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THE PREHISTORIC PEOPLING OF SOUTH AMERICA AS INFERRED FROM EPIGENETIC DENTAL TRAITS

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INTRODUCTION

The origins and genetic relations of New World populations have long been topics of scientific interest to physical anthropologists and archaeologists alike (Hrdlicka 1923, 1937). Because of a number of recently reported archaeological sites and human remains, the initial colonization of the New World is a topic of much discussion in both the popular press (Begley and Murr 1999; Malcomson 2000; *Nova*, "Mystery of the First Americans" 2000; Schurr 2000; Various Authors, *Discovering Archaeology* 2000) and scientific community (Jantz and Owsley 1998a, b; Neves and Blum 2000; Neves *et al.* 1999a, b, c, d, 2001; Powell 2000; Powell and Neves 1998, 1999; Powell and Rose 1999; Steele and Powell 1999). Turner's (1969, 1971, 1981, 1983, 1985, 1990) investigations of genetically controlled discrete dental trait variability are, perhaps, the most comprehensive investigations on the origins of New World human biological variation. His surveys of dental trait variability reveal that Northeast Asians and all Native American populations demonstrate a more complex pattern of tooth cusp and root number relative to Southeast Asians. Turner refers to populations exhibiting this increased complexity of dental traits as "sinodonts," whereas the more simple dental condition observed among southeast Asians, Australians, and Pacific Rim populations is referred to as "sundadonty." Turner (1985, 1986, 1987, 1990) estimates that sinodont dental traits evolved in northeast Asia from pre-existing, less elaborate "sundadont" tooth cusp and root traits approximately 20,000 years before present. For this study, I report on genetically influenced tooth root and cusp traits for 12 south central Andean mortuary populations and compare them to other previously reported samples in order to shed light on the

genetic origins and number of migrations for prehistoric South America. I then consider broader implications of these results in light of current archaeological and paleoclimatic data.

Based upon univariate comparisons and unstandardized Mean Measure of Divergence (MMD) analyses of discrete dental traits frequencies, Turner (1983: figure 11.2) proposes that northeast Asian human populations migrated into the New World through Siberia and Beringia in three distinct migratory "waves." Each of these waves closely corresponds to the three modern language groups found among Native Americans of North and South America as defined Greenberg (1987). According to this model, the Paleoindians represent the earliest of these population movements and are ancestral to all Amerind-speaking populations of North and South America. Na-Dene speaking Athapascan populations of the Greater Northwest Coast arrived in the second migratory wave and the Aleut-Eskimo speaking populations of Alaska and northern Canada account for the most recent migration.

Since its initial presentation, Turner's (1983, 1985, 1989) tripartite model has provided a valuable framework for directing and empirically testing scientific research regarding the number and timing of peopling events in the New World's prehistory. However, the validity of Turner's "three-wave hypothesis" depends, in part, on his characterization of dental variability among Native Americans. According to Turner (1985), all Macro-Indians, which includes the Paleoindians, all South Americans, and Amerind-speaking North American populations, and the Na-Dene and Aleut-Eskimo populations are characterized by relatively high frequencies of "sinodont" traits. While archaeological, linguistic, and

molecular data have been presented in support of Turner's hypothesis (Cavalli-Sforza *et al.* 1994; Greenberg 1987; Greenberg *et al.* 1986; Williams *et al.* 1985), his tripartite model is not without its critics. Recent molecular (Bonatto and Salzano 1997a, b; Cann 1994; Horai *et al.* 1993; Karafet *et al.* 1999; Kolman *et al.* 1996; Lorenz and Smith 1996; Merriwether *et al.* 1995; Schanfield 1992; Szathmary 1993; Torroni *et al.* 1993), linguistic (Nichols 1990, 1995), osteological (Jantz and Owsley 1998a, b, 2001; Lahr 1995, 1996, 1997; Neves and Pucciarelli 1989, 1991; Neves *et al.* 1996a, 1999a, b, 2001; Powell and Neves 1998, 1999; Powell and Steele 1992; Steele and Powell 1993), and dental studies (Haydenblit 1996; Lahr and Haydenblit 1995; Powell 1993, 1995, 2000; Powell and Neves 1998; Sutter 1997a, b) have challenged both the timing and number of migrations into the New World. Some have argued for as many as four (Horai *et al.* 1993; Lorenz and Smith 1996; Munford *et al.* 1995; Neves and Pucciarelli 1991; Schanfield 1992; Torroni *et al.* 1993) while others have argued for as few as a single migration (Bonatto and Salzano 1997a, b; Merriwether *et al.* 1995).

After re-analyzing Turner's dental trait data using cladistic and phenetic analytical procedures, Powell (1993) argues that Turner's Paleoindian sample is biologically distinct from New World populations represented in subsequent migrations. While supporting Turner's three principal migratory groups (*i.e.*, Macro-Indian, Na-Dane, Aleut-Eskimo), Powell's results indicate that the Paleoindians are more similar to Northeast Asians than to other Native Americans. He also finds that the dental variability of these samples demonstrates that substantial differences exist among the Paleoindians and later Macro-Indian populations. Subsequently, Scott and Turner (1997:279) have acknowledged these differences, but maintain that samples combined to form Turner's Macro-Indian samples—including Turner's South American Indians sample—represent direct descendants of the Paleoindians. However, it is difficult to evaluate the homogeneity of Turner's Macro-Indian dental samples and the validity of his three wave hypothesis, given that he has not yet published these data in detail. This difficulty is especially marked for his South American Indian

sample, which includes all prehistoric South American collections he examined, irrespective of their geographic location or antiquity (see Turner 1985:59).

Recent craniometric investigations of Paleoindian remains (Jantz and Owsley 1998a, b, 2001; Neves and Pucciarelli 1989, 1991; Neves *et al.* 1996a, b, 1999a, b, 2001; Powell and Neves 1999; Powell and Rose 1999; Powell and Steele 1992; Steele and Powell 1993) have also challenged Turner's "three-wave" hypothesis. The results of these studies have led some investigators to suggest that Turner's Macro-Indian sample is distinct from the Paleoindians and may represent either a subsequent or contemporaneous population movement into the New World (Lahr 1995, 1997; Lalueza 1996; Munford *et al.* 1995; Neves *et al.* 1996b, 1997). The broader implications of these skeletally-based studies are that there were at least four migrations into the New World. Other craniometric studies of Paleoindian and early Archaic Period remains also call into question the homogeneity of the Paleoindians and suggest that North American Paleoindian remains represent a highly variable population (Jantz and Owsley 1998a, b, 2001; Neves and Blum 2000; Powell 1993, 1995, 2000; Powell and Rose 1999; Steele and Powell 1993, 1999), while South American Paleoindian remains are closely related but relatively more homogenous (Neves *et al.* 1999b, c, d; Powell and Neves 1999).

At this time, investigations examining the microevolutionary relations among prehistoric South Americans and, more specifically, ancient Andeans, are just beginning to contribute to this debate. The biological relations among prehistoric Andeans can contribute to our understanding of critical scientific questions regarding prehistoric human biological variability, the peopling of South America, the relationship between ancient biological variability and the archaeological record, and the relationship between ancient biological variability and the observed pattern of genetic and linguistic variability among contemporary Andeans. The twelve populations examined in this study were recovered in southern coastal Peru and northern Chile. I compare the data reported here with previously

published dental data in order to understand dental variability for previously unreported prehistoric samples from the south central Andes, and to place these samples into a broader evolutionary context. I then interpret the results of these comparisons in light of current osteological, genetic, linguistic, and archaeological data for the Andes. In doing so, it is my goal to contribute to our ever-growing understanding of prehistoric population dynamics in South America and the New World. I intentionally avoid the route and timing of the initial colonization of South America, given that these separate issues are best dealt with by the archaeological community.

MATERIALS

The 12 archaeological samples analysed in this study come from 18 prehistoric coastal valley sites in the Moquegua Valley, Peru and the Azapa Valley, Chile (Figure 1). In total, these twelve mortuary populations represent the dentitions of 787 skeletal and mummified individuals from the south central Andes (Table 1). The human remains examined here represent more than 7,000 years of biocultural history (Figure 2) and a variety of socio-economic populations. To avoid confusion, my chronological discussions will follow the chronology used by other scholars working in the south central Andes. This is because the traditional Horizon/Period chronology (Lanning 1967; Rowe 1967) used throughout most of Peru does not accurately reflect cultural developments in the south central Andes. The Archaic Period (10,000-3800 cal BP or 8050-1850 B.C.) and associated sub-divisions (see Aldenderfer 1989; Santoro 1989) roughly correspond to Quilter's (1991) Preceramic periods, while the Initial Period, Early Horizon, and Early Intermediate Period roughly correspond to the Formative Period (3800-1500 cal BP or 1850 B.C.-450 A.D.) for the south central Andes as a whole (Stanish 1992), although regional chronologies vary. The Middle Horizon ranges between 1500-1000 cal BP (450 A.D.-950 A.D.), while the Late Intermediate Period (950-474 cal BP or A.D. 1000-1476) of southern Peru is traditionally referred to as the Desarrollo Regional for northern Chile. However, for the sake of simplicity I refer to this period as the Late Intermediate Period for both southern Peru and northern Chile.

The Moquegua Valley (Figure 3) is represented by four prehistoric samples. Remains belonging to the Ilo Preceramic sample are from two Archaic Period coastal sites 10 km north of Ilo, Peru. These include four Chinchorro-like, naturally mummified burials from Yara (Rasmussen 1998) and 11 "Quiani-style" flexed burials from the Kilometer 4 site (Wise *et al.* 1994). The other three Moquegua Valley samples all correspond to the Late Intermediate Period. La Yaral (not to be confused with Yara) is a Late Intermediate Period middle Moquegua Valley site characterized by a mixed agro-pastoral economy (Rice 1993). The sample from San Gerónimo represents a contemporaneous period fishing village at the mouth of the Ilo River in the town of Ilo (Jessup 1990a), while the Chiribaya Alta sample is from what is widely recognized as the administrative, ceremonial, and economic center of the Late Intermediate Period Chiribaya polity (Buikstra 1989, 1995; Jessup 1990b; Owen 1993).

