutan and GKS. It is the scatterplot based on multi-step Model 1 (Fig. 9b) that is most consistent with the expectations of a Neolithic dispersal of farmers and herders. As expected, TH and HAR occupy isolated positions on opposite sides of the array. The two pre-BMAC samples also occupy an isolated position, which is somewhat surprising given their geographic and temporal proximity to the BMAC and 'peripheral' BMAC samples, but they do exhibit closest affinities to one another. Likewise, the early BMAC era sample from SAP shows close affinities to the pooled sample of 'core' BMAC samples from Djarkutan. Somewhat surprising is the more strongly divergent position of the later BMAC sample from BUS. It may be that this sample reflects gene flow from neighboring Vakhsh and Beshkent culture populations from the nearby highlands of southern Tajikistan (Litvinski, 1973; P'yankova, 1986, 1993, 1994; Vinogradova, 1994, 2020; but see Teufer, 2020).

The Namazga Expansion

Authorities who maintain that the evidence for larger sites, more sites, and colonization of new areas in southern Central Asia provide archaeological evidence for considerable change during the Middle and Late Chalcolithic (*c.* 4000 – 3000 BCE) that involved establishment of desert-adapted settlements within the Geoksyur oasis (Khlopin, 1964; Lisitsina, 1969; Masson, 1992a) increased demand for non-local commodities (Gupta, 1979; Kohl, 1992; Tosi, 1973-74) spurred an outward world view (Salvatori, 2008) that led to contacts with populations of the Harappan Civilization and stimulated an expansion of the Namazga culture found in the piedmont zone of the Kopet Dagh foothill plain (Masson and Sarianidi, 1972). These authorities assert that increased food production facilitated by technological advances in irrigation and water management strategies not only led to establishment of large urban centres during the Early and Middle Bronze Age (*c.* 3000 – 2200 BCE) but also the colonization of Margiana, Bactria and beyond across the Iranian Plateau to Iranian and Afghan Seistan, the Helmand Valley and the western periphery of Indus Valley during the Late Bronze Age (*c.* 2200 – 1500 BCE) (Biscione and Vahdati, 2020; Hiebert, 1994; Hiebert and Lamberg-Karlovsky,1992; Lamberg-Karlovsky, 2002; Mutin and Lamberg-Karlovsky, 2020).

Because of these factors, the pattern of dispersal involving populations residing about the margins of the Iranian Plateau between the Neolithic and the beginning of the Iron Age — a period of some six millennia — was unlikely to exhibit the constancy and uniformity believed to characterize the spread of farming populations out of the Near East and into Europe (Ammerman and Cavalli-Sforza, 1984; Zvelebil, 2000). Instead four aspects render such a pure demic expansion model unlikely. The first is a dynamic throughout this timeframe in which the archaeological evidence attests to an episodic process in which long periods of *in situ* internal development were punctuated by bursts of dispersal to new localities initially in a general west to east direction (Kohl, 1984, 1992) and subsequently along a north to south vector (Biscione and Vahdati, 2020; Mutin and Lamberg-Karlovsky, 2020). Second, is evidence of periodic influxes of cultural developments from the south in central and northeastern Iran into the archaeological cultures occupying the margins of the Iranian Plateau (Berdiev, 1966; Biscione and Vahdati, 2020; Gupta, 1979; Masson and Sarianidi, 1972; Sarianidi, 1971; Mutin and Lamberg-Karlovsky, 2020). Third, although once believed by most Soviet scholars to have involved dispersal to previously unoccupied settings (Harris and Gosden, 1996; Masson and Sarianidi, 1972), it has become increasingly clear that such dispersal events often resulted in immigrants coming to occupied areas — perhaps under-occupied from the standpoint of irrigation enhanced productivity — at such localities as the Aral Sea region (Kohl, 1992), the Middle Zeravshan River Valley (Askarov, 1962, 1981; Lyonnet, 1996; Sarianidi, 1979), southern Tajikistan (P'yankova, 1993, 1994; Vinogradova and Lombardo, 2002), Seistan and the Helmand Valley (Biscione and Vahdati, 2020 as well as Margiana (Masimov, 1979, 1981; Masson, 1964; Salvatori, 2008) and Bactria (Francfort, 1984; Salvatori, 2008). Fourth, the establishment of desert-adapted settlements within the Geoksyur oasis is maintained to represent a fundamental shift in the adaptive landscape of populations residing about the margins and on the Iranian Plateau (Hiebert, 1994; Kohl, 1992; Lisitsina, 1969, 1978). As such, these cultural developments took place in ecological settings marked by severe differences between small pockets of useable arable lands separated by vast swaths of poorly watered, but often minerally productive wastelands.