I also analyzed eight samples from Azapa Valley sites (Figure 4). The Chinchorro sample represents the founding population of the Azapa Valley. The remains from four Chinchorro beach sites were combined into a single sample for statistical analyses. These include Morro-I (Standen 1991), Morro-I/V (Guillén 1992), Morro-I/VI (Focacci and Chacón 1989), and Playa Miller-8 (Alvarez 1969). Two samples represent the Formative Period. The sample referred to as Alto Ramírez includes Azapa phase (3000-2800 cal BP) burials from the site Azapa-71 and Alto Ramírez phase (2800-2500 cal BP) burials from the sites Azapa-14, Azapa-70, and Azapa-115. Sites of these phases provide the earliest evidence for coastal valley village life and incipient agriculture within the Azapa Valley (Focacci 1980; Muñoz O. 1980, 1983, 1987, 1989; Santoro 1980a, b). All sites included in the Alto Ramírez sample are inland, 10 to 12 km from the coast of Arica. The Playa Miller-7 sample comes from a coastal site that was a contemporaneous Formative Period fishing community of the El Laucho tradition, where the earliest pottery of the region was also found (Focacci 1974). The Late Intermediate Period is represented by samples from the agricultural Cabuza sites Azapa-6 and Azapa-71 (Focacci 1993), a sample from the mixed maritime-agropastoral Gentilar site Azapa-8 (Focacci

1960), and a sample from the mixed agropastoral Maitas-Chiribaya site Azapa-140 (Muñoz O. and Focacci 1985). Remains from the Playa Miller-4, a contemporaneous fishing community, are from a Late Intermediate Period coastal site (Focacci 1969, 1974).

METHODS

For this study, I use 28 genetically controlled dental crown and root traits to assess the biological affinities among the 12 prehistoric south central Andean samples examined here and those previously reported by Turner (Table 2). Dental traits have been used successfully to evaluate the evolutionary relations and biological affinities among a number of archaeological populations (Green 1982; Greenberg *et al.* 1986; Haydenblit 1996; Lukacs and Hemphill 1991; Powell 1995; Sofaer *et al.* 1986; Sutter 2000; Turner 1985, 1987, 1989, 1990). Many dental traits are known to be highly heritable among living populations (Berry 1978; Biggerstaff 1970, 1973; Escobar *et al.* 1976; Harris and Bailit 1980; Hassanali 1982; Ludwig 1957; Nichol 1989; Portin and Alvesalo 1974; Scott 1977, 1980). Although some investigators presume discrete dental traits to be quasi-continuous (Turner *et al.* 1991), others have found that many of these traits are controlled by major genes with variable expression and show varying degrees of environmental influence (Nichol 1989). Scott and Turner (1988) demonstrate that relatively few dental traits' expressions are sexually dimorphic or inter-correlated on a global level. Many of the dental traits are scored using an ordinal scale, while others are simply recorded as present or absent (see Scott and Turner 1997 and Turner *et al.* 1991 for detailed trait descriptions and a discussion of scoring procedures). These ordinally scaled dental traits are then dichotomized for subsequent biodistance and multivariate analyses.

For comparative purposes, I limited the selection of dental traits to those reported by Turner (1985, 1987) for the 23 Asian and Native American populations and those examined by this study (Tables 3 and 4). I visually examined and scored these traits using standardized casts and descriptions (see Turner *et al.* 1991). The dental trait scores for the prehis-

toric Andean remains reported here are dichotomized using the same presence/absence ranges reported by Turner (1985, 1987, 1990) (see Table 2). One advantage of dichotomization is that it reduces observational error. The reduction in error arises because it is generally easier to distinguish consistently presence from absence of a trait than it is to assign different levels of expression for traits.

The first goal of this investigation is to determine whether the 12 south central Andean samples are characterized by sinodonty or sundadonty by comparing their dental trait frequencies with dental data reported for the 23 New World and Asian populations reported by Turner (1985, 1987). Importantly, based upon visual inspection of the percentages of dental traits for each of his samples, Turner (1990) claims that eight traits effectively discriminate sinodont populations from sundadonts. These traits include upper central incisor shoveling, upper central incisor double shoveling, single rooted first premolars, enamel extensions of the first maxillary molar, peg-shaped/reduced third maxillary molar, three-rooted mandibular first molar, deflecting wrinkle of the first mandibular molar, and four-cusped second mandibular molars.

Although Turner (1983, 1985, 1989) has argued that all New World populations are characterized by sinodonty, others have reported the presence of sundadont dental trait frequencies for prehistoric remains from the Tierra del Fuego and Patagonia region (Lahr and Haydenblit 1995) and early Pre-ceramic New World remains (Haydenblit 1996; Powell 1993, 1995; Powell and Neves 1998; Powell and Rose 1999). For this study, the 12 south central Andean samples' dental profile (*i.e.*, sinodonty or sundadonty) is determined by classifying them using seven of the eight arcsine-transformed dental trait frequencies for Turner's 23 samples using discriminant functions analysis (DFA). This is the same procedure that has already been used by others to classify prehistoric populations as sinodonts or sundadonts using Turner's published data (Haydenblit 1996; Powell 1993). One of Turner's eight key traits, the deflecting wrinkle of the mandibular first molar, was excluded from DFA because most of the samples reported here had no observations for this

trait. The deflecting wrinkle is a trait that is often quickly obliterated shortly after the first molar erupts due to tooth wear or cavities, so it is rarely possible to score this trait in individuals older than 10 years of age (see Turner *et al.* 1991). For each of the 12 south central Andean samples examined here, Table 4 presents the dental profiles based upon DFA using the remaining seven key traits.

To place the 12 south central Andean samples that were examined into a broader evolutionary context, I compared the Andean samples reported here to the 23 Asian and New World samples reported by Turner (1985, 1987, 1990) using all traits from Tables 3 and 4. Each sample's arcsine-transformed dental trait frequencies are used to calculate the mean measure of divergence (MMD) according to procedures suggested by Green and Suchey (1976). The equation for the mean measure of distance is calculated as follows:

where r is the number of traits used in the comparison, θ_{1i} and θ_{2i} are the transformed frequencies in radians of the i^{th} trait in the two groups being compared, and n_{1i} and n_{2i} are the numbers of individuals

$$MMD = \frac{\sum_{i=1}^r (\theta_{1i} - \theta_{2i})^2 - [1/(n_{1i} + 1/2) + 1/(n_{2i} + 1/2)]}{r}$$

scored for the i^{th} trait in the two groups. It should be noted that the MMD can produce negative distances (Green 1982; Sjøvold 1973). This occurs when there is very little or no difference in the arcsine-transformed frequencies across a number of traits for the populations being compared. In such cases, the estimated variance of the measure of distance for a given trait (*i.e.*, the bracketed term in the numerator of the MMD equation) will be subtracted from a zero or near zero value for the squared difference in the arcsine-transformed trait frequencies. While negative MMD values are not meaningful in a statistical sense, they do indicate that the populations being compared are similar for the traits being considered.

Standard deviations and standardized distances for MMD values are calculated as suggested by

Sjøvold (1973). The variance of the MMD is calculated using the equation:

$$Var_{MMD} = \frac{2}{r^2} \sum_{i=1}^r (1/(n_{1i} + 1/2) + 1/(n_{2i} + 1/2))^2$$

Once the variance of the MMD is found, the standard deviation of the MMD is calculated using the equation:

$$sd_{MMD} = \sqrt{Var_{MMD}}$$

Finally, the standardized MMD is determined by:

$$\text{Standardized MMD} = \frac{MMD}{sd_{MMD}}$$

As Sjøvold (1973) correctly points out, standardized mean measures of divergence are more appropriate than the mean measure of distance for evaluating biological relatedness when comparing the populations of different sample sizes. The standardized MMD is particularly important when the number of observations for some traits is small, because its value is a more accurate reflection of biodistances than unstandardized MMD values. Standardized distances are considered statistically significant if their value is greater than 2. Table 5 lists standardized MMD values for the 12 south central Andean samples and those reported by Turner. One problem in making comparisons when using published data is that it is not possible to address inter-observer error directly in the scoring of data collected by this project and previously published data. However, while the magnitude of MMD comparisons might be suspect, when intra-observer error is low, the general patterns made by such comparisons still provide valuable information.

I used nonmetric multidimensional scaling procedures to analyze the matrix of standardized MMDs (Figure 5). Multidimensional scaling is a useful procedure for producing easily interpretable visual representations of complex distance matrices (Norusis 1994). This procedure produces accurate graphical representations of data matrices using the number of dimensions specified by the investigator.

RESULTS

Despite his (Turner 1985, 1987, 1990) assertion that all New World populations are sinodonts, this investigation reveals that some prehistoric south central Andean populations do not strictly adhere to Turner's sinodont/sundadont dichotomy. In fact, the results of the DFA classify as sundadonts the Archaic Period Ilo Preceramic of the Moquegua Valley, Peru, and Chinchorro and Formative Period El Laucho (Playa Miller-7) and Alto Ramirez samples of the Azapa Valley, Chile (Table 4). The Late Intermediate Period samples from the Azapa Valley, Chile (Azapa-140, Azapa -8, and Playa Miller-4) are also classified as sundadonts, while other, contemporaneous Late Intermediate Period Azapa Valley samples (*i.e.*, Azapa-6 and Azapa-71) are characterized by the sinodont dental pattern. Significantly, all three Late Intermediate Period Moquegua Valley samples (Chiribaya Alta, San Gerónimo, and El Yaral) are also classified as sinodonts using DFA. Results of this study clearly indicate that Turner's characterization of all South Americans as being characterized by sinodonty must be rejected. Consequently, the sinodont/sundadont dichotomy first proposed by Turner does not accurately reflect all of the dental trait variability in Asia and the New World. Others examining prehistoric dental trait variation in North America (Powell 1995), Mexico (Haydenblit 1996), and Tierra del Fuego (Lahr and Haydenblit 1995) have arrived at a similar conclusion.

Two (8.5%) of Turner's 23 Asian and New World samples—Hong Kong and South China Proper—are incorrectly classified by DFA using seven of the eight key traits defined by Turner (1990). This reanalysis is similar to results obtained by Powell (1995), who classified his samples based upon all eight of the key traits defined by Turner.

Because it was not possible to address inter-observer error, the magnitude of specific comparisons of standardized MMD values among south central Andean samples and those reported by Turner (1985, 1987) are suspect. However, while concerns regarding inter-observer error are real, it is unlikely that the general patterns in dental trait frequencies

among the south central Andean samples are due to observational error, especially when many of these traits are scored as either present or absent.

As reported elsewhere (Sutter 1997a, b, 2000), there is a clear diachronic increase in the frequency of sinodont traits among the 12 south central Andean samples reported here. More specifically, the frequency of incisor winging, the upper first molar metaconule (cusp 5), the upper first premolar root number, odontomes, lower first molar entoconulid (cusp 6), and lower first molar protostylid (cusp 7), increase through time and geographically from south to north. These and other sinodont traits are observed at their highest frequencies among the three Late Intermediate Period samples from Moquegua, Peru (Tables 3 and 4). Based upon these differences, I argue elsewhere (Sutter 2000) that the Late Intermediate Period samples from Moquegua, Peru, are substantially different from all Azapa Valley populations and the founding Moquegua Valley Ilo Preceramic sample. These interpretations are supported by archaeological evidence that indicates the arrival of an immigrant population in the Moquegua Valley at the beginning of the Late Intermediate Period (Owen 1993).

The nonmetric multidimensional scaling solution (MDS) of standardized MMD values presents patterns that provide compelling information regarding the nature of dental trait variability among the south central Andean samples. Within the MDS solution the three Late Intermediate Period Moquegua Valley samples from Chiribaya Alta, San Gerónimo, and El Yaral are most negative of all south central Andean samples along Dimension 1, indicating that the Late Intermediate Period Moquegua Valley groups scale more highly as sinodonts than other prehistoric south central Andeans (Figure 5 and Table 6). Further, when nearby comparative samples are examined, the Late Intermediate Period Moquegua Valley samples are most similar to Native American sinodont populations from North and South America, relative to other south central Andean samples. In addition, dental trait frequencies among south central Andean Archaic Formative Period Chinchorro and Ilo Preceramic samples are intermediate to those expressed by sinodont and

sundadont populations reported by Turner and are most similar to the Turner's Paleoindian sample (Figure 5 and Table 5).

DISCUSSION

According to Turner's (1983, 1985) three-wave hypothesis, all South American and Amerind-speaking North American Indian populations descended from the founding Paleoindian population, who came to the New World in the initial wave. Turner (1983, 1985) claims that all three of these populations belong to a single Macro-Indian group. However, the broader implications of my results are that Turner's Macro-Indian sample likely represents at least two migratory events. A number of investigators from a variety of disciplines also contend that a single migration cannot account for all of the genetic, phenotypic, linguistic, and archaeological variability present in Turner's Macro-Indian group (Lahr 1995, 1996; Lahr and Haydenblit 1995; Munford *et al.* 1995; Neves and Pucciarelli 1989, 1991; Nichols 1990, 1995; Powell 1993; Schanfield 1992; Steele and Powell 1992; Torroni *et al.* 1993).

Although there is considerable variability in the dental trait morphology of prehistoric south central Andean populations reported here, there is a clear chronological and directional trend indicating that the number and complexity of tooth cusps and roots increase through time (*i.e.*, dental traits become more complex or sinodont-like) and are observed at their highest frequencies in the north (the Moquegua Valley) and decrease in the south (the Azapa Valley). Haydenblit (1996) reports a similar temporal trend from sundadonty to sinodonty among prehistoric Mesoamericans.

Multidimensional scaling analysis of standardized MMD values indicates (Figure 5, Tables 5 and 6) that Archaic and Formative Period samples examined here (the Ilo Preceramic, Chinchorro, Alto Ramírez, and Playa Miller-7 samples) and the Late Intermediate Period Azapa Valley samples from Azapa-8 and Playa Miller-4 exhibit dental profiles that are intermediate to the sinodont/sundadont dichotomy defined by Turner. In contrast, the Late Intermediate Period samples from Chiribaya Alta, La

Yaral, and San Gerónimo of the Moquegua Valley, Peru, and Azapa-6 and Azapa-71 of the Azapa Valley, Chile, are characterized by higher frequencies of complex tooth cusp and root traits. More specifically, dental trait frequencies (Tables 3 and 4) and biodistance results (Table 5) presented here indicate that, among prehistoric south central Andean populations, the dental profiles of Late Intermediate Period samples from the Moquegua Valley (Chiribaya Alta, La Yaral, and San Gerónimo) are most like those previously reported by Turner (1985, 1987) for other New World populations.

Previously reported archaeological and biodistance data both indicate that the Late Intermediate Period Moquegua Valley samples represent an immigrant population (Owen 1993; Sutter 1997a, 2000). Based upon the frequencies of seven key traits, these populations are classified as sinodonts by DFA, whereas the earlier Archaic Period Ilo Preceramic sample of the Moquegua Valley is characterized by a sundadont dental pattern (Table 4). Recent mitochondrial DNA (mtDNA) analysis of the preceramic and Chiribaya Alta samples reported here support the inferences made from both biodistance and archaeological analyses (Williams *et al.* 2001). Williams and her colleagues analyzed preceramic remains from Kilometer-4 and report that they were homogenous with respect to their mtDNA. In contrast, the Chiribaya from Chiribaya Alta were highly variable, indicating a substantial amount of gene flow into the coastal Moquegua Valley sometime following the Preceramic Period.

With the exception of the Late Intermediate Period samples from Azapa-6 and Azapa-71, all of the Azapa Valley samples have relatively simple dental patterns that are intermediate to those exhibited by sinodonts and sundadonts when compared to other New World and south central Andean samples (Figure 5 and Table 5). When these samples are classified into one of two dental groups based upon their dental trait frequencies for the seven key traits defined by Turner (1990), they are classified as sundadonts (Table 4). Previously reported biodistance results published elsewhere (Guillén 1992; Rothhammer *et al.* 1984; Sutter 1999) indicate 5,000 years of genetic continuity

among the Azapa Valley samples. The presence of South American populations characterized by sundadont dental trait frequencies has also been reported for both South American Paleoindians from Brazil (Powell and Neves 1998) and prehistoric populations from Tierra del Fuego and Patagonia (Lahr and Haydenblit 1995), a point to which I will return below.

While *in situ* microevolution may account for some of the observed differences in dental trait variability among prehistoric south central Andean populations, I hypothesize that this variability is the result of two migratory events into South America (Figure 6). According to this scenario, the first migration corresponds to the initial colonization of South America by the Paleoindians while the second migration is represented by northern and central Andean populations characterized by relatively higher frequencies of increased tooth cusp and root number. I suggest that the second wave followed a north to south route along the Andean highlands, and later proceeded from the highlands to the coastal valleys.

Rather than implying large scale migration resulting in population replacement, I argue the second wave likely represents the increased fertility among the earliest agriculturalists arriving in South America from the north from Mesoamerica via the Isthmus of Panama. I hypothesize that these agriculturalists would have been characterized by relatively higher frequencies of complex tooth cusp and root traits relative to the earlier South American populations that represent direct descendants of the Paleoindians. This second migration resulted in substantial and directional gene flow associated with these cultural changes and is best described as a demic expansion (also referred to as demic diffusion)—a well-established concept in molecular studies that other investigators have applied in explaining observed genetic and morphological changes among prehistoric populations as the result of demic expansion of food-producing populations (Barbujani *et al.* 1994; Cavalli-Sforza *et al.* 1993, 1994; Jacobs 1994; Semino *et al.* 1996; Sokal and Menozzi 1982; Sokal *et al.* 1991). The higher fertility rates of intensive agriculturalists as compared to foragers and horticulturalists is well documented in the anthropological literature (Armelagos *et al.* 1991; Bentley *et al.* 1993a, b; Campbell and Wood 1988; Clark and Brandt 1984). Research also shows that populations characterized by relatively low fertility are more susceptible to lineage extinction compared to those populations characterized by higher fertility rates (Harpending 1994; Harpending *et al.* 1993; Rogers and Harpending 1992).

Although the exact timing of the demic expansion into South America is difficult to estimate, compelling circumstantial evidence exists. Theoretically, this demic expansion would be closely related to the beginning of food production in the Formative Period of different regions of South America. Accordingly, this expansion had its origins in Central America and then proceeded south into northwestern South America where the earliest evidence for the cultivation of C4 domesticates is found (Pearsall 1992).¹ Importantly, many domesticates—especially maize—have been recovered primarily from ceremonial contexts but do not appear to have been dietary staples until after 5800 cal BP (Burger and Van der Merwe 1990; Grieder *et al.* 1988; Pearsall 1995; Piperno 1995; Quilter 1991; Quilter and Stocker 1983; Quilter *et al.* 1991; Staller 2003; Staller *et al.* 2001). The economic shift to agriculture and the hypothesized demic expansion also closely correspond with environmental changes during the South American mid-Holocene Climatic Optimum. According to Sandweiss' (2003) recent review of available paleoclimatic data, the mid-Holocene Climatic Optimum in northern Peru corresponds to 9000-5800 cal BP. In that region, the period was characterized by a warmer and wetter, more stable seasonal climate from 9000 to 5800 cal BP relative to the preceding period, followed by a cool climate punctuated by less frequent ENSO events than today between 5800 and 3000 cal BP (Sandweiss 2003; Thompson *et al.* 1992). In southern Peru and northern Chile, the mid-Holocene Climatic Optimum was apparently expressed as a period of ex-

¹ C4 domesticates are plants, mainly tropical grasses, which follow a metabolic pathway resulting in their preferential incorporation of the Carbon 14 isotope.

treme aridity from ca. 8000-4000 cal BP, but it is likely that some climatic change occurred around 5800 cal BP as it did further north and throughout the Pacific Basin (e.g., Sandweiss 2003; Sandweiss *et al.* 2001). Archaeologically, this period is associated with the restricted distribution of crucial resources, and humans responded to these changes intensifying the exploitation of important resources and experimenting with new forms of subsistence.

While many plants were already under cultivation prior to 5800 cal BP (Pearsall 1992; Quilter 1991; Quilter and Stocker 1983), conditions following the mid-Holocene Climatic Optimum (5800-3000 cal BP) are implicated in the increased productivity of C4 plants (Sage *et al.* 1995) such as maize, sedges, and other important New World cultigens (Street-Perrott *et al.* 1997). This period is characterized by a decrease in temperature and an increase in coastal humidity and atmospheric CO₂ levels. This period also marks the emergence of modern ocean levels, ocean currents, and the El Niño (ENSO) phenomena (Sandweiss 2003; Sandweiss *et al.* 1996, 2001; Thompson *et al.* 1992). The greatly increased productivity of the C4 plants is associated with the economic shift from simple cultivation of domesticates to intensive agriculture in northern Perú.