Advocates for the impact of the Namaza era expansion identify the development of irrigation technology and the initial colonization of the Geoksyur oasis as key events that ushered in a new long-distance desert-adapted lifeway (Hiebert, 1994; Masson and Sarianidi, 1972; Sarianidi, 1971). This lifeway initiated a new acquisitive outward perspective that resulted in strategic contacts for procurement of vital resources that had no local sources and stimulated colonization of new areas. If this scenario is correct then the following five corollaries must also be true:

- As with the Neolithic farming hypothesis, the ultimate origin of Neolithic-Early Chalcolithic populations residing about the margins and on the Iranian Plateau is to be found among the descendants of Neolithic farming populations of the Zagros Mountain region.
- Due to temporal and spatial proximity, the Late Chalcolithic inhabitants of Geoksyur (GKS), ought to be most similar to the Middle Bronze Age inhabitants of Altyn depe (ALT) on the one hand and the Period II and III inhabitants of Tepe Hissar on the other.
- Apart from the two exceptions noted below, a pattern of long-term *in situ* continuity within regions suggests a general pattern of within-region homogeneity coupled with inter-regional heterogeneity in phenetic affinities.
- Due to possible founder effects and genetic drift concurrent with the colonization of the Tedjen delta, phenetic affinities between the inhabitants of Late Chalcolithic Geoksyur and Middle Bronze Age Altyn depe ought to be of moderate strength.
- Due to temporal and spatial proximity, the Middle Bronze Age inhabitants of Altyn depe ought to share closer phenetic affinities to BMAC era populations of Bactria than Geoksyur.

As previously noted, univariate and multivariate comparisons of nonmetric trait frequencies consistently identify HAR as the most unique sample and often this sample is marked by the greatest divergence from TH. Such results are in accord with the single bout of dispersal from west to east expected if the development of food production and animal husbandry spread across the Iranian Plateau and adjacent regions. However, apart from results obtained from correspondence analysis with single-step Model 2 (Figs. 2b, 2c), none of the other analyses indicate any affinities between TH and GKS. Instead, GKS is most often identified as an outlier to all other samples, except ALT to which it shares moderate (Figs. 6b, 7a) to close affinities (Figs. 2b, 2c, 3b, 4a, 5b; but see Figs. 3b, 4b, 7b). Such results may be explained by founder effect in the establishment of settlements in the Geoksyur oasis followed by subsequent population growth the resulted in an expansion to Altyn depe in the eastern Kopet Dagh foothills. Results obtained with multi-step Model 1 are especially useful for understanding the relationship between GKS and ALT. With this model correspondence analysis (Figs. 8b, 8c), neighbor-joining cluster analysis (Fig. 9a), and multidimensional scaling (Fig. 9b) all attest to the fairly close affinities between these two samples.

The three temporally successive BMAC era samples from Djarkutan (DJR, KUZ, MOL) are identified by all four models as possessing closest affinities to another. In fact, MMD distances based on trait inclusion with Holm's (1979) sequentially rejective Bonferroni adjustment fail to find any significant distances between them. Neighbor-joining cluster analysis yields dendrograms in which these BMAC period samples tend to occupy central positions with closest affinities to one another, but there are exceptions. Single-step model 1 (Fig. 3a) indicates that TH shares closer affinities to the BUS period sample than the other BMAC era samples from Djarkutan, while the dendrograms based on single-step models 2 and

3 (Figs. 5a, 7a) suggest a more distant association with TH. This tendency to pull the time successive BMAC era samples apart from one another is more evident from the three-dimensional MDS plots. Single-step models 1 and 2 (Figs. 3b, 5b) suggest a centrifugal dynamic affecting these samples in which KUZ is pulled toward the phenetic space occupied by ALT, BUS by TH, and DJR by GKS. In both plots, the Molali period sample (MOL) serves as a sort of central hub holding the other three time successive samples in the center-right of the array together. In contrast, single-step Model 3 (Fig. 5b) shows most of the time successive BMAC era samples from Djarkutan (DJR, KUZ, MOL) as sharing close affinities to one another; the only exception being the latest BMAC period sample, BUS, which is identified as sharing distant (Model 4) affinities to TH (Fig. 7b). Such a centrifugal dynamic may indicate that the Namazga expansion of other regions was not a unidirectional arrow of increasing phenetic distance, but a bidirectional circle of commerce and residency (Mutin and Lamberg-Karlovski, 2020).