My results beg the question of where these sinodont populations originated. At this time the data are inconclusive. However, I submit two possibilities: first, it is possible that sinodonty was already present among the initial colonists of the New World. This is not a novel proposition, as others report that North American Paleoindian dental (Powell 1993, 1995, 2000; Powell and Neves 1998; Powell and Rose 1999; Scott and Turner 1997) and craniometric morphology (Jantz and Owsley 1998a, b; Neves *et al.* 1996a, b; Neves *et al.* 1999a, b, c, d, 2001; Powell 1995; Powell and Neves 1999; Powell and Rose, 1999) is highly variable, but much less so among South American Paleoindians (Munford *et al.* 1995; Neves *et al.* 1996a, b, 1999a, b, c, d, 2001; Neves and Pucciarelli 1991; Powell and Neves 1998). It is possible that microdifferentiation among the initial colonizers of the New World led to some Paleoindians being characterized by sinodonty while others may have been characterized by sunda-

donty. If this were the case, then the initial colonizers of South America — being characterized by a sundadont dental pattern — would not be representative of other prehistoric Central and North Americans. In other words, the atypical sundadont dental trait pattern characteristic of the founding South Americans would be due to founder's effect, a special case of genetic drift where a founding or colonizing population is genetically unrepresentative of the larger population from which it separated.

The second possibility is that the Paleoindians and their descendants—who would have been characterized by sundadonty and a “proto-Mongoloid” (Munford *et al.* 1995; Neves *et al.* 1996a) or “generalized Mongoloid” (Lahr 1995, 1996, 1997) morphology—are genetically and morphologically distinct from other Amerindians and Northeast Asians who are characterized by sinodonty and Mongoloid craniometric morphology. Once again, this is not a novel proposition as others also suggest that Amerindians reported by Turner (1983, 1985) and Greenberg *et al.* (1986) actually represent two or more genetically and morphologically distinct populations (Lahr, 1995, 1996, 1997; Munford *et al.* 1995; Neves and Pucciarelli 1991; Neves *et al.* 1996b; Neves *et al.* 1999a, c; Neves *et al.* 2001; Powell 1993; 1995; 2000; Powell and Neves 1998; 1999). According to this scenario, the prehistoric peopling of the New World occurred as four migratory events, not three.

As Lahr (1995:188) correctly points out, this scenario does not necessarily suggest a revised timing for the arrival of the Paleoindians and other Amerindians, nor does it necessarily preclude their arrival in two simultaneous but morphologically distinct populations. Whichever of the two scenarios accounts for the origin of New World sinodont populations, data presented here and by others (Lahr and Haydenblit 1995; Powell and Neves 1998) suggest that the earliest inhabitants of South America and their Preceramic Period (pre-3800 cal BP) descendants would have been characterized by sundadonty, while the subsequent demic expansion would be associated with populations characterized by a sinodont dental pattern.

Previous investigations estimating the genetic affinities among South American populations also suggest that substantial craniometric differences existed among Preceramic Period coastal and highland Andean populations, and that these differences significantly decreased through time (Ericksen 1962; Newman 1943, 1948, 1951; Rothhammer *et al.* 1984). Indeed, it is important to point out that Turner's own dental data from the central coast of Peru indicate that the dentition associated with the Late Preceramic (5800-3800 cal BP) remains from coastal site La Paloma are significantly different from earlier dentitions from the same site (see Benfer 1984:533). The transition between these two periods in central Peru is associated with the appearance of pottery and significant changes in population growth, subsistence strategies, iconography, trade, and settlement and architectural patterns in the Andes (Cohen 1977; Moseley 1992; Quilter 1991; Quilter and Stocker 1983; Sandweiss *et al.* 1999; Weir *et al.* 1988).

Ericksen (1962) suggested that these changes in subsistence patterns following the Late Preceramic Period broke down the genetic isolation of coastal South American populations. Dental data presented here suggest that populations associated with higher frequencies of sinodont traits arrived on the coast of the south central Andes sometime shortly after the beginning of the Formative Period which I postulate occurred here approximately 2500-1500 cal BP. If my hypothesis of initial movement through the highlands is correct, the second wave would have arrived in the Lake Titicaca Basin prior to their arrival on the coast. The impact of this demic expansion on the Lake Titicaca region appears to coincide with archaeological changes associated with the beginning of the Lower Formative Period, which in this region begins approximately 2800 cal BP (Stanish 1992).

Recent linguistic and genetic investigations also provide particularly compelling support for this second north-to-south demic expansion in the Andes. Nichols' (1995: figure 7) review of linguistic variability indicates that southern Andean and eastern Brazilian populations speak a "frontier language" that is descended from the colonizing lan-

guage group of the New World. According to Nichols, central Andean and northwestern South American populations are linguistically characterized by the second and third linguistic strata found within the New World. The first principal component of Rothhammer and Silva's (1992: figure 2a) presentation of allelic variation at 13 loci closely corresponds to Nichols' diagram of South American linguistic variability and indicates that Southern Andean and Amazonian populations exhibit considerably more variability among the 13 loci than Andean and northeastern South American populations. This variability suggests a greater period of genetic divergence among southern Andean and Amazonian populations than among other South American populations.

Investigations of mtDNA variability among New World populations have also shed light on the peopling of South America. In surveys of genetic data for 26 Asian and New World populations, Schurr *et al.* (1990), Wallace and Torroni (1992), and later Torroni *et al.* (1993), identify four different haplogroup of mtDNA (referred to as haplogroups A, B, C, and D) that are exclusive to Asian populations and their descendants (*i.e.*, Native Americans). According to the investigators, each of these haplogroups corresponds to founding lineages of maternal mtDNA among Native American populations. The investigators (Schurr *et al.* 1990; Torroni *et al.* 1992; 1993; Wallace and Torroni 1992) report that Amerind-speaking tribes are found to carry all four haplogroups, while Na-Dene speaking populations are largely characterized by haplogroup A with very low frequencies of C and D. These findings lead the investigators to suggest that only two migrations account for all the variation observed in Native American mtDNA. However, in a subsequent publication, Torroni *et al.* (1993) report haplogroup B to be absent among Aleut-Eskimo and Siberian populations, who are characterized by relatively higher frequencies of haplogroups A and D.

Merriwether *et al.* (1995) report mtDNA data for 14 additional New World populations and compare it with previously reported data. The investigators note a number of general trends in the mtDNA haplogroup data for the New World.

Native American populations exhibit a north to south increase in the presence of haplogroup B, and a north to south decrease in the frequency of haplogroups A and C. Based upon their findings, Merriweather *et al.* dispute Torrani *et al.*'s (1993) characterization of mtDNA variability among Native Americans, suggesting that the four haplogroups identified by Torrani and colleagues were present among all three New World linguistic groups. Further, Merriweather *et al.* (1995) suggest that additional haplogroups exist in low frequencies among some North American populations. For these reasons, the authors contend that all mtDNA variability among Native Americans can be explained by a single migratory event with subsequent *in situ* microevolutionary forces creating the presently observed genetic variability.

Lorenz and Smith (1996) report mtDNA data for 40 North American Na-Dene and Amerind samples that appear to support Torrani *et al.*'s (1993) previous characterization of New World mtDNA variation. While the investigators corroborate Merriweather *et al.*'s (1995) observation that all four mtDNA haplogroup variants are present among all three of Greenberg's language groups (Amerind, Na-Dene, Aleut-Eskimo), Lorenz and Smith (1996) argue that significant differences in the frequencies of these haplogroups exist among living members of the three language groups. Further, these investigators report that significant differences in haplogroup frequencies exist among Amerind populations for North, Central, and South America. Lorenz and Smith (1996) suggest that the haplogroup differences observed among living Amerinds (direct descendants of the Paleoindians according to Turner's hypothesis) reflect an extended period of *in situ* microevolution with relatively little gene flow among North, South, and Central American Amerind speakers.

Despite the claims by Merriweather *et al.* (1995) that all mtDNA variability among Native Americans can be explained by as few as a single, or at most, two migrations into the New World, the distribution of mtDNA haplogroups among South American populations suggests otherwise (Figure 7). Southern Andean and northeastern South American populations exhibit relatively low frequencies of haplo-

groups A and B, and high frequencies of haplogroups C and D, whereas Northern Andean and northwestern South American populations exhibit relatively high frequencies of haplogroups A and B and low frequencies of C and D.

Independent ancient mtDNA studies by Rogan and Salvo (1990) and Merriweather *et al.* (1994) report on the haplogroup B, or 9-bp Region V deletion, for a total of 27 Middle Preceramic (Chinchorro culture) and Formative Period (Alto Ramirez culture) mummies from the Azapa Valley. None of the 27 mummies examined by these investigators are characterized by haplogroup B. Likewise, Matheny *et al.* (n.d., cited in Turbón *et al.* 1994) report the absence of haplogroup B for terminal Paleoindian remains from the Azapa Valley site Acha-2.

Merriweather *et al.* (1994) note that modern Quechua, Aymara, and Atacameño populations from the nearby altiplano are reported to exhibit relatively high (>30%) frequencies for haplogroup B, while modern coastal populations from southern Chile, such as the Pehuelche and Yaghan, exhibit relatively low (<10%) to absent frequencies for the 9-bp Region V deletion. Merriweather *et al.* (1994) suggest that the prehistoric Azapa Valley populations may be ancestral to the modern south coast populations of Chile, while the modern Quechua, Aymara, and Atacameños descended from populations characterized by high frequencies of haplogroup B (*i.e.*, north and central Andean populations).

Subsequent to Merriweather *et al.*'s (1994) presentation of central Andean mtDNA frequencies, others have also report the absence of haplogroups A and B among prehistoric and historic populations of the Tierra del Fuego and Patagonia region (Lalueza 1996; Lalueza *et al.* 1997; Turbón *et al.* 1994). These researchers suggest that populations from Tierra del Fuego and Patagonia represent direct descendants of the Paleoindians and argue that the absence of haplogroup B, in particular, among these remote populations indicates that haplogroup B is associated with a subsequent wave of populations currently occupying the northern and central Andes. The researchers point out the lack of haplogroup B among Early Archaic Period remains from North

America (Pääbo *et al.* 1988) and South America (Matheny *et al.* n.d., cited in Turbón *et al.* 1994) to support their assertion.

Lahr's studies on both metric (Lahr 1995) and non-metric (Lahr 1996) cranial trait variation also indicate similar patterns for Southern Cone populations of South America. Lahr proposes that Southern Cone populations are phenotypically characterized as generalized mongoloids (*i.e.*, dolichocephalic, sundadont dental pattern) and suggests that these characteristics are associated with an absence of haplogroup B (Lahr 1995:188, 1996:323, 1997:4). Others have also reported that the craniometric measures of South American Paleoindians and Archaic Period remains are significantly different from subsequent South Americans (Munford *et al.* 1995; Neves *et al.* 1999a, b, d, 2001; Rivera and Rothhammer 1986; Rothhammer *et al.* 1984; Soto *et al.* 1975).

These aforementioned trends in the genetic and phenotypic data closely fit a 2-wave model to explain genetic variability among native South Americans: the first wave would correspond to populations with relatively high frequencies of mtDNA haplogroups C and D, whereas the second wave would correspond to central Andean and northwest South American populations that were characterized by relatively higher frequencies of mtDNA haplogroups A and B.