Finally, advocates who emphasize the influence of the Namazga expansion on interactions among populations on and adjacent to the Iranian Plateau claim that due to gene flow from populations located on the Iranian Plateau in Iranian Khorassan (Biscione and Vahdati, 2020) and due to an ‘urban crisis’ affecting the Middle Bronze Age urban center of Altyn depe this led to colonisation initially of Margiana and subsequently Bactria (Biscione, 1977; Hiebert, 1994; but see Francfort, 1984). This colonisation event ought to be reflected by close affinities between the sample from Altyn depe and the BMAC era samples, especially the earliest one, from Sapalli tepe. None of the analyses identify an especially close relationship between Altyn depe and any of the BMAC era samples. Such results stand iin direct opposition to the claim that the inhabitants of Bactria owe their origins to colonists from Altyn depe as argued by Francfort (1985) and Salvatori (2008, 2016).

Bronze Age Interregional Interaction

The vast majority of those who emphasize the impact of Bronze Age interregional interaction model maintain that there was a significant entry of either pastoralist populations from the steppe zone of Central Asia or dwellers of the urban centers of the BMAC during the mid-2nd millennium that led these immigrants to cross the Hindu Kush and descend on the cities of the Harappan Civilization bringing that indigenous cultural development to an abrupt end (Erdosy, 1995; Wheeler, 1968). Proponents of this model further maintain that these populations brought Indo-Iranian languages to the borderlands separating the Indus Valley from the lowlands of Central Asia and that once established in South Asia (Nichols, 1997; Parpola, 1988, 1993a, 1995), these now-Indic-speaking foreigners spread their influence to the Upper Doab region of North India and eventually throughout the entire subcontinent through various combinations of religious conversion to Hinduism and elite dominance (Bamshad *et al.*, 1998, 2001; Cavalli-Sforza *et al.*, 1994).

Supporters of the influence of Bronze Age interregional intraction upon populations residing on and adjacent to the Iranian Plaetau are divided over the identification of the source populations for this entry of Central Asians into South Asia. Historically, the majority of proponents of the Bronze Age interregional interaction model have identified populations of the Andronovo steppe culture and its various regional manifestations found in the southern steppe zone of Russia and Kazakhstan as the most likely source for the introduction of foreign cultural elements, practices, and genes into South Asia (Anthony, 2007; de Barros *et al.*, 2018; Kuzmina, 2001; Masson, 1996; Narasimhan *et al.*, 2018; P’yankova, 1994). However, in more recent years an array of scholars have specifically identified the populations residing within the BMAC urban centers (Erdosy, 1995; Parpola, 1993a, 1995) or perhaps an admixed Andronovo-BMAC population due to an extended period of co-residency within the Margianan and Bactrian oases (Rouse and Cerasetti, 2014, 2018; Spengler *et al.*, 2014). Still others suggest that the impetus for such interaction was not from north to south, but from south to north and is signaled by the presence of the Harappan outpost of Shortughaï found in the East Bactrian oasis of northern Afghanistan (Francfort, 1981a, 1981b, 1984, 1989; Götzelt, 1995; Salvatori, 2008).

Regardless of the polarity of interaction, two inter-sample similarities and differences are expected if the Bronze Age interregional interaction model is true:

- Since neither Iranian nor pre-BMAC 'farming' populations of southern Central Asia are believed to have played any role in this interaction, there ought to be no phenetic affinities linking them to any Indus Valley population either pre- or post-Harappan.
- If populations of the urban centers of the BMAC are the source population for these Central Asian invaders into the Indus Valley in the mid-2nd millennium BCE, and if such gene flow was not exclusively unidirectional, then phenetic affinities of BMAC era samples ought to reflect a rappoachement with HAR relative to earlier pre-BMAC era samples from Central Asia.

None of the analyses based on any of the four models tested in the current research offer any 4b) support for the Bronze Age interregional interaction model. Correspondence analyses (Figs. 2b, and the dendrograms yielded by neighbour-joining cluster analyses (Figs. 3a, 5a, 6a, 9a) consistently identify HAR as a distant outlier to all other samples, however it is also true that these same analyses also identify HAR as sharing closer affinities to BMAC era samples than to pre-BMAC samples from ALT and GKS. Especially illuminating in this regard are the results obtained with the multidimensionally scaled scatterplots. All of the single-step models as well as the multi-step model identify HAR as a distant outlier with no affinities to any of the other samples considered. Such results run counter to the expectations of gene flow between the urban populations of southern Central Asia, both BMAC and pre-BMAC, and the Indus Valley regardless of the direction of this gene flow. This finding confirms previous craniometric investigations involving steppe Andronovo samples, steppe-influenced samples from southern Central Asia, and post-Harappan samples from the Indus Valley (Hemphill 1998, 1999a; Hemphill and Mallory 2004).