Within the context of this study, those samples that exhibit relatively fewer tooth cusp and root number (Ilo Pre-ceramic, Chinchorro, Alto Ramírez, Playa Miller-4, Playa Miller -7, Azapa-8, Azapa -140) likely represent direct descendants of South American Paleoindians. I expect that future mtDNA studies will find these populations have high frequencies of haplogroups C and D and relatively low frequencies of mtDNA haplogroups A and B. Conversely, south central Andean samples associated with relatively higher frequencies of tooth cusp and root number, such as the Late Intermediate Period samples from Chiribaya Alta, San Gerónimo, El Yaral, Azapa-6, and Azapa-71, should exhibit relatively high frequencies of mtDNA haplogroups A and B and lower frequencies of mtDNA haplogroups C and D. The composition of these samples should

reflect genetic contributions from the second demic expansion into South America.

Apart from the dental trait frequencies for Turner's South American Indian sample, relatively little is known concerning dental trait variability among prehistoric South Americans. Therefore, this study presents important information for a region where detailed dental data are lacking. When compared with other lines of evidence, the general patterns of dental trait variability among south central Andean samples provides important information on the prehistoric population dynamics in South America.

This study identifies a significant geographic and temporal trend towards sinodonty among prehistoric south central Andeans. Phenotypically, early prehistoric northern Chileans are characterized by low frequencies of sinodont traits and are most similar to the Paleoindian sample, while, in contrast, the Late Intermediate Period Moquegua Valley samples exhibit high and significantly different frequencies of sinodont traits. These populations exhibit dental trait frequencies most similar to those reported by Turner for other Macro-Indian populations.

Based upon the differences in dental trait morphology reported here and other sources of evidence, I suggest that there were at least two prehistoric peopling events that occurred in South America. According to this hypothesis, the earliest inhabitants of South America (the Paleoindians and their Archaic Period descendants) had relatively low frequencies of complex dental cusp and root traits (shoveling, winging, increased number of cusps, and decreased number of roots), similar to those reported by Turner (1985, 1987) for southeast Asian populations, whereas the subsequent prehistoric migration into South America was by made people with higher frequencies of complex dental cusp and root traits, similar to those reported for other New World and northeast Asian populations. The second migratory event can best be described as a demic expansion (Cavalli-Sforza *et al.* 1993; Sokal and Menozzi 1982), rather than representing outright population replacement. This second prehistoric migratory event in South America was likely associated with the in-

creased fertility of early agricultural populations characterized by high frequencies of sinodont traits.

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Sample	Site(s) represented by	Sample size (n)	Cultural	Location of site(s)	Time period
ChA	Chiribaya Alta	185	Chiribaya	Moquegua, Coastal Valley	Late Intermediate AD 1000-1476
SG	San Gerónimo	57	Chiribaya	Moquegua, Coast	Late Intermediate AD 1000-1476
YARAL	La Yaral	52	Chiribaya	Moquegua, Coastal Valley	Late Intermediate AD 1000-1476
ILOPC	Kilometer 4 and Yara	16	Preceramic	Moquegua, Coast	Archaic 3000-1000 BC
ALTRAM	Azapa-14, 70, and 115	72	Alto Ramírez	Azapa, Coastal Valley	Formative 1000 BC-AD 750
AZ140	Azapa-140	82	Maitas-Chiribaya	Azapa, Coastal Valley	Late Intermediate AD 1000-1476
AZ6	Azapa-6	45	Cabuza	Azapa, Coastal Valley	Late Intermediate AD 1000-1476
AZ71	Azapa-71	64	Cabuza	Azapa, Coastal Valley	Late Intermediate AD 1000-1476
AZ8	Azapa-8	25	Gentilar	Azapa, Coastal Valley	Late Intermediate AD 1000-1476
PLM4	Playa Miller-4	43	San Miguel & Gentilar	Azapa, Coast	Late Intermediate AD 1000-1476
PLM7	Playa Miller-7	62	El Laucho	Azapa, Coast	Formative 1000 BC-AD 750
CHINCH	Morro-I, Morro-V, Morro-VI, PLM8	84	Chinchorro	Azapa, Coast	Archaic 3000-1000 BC

Table 1. Prehistoric south central Andean samples examined by this study.

<i>Maxillary Traits</i>	<i>Abbrev.</i>	<i>Teeth Examined for Trait Presence</i>	<i>Range</i>	<i>Presence¹</i>
Winging	WING	Maxillary central incisors	0-1	1
Shoveling	SHOV	Maxillary incisors and canines	0-7	2-7
Labial Convexity	LABC	Maxillary incisors	0-4	1-4
Double Shoveling	DSHOV	Maxillary incisors, canine, and first premolar	0-6	2-6
Tuberculum Dentale	TD	Maxillary and mandibular canines	0-6	1-6
Interruption Groove	INTG	Maxillary incisors	0-1	1-2
Distal Accessory Ridge	UCDAR	Maxillary and mandibular canines	0-5	2-5
Mesial Ridge	UCMR	Maxillary canines	0-3	1-3
Distosagittal Ridge	DSR	Maxillary premolars	0-1	1
Odontome	ODONT	Maxillary premolars	0-1	1
Premolar Root Number	PMRT	Maxillary premolars	1-3	1
Metacone	META	Maxillary molars	0-6	5-6
Hypocone	HYPO	Maxillary molars	0-6	5-6
Metaconule	CUSP5	Maxillary molars	0-5	1-5
Carabelli's Trait	CARA	Maxillary molars	0-7	2-7
Parastyle	PARA	Maxillary molars	0-5	1-5
Enamel Extensions	EE	Maxillary molars and premolars	0-3	2-3
Peg/Reduced/Congenital Absence	P/R/CA	Maxillary 3 rd molar, Maxillary 2 nd premolar lateral incisor	0-1	1
<hr/>				
<i>Mandibular Traits</i>	<i>Abbrev.</i>	<i>Teeth Examined for Trait Presence</i>	<i>Range</i>	<i>Presence¹</i>
Shoveling	SHOV	Mandibular incisors	0-3	1-3
Tome's Root	TOME	Mandibular first premolar	0-7	4-7
Distal Accessory Ridge	LDAR	Mandibular canine	0-5	2-5
Canine Root Number	LCRT	Mandibular canine	1-2	2
Odontome	ODONT	Mandibular premolars	0-1	1
Groove Pattern	PATT	Mandibular molars	Y,+,X	Y
Cusp Number	CUSPNO	Mandibular M3 and M2	4-6	4
		Mandibular M1	4-6	6
Protostylid	PROTO	Mandibular molars	0-7	2-7
Hypoconulid (Cusp 5)	CUSP5	Mandibular molars	0-5	1-5
Entoconulid (Cusp 6)	CUSP6	Mandibular molars	0-5	1-5
Metaconulid (Cusp 7)	CUSP7	Mandibular molars	0-4	1-4
Lower Molar Root Number	LMRT	Mandibular M3 and M2	1-3	2
		Mandibular M1	1-3	3
Congenital Absence	CA	Mandibular 3 rd molar, 1 st premolar, and central incisor	0-1	1

¹Note: Presence/absence ranges based upon those used by Turner (1985, 1987).

Table 2. Discrete dental traits examined by this study.

<i>Population</i>	<i>Dentition</i>	<i>UI¹Winging</i>		<i>UI¹Shov</i>		<i>UI¹DShov</i>		<i>UI²TD</i>		<i>UCDAR</i>	
Amur Basin	1 Sinodont	34	50.0	15	100.0	17	82.4	25	32.0	13	53.8
Northeast Siberia	1 Sinodont	70	30.0	41	97.6	22	59.1	51	72.5	20	55.0
Paleoindian	1 Sinodont	4	25.0	6	100.0	5	80.0	5	60.0	4	100.0
Eskimo	1 Sinodont	107	17.8	103	98.1	91	59.3	105	76.2	77	58.4
Aleut	1 Sinodont	70	37.1	40	97.5	38	50.0	66	60.6	29	86.2
Greater Northwest Coast	1 Sinodont	222	32.9	168	98.8	156	57.7	194	73.7	109	81.7
North American Indian	1 Sinodont	795	47.4	874	99.9	796	75.0	910	64.0	429	73.4
South American Indian	1 Sinodont	363	55.4	451	99.8	417	90.2	414	65.2	254	79.5
North China and Mongolia	1 Sinodont	261	24.9	200	84.0	213	30.0	246	19.1	125	66.4
Recent Japan	1 Sinodont	265	21.9	276	65.9	267	19.5	304	15.5	240	57.9
Jomon	1 Sundadont	166	19.9	117	25.6	138	1.4	201	23.9	49	69.3
Hong Kong	1 Sundadont	295	23.1	307	63.8	299	28.4	298	19.1	249	54.6
South China Proper	1 Sundadont	35	34.3	35	74.3	33	24.2	44	11.4	26	80.7
Prehistoric Taiwan	1 Sundadont	15	20.0	22	59.1	21	0.0	14	14.3	7	42.9
Philippines	1 Sundadont	51	13.7	54	42.6	29	17.2	58	22.4	39	61.5
Early Southeast Asia	1 Sundadont	96	29.2	99	32.3	100	10.0	113	27.4	44	56.8
Recent Southeast Asia	1 Sundadont	16	37.5	13	46.2	14	28.6	17	23.5	47	40.4
Recent Thailand	1 Sundadont	128	39.1	127	37.0	111	9.0	128	19.5	80	47.5
Burma	1 Sundadont	11	18.2	15	13.3	13	7.7	26	11.5	16	62.6
Nepal	1 Sundadont	9	22.2	10	20.0	11	9.1	9	22.2	9	66.7
Recent Indo-Malaysia	1 Sundadont	56	16.1	49	24.5	36	11.1	57	28.1	39	71.8
Early Malay Archipelago	1 Sundadont	23	13.0	71	29.6	67	28.4	84	32.1	63	50.8
East Malay Archipelago	1 Sundadont	11	0.0	12	8.3	3	0.0	13	23.1	9	88.9
Chiribaya Alta (Moquegua-Late Intermediate)	3	139	47.5	80	88.8	91	69.2	75	32.0	26	96.2
San Gerónimo (Moquegua-Late Intermediate)	3	42	54.8	29	79.3	36	72.2	27	55.6	7	100.0
La Yaral (Moquegua-Late Intermediate)	3	48	64.6	29	96.6	34	52.9	24	41.7	11	100.0
Ilo Preceamic (Moquegua-Archaic)	3	12	0.0	5	40.0	4	50.0	5	20.0	4	100.0
Alto Ramírez (Azapa-Formative)	3	59	20.3	24	45.8	28	64.3	28	21.4	11	45.5
Azapa-140 (Azapa-Late Intermediate)	3	75	24.0	45	62.2	45	46.7	45	40.0	27	18.5
Azapa-6 (Azapa-Late Intermediate)	3	40	22.5	14	85.7	15	66.7	14	28.6	13	23.1
Azapa-71 (Azapa-Late Intermediate)	3	44	20.5	29	75.9	33	66.7	23	21.7	8	75.0
Azapa-8 (Azapa-Late Intermediate)	3	23	39.1	3	33.3	5	20.0	7	14.3	4	75.0
Playa Miller-4 (Azapa-Late Intermediate)	3	41	17.1	7	71.4	8	62.5	9	0.0	7	57.1
Playa Miller-7 (Azapa-Late Intermediate)	3	49	2.0	10	50.0	6	83.3	13	7.7	16	25.0
Chinchorro (Azapa-Archaic)	3	49	2.0	22	59.1	23	56.5	30	36.7	8	62.5

¹Sample reported by Turner 1985: 67-74.
²Sample reported by Turner 1987: 312-315.
³Sample reported by this study.

Table 3. Maxillary dental trait frequencies for sinodont and sundadont samples.

Population	Dentition	UM ² Hypo		UM ¹ Cusp5		UM ¹ Cara		UM ³ Para		UM ¹ EE	
Amur Basin	1 Sinodont	51	86.3	42	21.4	56	28.6	26	0.0	81	86.4
Northeast Siberia	1 Sinodont	134	80.6	59	3.4	106	17.9	99	1.0	227	79.7
Paleoindian	1 Sinodont	5	100.0	3	33.3	4	100.0	6	16.7	7	57.1
Eskimo	1 Sinodont	257	79.8	182	23.1	211	17.5	219	5.9	416	78.4
Aleut	1 Sinodont	117	68.4	108	12.0	112	6.2	79	6.3	231	68.8
Greater Northwest Coast	1 Sinodont	451	91.8	376	21.3	386	24.9	354	2.8	689	69.7
North American Indian	1 Sinodont	1358	91.7	1161	18.4	1282	35.6	897	4.1	1849	62.2
South American Indian	1 Sinodont	852	92.6	588	13.6	655	41.8	575	6.3	1117	68.5
North China and Mongolia	1 Sinodont	406	90.4	295	28.1	374	30.5	131	9.2	514	51.4
Recent Japan	1 Sinodont	482	86.5	390	19.7	458	31.2	234	1.7	522	54.6
Jomon	1 Sundadont	206	82.0	146	31.5	181	8.3	207	5.3	278	9.7
Hong Kong	1 Sundadont	299	90.3	276	21.7	301	37.5	145	3.4	97	55.7
South China Proper	1 Sundadont	93	86.0	62	16.1	99	25.3	68	4.4	107	59.8
Prehistoric Taiwan	1 Sundadont	27	85.2	9	22.2	15	33.3	18	0.0	28	50.0
Philippines	1 Sundadont	148	83.8	132	27.3	146	37.0	101	1.0	131	40.5
Early Southeast Asia	1 Sundadont	189	93.1	132	37.1	140	37.1	122	4.9	203	25.6
Recent Southeast Asia	1 Sundadont	102	87.3	74	13.5	93	41.9	74	4.1	116	40.5
Recent Thailand	1 Sundadont	196	89.8	143	28.7	179	40.2	128	7.0	166	38.6
Burma	1 Sundadont	95	94.7	72	33.3	93	30.1	68	0.0	126	36.5
Nepal	1 Sundadont	58	86.2	50	32.0	50	26.0	26	7.7	70	27.2
Recent Indo-Malaysia	1 Sundadont	215	91.2	177	36.2	207	46.4	135	6.7	246	36.6
Early Malay Archipelago	1 Sundadont	156	89.1	90	24.4	100	23.0	93	6.5	87	18.4
East Malay Archipelago	1 Sundadont	29	86.2	22	45.5	28	50.0	23	0.0	31	35.5
Chiribaya Alta (Moquegua-Late Intermediate)	3	103	43.7	91	28.6	112	21.4	67	7.5	122	43.4
San Gerónimo (Moquegua-Late Intermediate)	3	38	55.3	28	17.9	36	25.0	28	0.0	34	29.4
La Yaral (Moquegua-Late Intermediate)	3	38	31.6	31	25.8	41	24.4	33	3.0	44	29.5
Ilo Preceamic (Moquegua-Archaic)	3	8	25.0	2	0.0	6	16.7	7	0.0	7	28.6
Alto Ramírez (Azapa-Formative)	3	38	52.6	16	18.8	34	17.6	31	0.0	37	18.9
Azapa-140 (Azapa-Late Intermediate)	3	63	50.8	56	19.6	63	25.4	42	2.4	64	14.1
Azapa-6 (Azapa-Late Intermediate)	3	32	46.9	35	11.4	35	22.9	23	0.0	31	41.9
Azapa-71 (Azapa-Late Intermediate)	3	38	50.0	29	31.0	42	33.3	33	3.0	35	42.9
Azapa-8 (Azapa-Late Intermediate)	3	17	23.5	9	22.2	18	22.2	13	7.7	18	38.9
Playa Miller-4 (Azapa-Late Intermediate)	3	31	25.8	22	18.2	34	41.7	14	0.0	30	50.0
Playa Miller-7 (Azapa-Late Intermediate)	3	37	54.4	34	20.6	40	27.5	16	0.0	38	23.7
Chinchorro (Azapa-Archaic)	3	39	43.6	17	29.4	38	21.1	41	4.9	36	38.9

¹Sample reported by Turner 1985: 67-74.
²Sample reported by Turner 1987: 312-315.
³Sample reported by this study.

Table 3 (continued). Maxillary dental trait frequencies for sinodont and sundadont samples.

<i>Population</i>	<i>Dentition</i>	<i>ULP¹²Odont</i>		<i>UP¹Rt</i>		<i>UM³P/C/A</i>	
Amur Basin	1 Sinodont	39	5.1	103	98.1	95	43.2
Northeast Siberia	1 Sinodont	50	0.0	251	90.8	245	21.6
Paleoindian	1 Sinodont	4	0.0	12	100.0	9	0.0
Eskimo	1 Sinodont	171	6.4	460	95.7	472	20.6
Aleut	1 Sinodont	116	3.4	252	93.3	212	25.9
Greater Northwest Coast	1 Sinodont	368	6.2	684	93.1	566	18.6
North American Indian	1 Sinodont	1181	3.7	1534	85.0	1551	17.5
South American Indian	1 Sinodont	560	5.7	1033	87.2	1096	20.9
North China and Mongolia	1 Sinodont	231	3.9	419	77.1	380	52.9
Recent Japan	1 Sinodont	462	5.0	506	75.1	504	42.1
Jomon	1 Sundadont	260	0.4	241	75.5	338	13.0
Hong Kong	1 Sundadont	314	7.6	113	61.9	238	37.4
South China Proper	1 Sundadont	94	0.0	113	67.3	124	25.0
Prehistoric Taiwan	1 Sundadont	17	0.0	22	81.8	28	14.3
Philippines	1 Sundadont	116	2.6	171	67.8	171	22.8
Early Southeast Asia	1 Sundadont	83	1.2	154	54.5	160	14.4
Recent Southeast Asia	1 Sundadont	63	3.2	119	66.4	125	12.8
Recent Thailand	1 Sundadont	189	4.2	168	66.1	206	18.4
Burma	1 Sundadont	57	1.8	138	65.9	142	17.6
Nepal	1 Sundadont	38	2.6	73	61.6	70	30.0
Recent Indo-Malaysia	1 Sundadont	147	0.7	301	53.8	252	25.4
Early Malay Archipelago	1 Sundadont	120	4.2	62	67.7	104	0.0
East Malay Archipelago	1 Sundadont	25	0.0	30	53.3	32	25.0
Chiribaya Alta (Moquegua-Late Intermediate)	3	372	1.0	130	86.2	123	17.1
San Gerónimo (Moquegua-Late Intermediate)	3	140	1.0	44	81.8	41	22.0
La Yaral (Moquegua-Late Intermediate)	3	146	1.0	42	69.0	42	16.7
Ilo Preceamic (Moquegua-Archaic)	3	37	5.0	14	92.9	10	30.0
Alto Ramírez (Azapa-Formative)	3	124	0.0	51	94.1	59	18.6
Azapa-140 (Azapa-Late Intermediate)	3	242	0.0	53	77.4	72	25.0
Azapa-6 (Azapa-Late Intermediate)	3	85	0.0	32	78.1	39	23.1
Azapa-71 (Azapa-Late Intermediate)	3	99	7.0	41	87.8	48	8.3
Azapa-8 (Azapa-Late Intermediate)	3	64	2.0	16	62.5	22	31.8
Playa Miller-4 (Azapa-Late Intermediate)	3	87	3.0	36	97.2	39	38.5
Playa Miller-7 (Azapa-Late Intermediate)	3	84	4.0	47	97.9	49	32.7
Chinchorro (Azapa - Archaic)	3	122	0.0	58	94.8	62	21.0

¹Sample reported by Turner 1985: 67-74.
²Sample reported by Turner 1987: 312-315.
³Sample reported by this study.

Table 3 (concluded). Maxillary dental trait frequencies for sinodont and sundadont samples.