Conclusions

This research has demonstrated that the selection of cranial nonmetric traits employed in analyses of biodistance analysis can exert profound influences on the patterning of affinities identified among them. Passive use of a list of nonmetric traits (single-step Model 1) introduces an excessive amount of statistical noise that saps multivariate statistical techniques of power and sensitivity to detect patterns of phenetic affinities among samples. This leads to volatility in the results obtained by different multivariate analytic procedures. Use of a general threshold, such as an alpha value below 0.5 as recommended by Harrris and Sjovøld (2004), improves the explanatory power of the analysis (single-step Model 2) due to the elimination of non-contributing variables, but the power of the model is weak and there remains considerable volatility in the results obtained by different analytical procedures. Employment of Bonferroni's adjustment for multiple comparisons improves the explanatory power of the model considerably, especially with regard to detection of which variables drive the diversity among samples, but this overly conservative method leads to such an extensive loss of variables that more subtle differences among related samples are either ignored or obscured. The best results were obtained with a multi-step procedure that pooled closely related samples (in this case the time successive BMAC era samples from Djarkutan, Kuzali, and Molali periods at Djarkutan) and employed Holm's (1979) nested rejective Bonferroni adjustment for multiple comparisons. This methodology not only had the greatest discernment among samples, but also yielded the most robust results across multiple multivariate statistical procedures.

The pattern of phenetic affinities observed among the Chalcolithic and Bronze Age era samples from the periphery of the Iranian Plateau was assessed in light of three proffered bouts of interregional influence. None of the scenarios were supported in their entirety. There is no support for substantial impact during the Bronze Age as there is simply no evidence of gene flow between Central Asians from the urban centers of the Kopet Dagh or of Bactria and Indus Valley inhabitants from Cemetery R37 at Harappa. There is some support for influences due to the Namaza era expansion. As expected, due to founder effects followed by subsequent population growth the Middle Chalcolithic sample from Tepe Hissar shows moderate to strong affinities to the Middle Bronze Age inhabitants of Altyn depe, but no evidence of a legacy from a Neolithic era dispora of farmers and herders from the west (Tepe Hissar). However, there is no evidence of a rapproachement of biodistances between Harappa and Altyn depe as expected if the Harappan items recovered from NMG IV signal the presence of Harappans at this site in southern Central Asia. As such, this would appear to reflect purely commercial interactions between the resident of these two regions with an unknown number of middlemen in between them.

The results obtained in the current study suggest that it was the spread of farmining and animal husbandry during the Neolithic that set the fundamental pattern of population affinities across the Iranian Plateau. As expected, the overall arrangement of phenetic affinities reflects a general pattern of isolation by temporal and spatial distance, while within regions there appears to be evidence of *in situ* genetic drift. As expected, the two most distant samples geographically — Tepe Hissar and Harappa — are most often the most distant with regard to phenetic affinities. However, in southern Central Asia, while phenetic affinities largely track temporal distances among most BMAC era samples, this is not the case for the Bustan period sample. Instead of showing closest affinities to the Molali phase sample, followed by the Kuzai phase sample, Bustan is identified by most analyses as divergent. While this result may be a consequence of the small size of the BUS sample it may also reflect gene flow from neighboring Bashkent and especially Vakhsh populations residing just to the east in southern Tajikistan. Indeed, the combination of late period BMAC ceramic wares and steppe-influenced brone objects at Beshkent culture sites (P'yankova, 1994; Vinogradova, 2020), coupled with inhumations under kurgans at the latter (Tufer, 2020) may indicate some level of gene flow from steppe-influenced populations from the Ara Sea region (Kokcha 3, Tazabagyab culture) as well as from steppe cultures of southwestern Kazakhstan (Teufer, 2020), perhaps via the Inner Asian Mountain Corridor (Frachetti, 2012). Further resolution of the nature of interregional interaction among Chalcolithic-Bronze Age populations occupying the periphery of theIranian Plateau requires collection of cranial nonmetric data, especially from Shahr-i Sokhta in Iranian Seistan, steppe-influenced assemblages from Tigrovaja Balka, Makon-i Mor, Kokcha III in southern Central Asia and from pre- and post-Harappan samples from the Indus Valley (Mehrgarh, Timargarha, Sarai Khola).

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