Population	Dentition	LM ² YPatt		LM ¹ Cusp6		LM ² CNU MB		LM ¹ Proto		LM ¹ Cusp7		LM ¹ Rt		LM ² Rt		LP ¹ Tomes	
		n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Amur Basin	1 Sinodont	54	14.8	43	51.2	51	11.8	52	7.7	53	5.7	71	31.0	74	62.2	36	2.8
Northeast Siberia	1 Sinodont	85	21.2	46	50.0	84	3.6	85	32.9	95	5.3	158	23.4	138	20.3	62	1.6
Paleoindian	1 Sinodont	7	28.6	3	0.0	8	0.0	2	0.0	5	0.0	12	25.0	11	27.3	9	11.1
Eskimo	1 Sinodont	214	20.1	178	39.9	209	3.8	224	16.5	248	12.9	325	26.5	285	33.3	198	3.0
Aleut	1 Sinodont	143	19.6	104	43.3	112	10.7	116	25.9	131	8.4	273	40.7	237	31.2	181	0.6
Greater Northwest Coast	1 Sinodont	401	11.0	406	40.6	471	4.2	450	33.6	467	8.6	730	16.7	647	38.9	485	9.3
North American Indian	1 Sinodont	1631	10.7	1388	49.2	1597	8.1	1679	41.9	1788	10.2	2077	6.7	1672	30.5	1297	13.0
South American Indian	1 Sinodont	805	7.7	545	55.8	779	9.0	786	29.8	852	9.6	1117	6.2	900	38.3	498	2.0
North China and Mongolia	1 Sinodont	338	6.5	211	37.4	258	17.1	332	30.1	341	9.4	406	34.0	358	42.2	94	5.3
Recent Japan	1 Sinodont	352	13.4	314	42.7	345	13.6	353	21.2	382	6.5	426	24.2	407	32.9	200	10.0
Jomon	1 Sundadont	290	32.1	214	46.7	244	28.7	233	13.3	285	5.3	377	3.4	336	9.8	282	3.2
Hong Kong	1 Sundadont	228	7.5	267	33.7	296	24.3	274	21.9	295	8.8	98	18.4	98	36.7	107	14.0
South China Proper	1 Sundadont	80	12.5	60	40.0	77	19.5	85	24.7	85	10.6	100	15.0	92	33.7	47	31.9
Prehistoric Taiwan	1 Sundadont	19	10.5	15	46.7	21	19.0	29	6.9	33	6.1	25	4.0	21	38.1	13	7.7
Philippines	1 Sundadont	123	13.0	98	38.8	122	27.9	122	18.9	129	6.2	126	17.5	121	28.1	62	19.3
Early Southeast Asia	1 Sundadont	187	17.1	136	36.8	163	38.7	171	28.1	217	9.7	237	9.7	165	17.0	84	23.8
Recent Southeast Asia	1 Sundadont	83	15.7	61	27.9	79	31.6	74	13.5	84	7.1	94	17.0	95	29.5	28	25.0
Recent Thailand	1 Sundadont	176	19.3	120	28.3	163	25.8	166	28.3	178	6.2	186	10.8	180	31.1	91	18.7
Burma	1 Sundadont	33	6.1	21	52.4	28	21.4	30	13.3	35	8.6	37	13.5	38	44.7	18	22.3
Nepal	1 Sundadont	30	23.3	21	42.9	28	53.6	33	15.2	34	5.9	36	25.0	34	11.8	9	44.4
Recent Indo-Malaysia	1 Sundadont	142	18.3	97	36.1	134	29.9	124	21.8	137	13.1	178	14.6	168	21.4	88	21.5
Early Malay Archipelago	1 Sundadont	139	19.4	99	45.5	130	24.6	124	12.9	131	4.6	142	6.3	105	33.3	76	18.4
East Malay Archipelago	1 Sundadont	25	20.0	18	38.9	24	45.8	23	8.7	25	4.0	28	14.3	27	29.6	19	36.9
Chiribaya Alta (Moquegua-Late Intermediate)	3	101	28.7	104	45.2	85	3.5	120	58.3	117	17.1	135	3.7	110	20.0	115	7.8
San Gerónimo (Moquegua-Late Intermediate)	3	38	36.8	33	18.2	24	0.0	42	52.4	39	20.5	45	0.0	42	35.7	43	4.7
La Yaral (Moquegua-Late Intermediate)	3	30	26.7	31	41.9	27	0.0	40	62.5	35	45.7	44	6.8	38	34.2	37	2.7
Ilo Preceamic (Moquegua-Archaic)	3	9	44.4	5	40.0	6	0.0	10	30.0	10	0.0	11	0.0	11	18.2	13	15.4
Alto Ramírez (Azapa-Formative)	3	25	28.0	17	35.3	17	0.0	31	16.1	34	2.9	41	0.0	33	6.1	39	5.1
Azapa-140 (Azapa-Late Intermediate)	3	49	8.2	47	34.0	36	11.1	65	43.1	58	10.3	65	0.0	54	18.5	44	13.6
Azapa-6 (Azapa-Late Intermediate)	3	21	47.6	19	52.6	16	18.8	25	28.0	26	11.5	27	0.0	24	25.0	23	17.4
Azapa-71 (Azapa-Late Intermediate)	3	29	24.1	25	44.0	20	20.0	34	47.1	38	18.4	43	0.0	36	19.4	46	17.4
Azapa-8 (Azapa-Late Intermediate)	3	16	12.5	12	50.0	9	0.0	17	29.4	19	10.5	19	0.0	21	14.3	20	10.0
Playa Miller-4 (Azapa-Late Intermediate)	3	17	23.5	17	17.6	14	7.1	20	25.0	21	4.8	21	0.0	20	10.0	20	0.0
Playa Miller-7 (Azapa-Late Intermediate)	3	21	33.3	14	28.6	16	6.2	23	4.3	23	17.4	24	0.0	22	9.1	20	5.0
Chinchorro (Azapa-Archaic)	3	43	41.9	26	34.6	36	0.0	42	7.1	47	6.4	66	1.5	57	8.8	47	2.1

¹Sample reported by Turner 1985: 67-74.
²Sample reported by Turner 1987: 312-315.
³Sample reported by this study.

Table 4. Mandibular dental trait frequencies for sinodont and sundadont samples.

<i>Sample</i>	<i>Classification</i>
Amur Basin	Sinodont
Northeast Siberia	Sinodont
PaleoIndian	Sinodont
Eskimo	Sinodont
Aleut	Sinodont
Greater Northwest Coast	Sinodont
North American Indian	Sinodont
South American Indian	Sinodont
North China & Mongolia	Sundadont
Recent Japan	Sundadont
Jomon	Sundadont
Hong Kong*	Sinodont
South China Proper*	Sinodont
Prehistoric Taiwan	Sundadont
Philippines	Sundadont
Early Southeast Asia	Sundadont
Recent Southeast Asia	Sundadont
Recent Thailand	Sundadont
Burma	Sundadont
Nepal	Sundadont
Recent Indo-Malaysia Archipelago	Sundadont
Prehistoric Malaysia	Sundadont
East Malaysia Archipelago	Sundadont
Chiribaya Alta (Moquegua LIP)	Sinodont
San Gerónimo (Moquegua LIP)	Sinodont
El Yaral (Moquegua LIP)	Sinodont
Ilo Preceamic (Moquegua Archaic)	Sundadont
Alto Ramírez (Azapa Formative)	Sundadont
Azapa-140 (Azapa LIP)	Sundadont
Azapa-6 (Azapa LIP)	Sinodont
Azapa-71 (Azapa LIP)	Sinodont
Azapa-8 (Azapa LIP)	Sundadont
Playa Miller-4 (Azapa LIP)	Sinodont
Playa Miller-7 (Azapa Formative)	Sundadont
Chinchorro (Azapa Archaic)	Sundadont
<i>*Originally classified as sundadont</i>	

Table 5. Discriminant functions analysis of sinodont and sundadont samples assigned using seven "key" dental trait frequencies defined by Turner (1990).

<i>Sample</i>	<i>Dim 1</i>	<i>Dim 2</i>	<i>Dental Profile</i>
Amur Basin	-0.705	-0.697	Sinodont
Northeast Siberia	-1.063	-0.210	Sinodont
Paleoindian	-0.306	-0.198	Sinodont
Eskimo	-1.132	-0.922	Sinodont
Aleut	-0.971	-0.571	Sinodont
Greater Northwest Coast	-1.421	-0.536	Sinodont
North American Indian	-1.447	0.663	Sinodont
South American Indian	-1.793	0.343	Sinodont
North China and Mongolia	0.199	-1.297	Sinodont
Recent Japan	0.598	-1.034	Sinodont
Jomon	1.224	0.922	Sundadont
Hong Kong	0.731	-0.842	Sundadont
South China Proper	0.213	-0.707	Sundadont
Prehistoric Taiwan	0.262	-0.299	Sundadont
Philippines	0.823	-0.211	Sundadont
Early Southeast Asia	1.264	0.294	Sundadont
Recent Southeast Asia	0.555	-0.273	Sundadont
Recent Thailand	1.205	-0.250	Sundadont
Burma	0.836	-0.024	Sundadont
Nepal	0.641	0.072	Sundadont
Recent Indo-Malaysia	1.225	0.099	Sundadont
Early Malay Archipelago	0.866	0.568	Sundadont
East Malay Archipelago	0.609	0.089	Sundadont
Chiribaya Alta (Moquegua LIP)	-0.602	1.110	Sinodont
San Gerónimo (Moquegua LIP)	-0.711	0.423	Sinodont
El Yaral (Moquegua LIP)	-0.655	0.864	Sinodont
Ilo Preceramic (Moquegua Archaic)	-0.005	0.106	Sinodont
Alto Ramírez (Azapa Formative)	0.094	0.457	Sundadont
Azapa-140 (Azapa LIP)	0.143	0.934	Sundadont
Azapa-6 (Azapa LIP)	-0.343	0.123	Sinodont
Azapa-71 (Azapa LIP)	-0.268	0.140	Sinodont
Azapa-8 (Azapa LIP)	0.058	-0.001	Sundadont
Playa Miller-4 (Azapa LIP)	-0.137	-0.080	Sinodont
Playa Miller-7 (Azapa Formative)	0.128	0.533	Sundadont
Chinchorro (Azapa Archaic)	-0.114	0.413	Sinodont

Table 6. Multidimensional scaling scores of sinodont and sundadont samples for the two dimension solution.

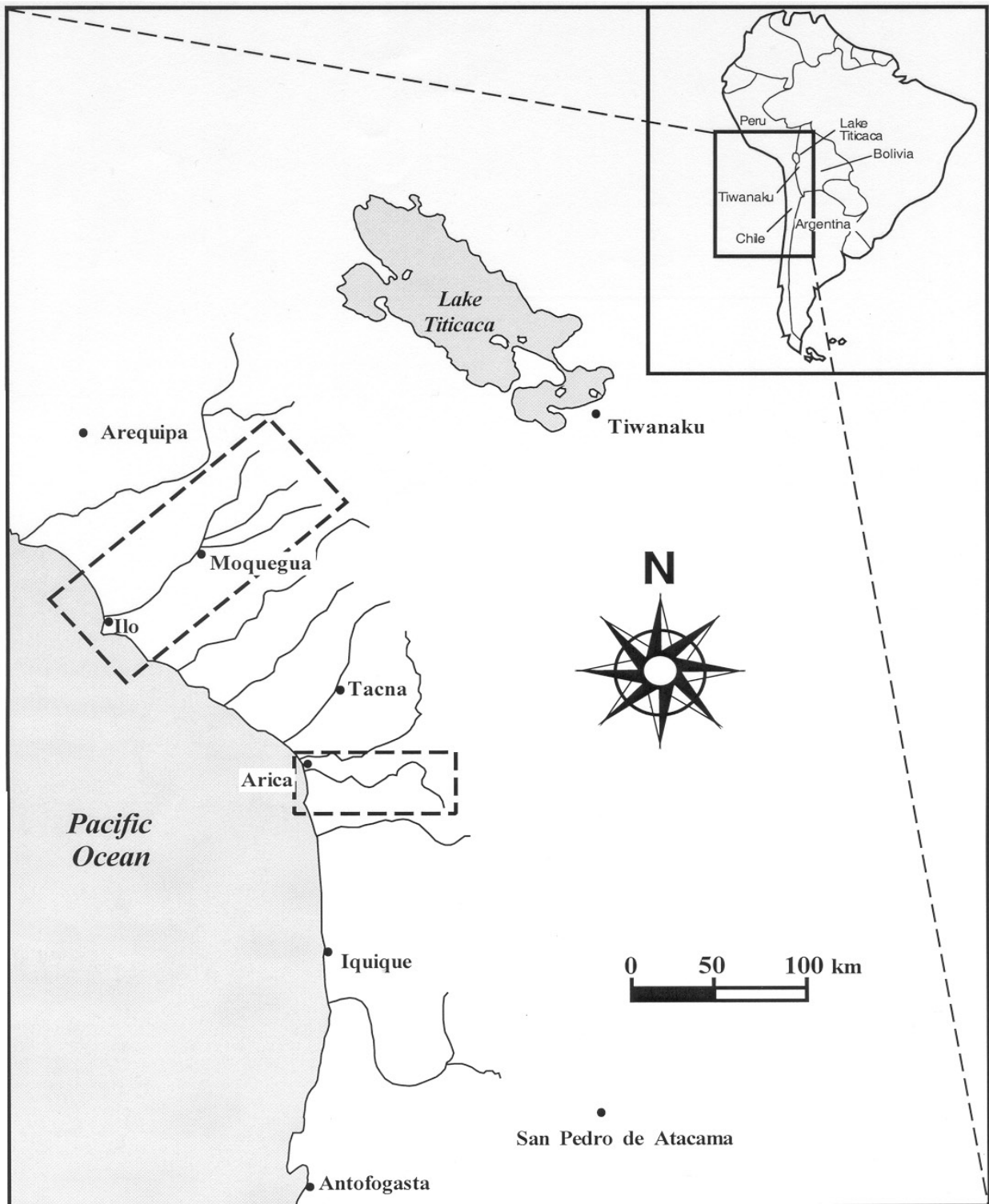


Figure 1. The south central Andes (from Sutter 1997a: figure 1; 2000: figure 1; Sutter and Mertz 2004: figure 1).

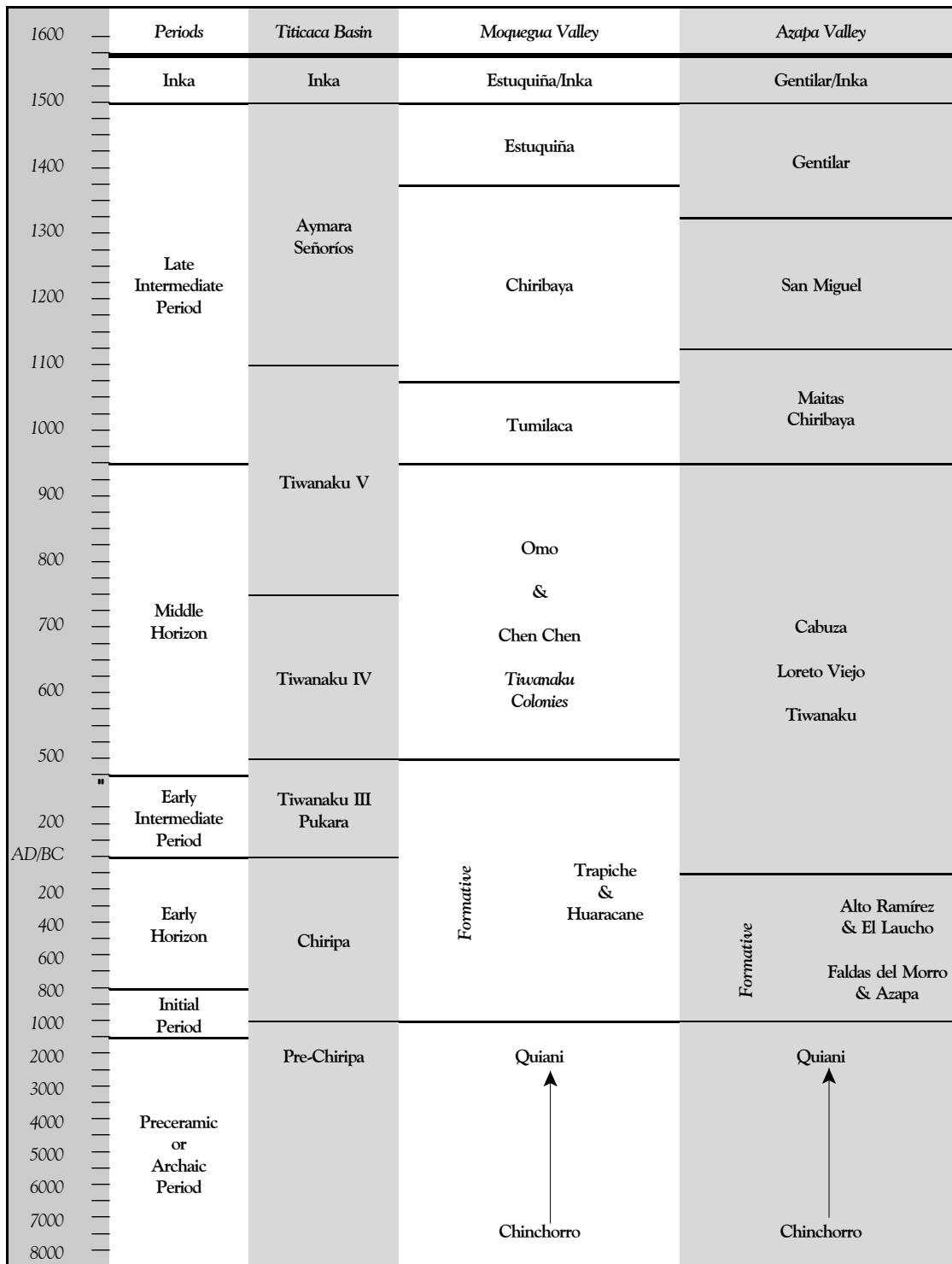


Figure 2. Culture history for select regions of the south central Andes (after Sutter 2000).

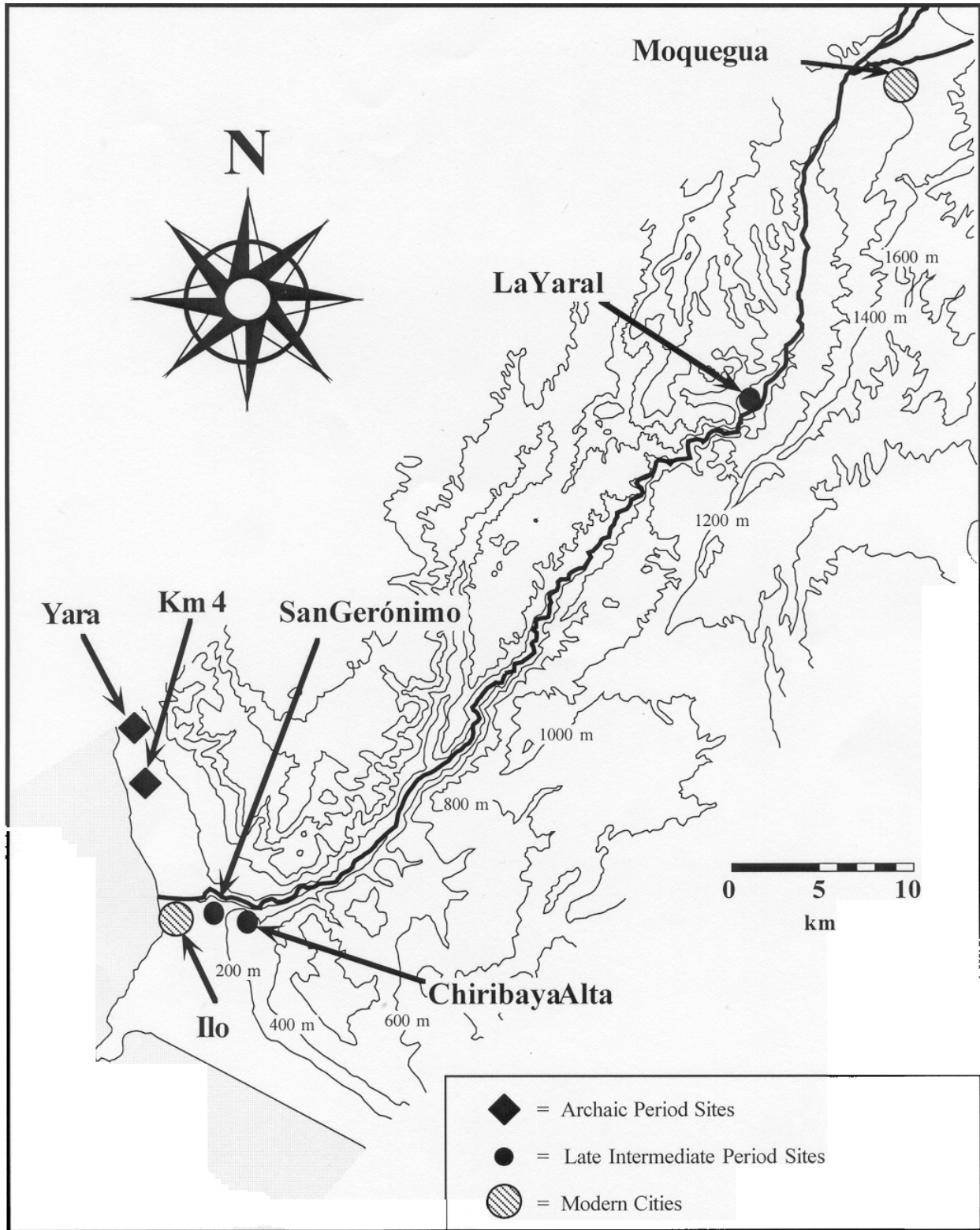


Figure 3. Archaeological sites for the Moquegua Valley mentioned in the text (after Sutter 1997a: Figure 13, 2000: figure 3; Owen 1993:5).

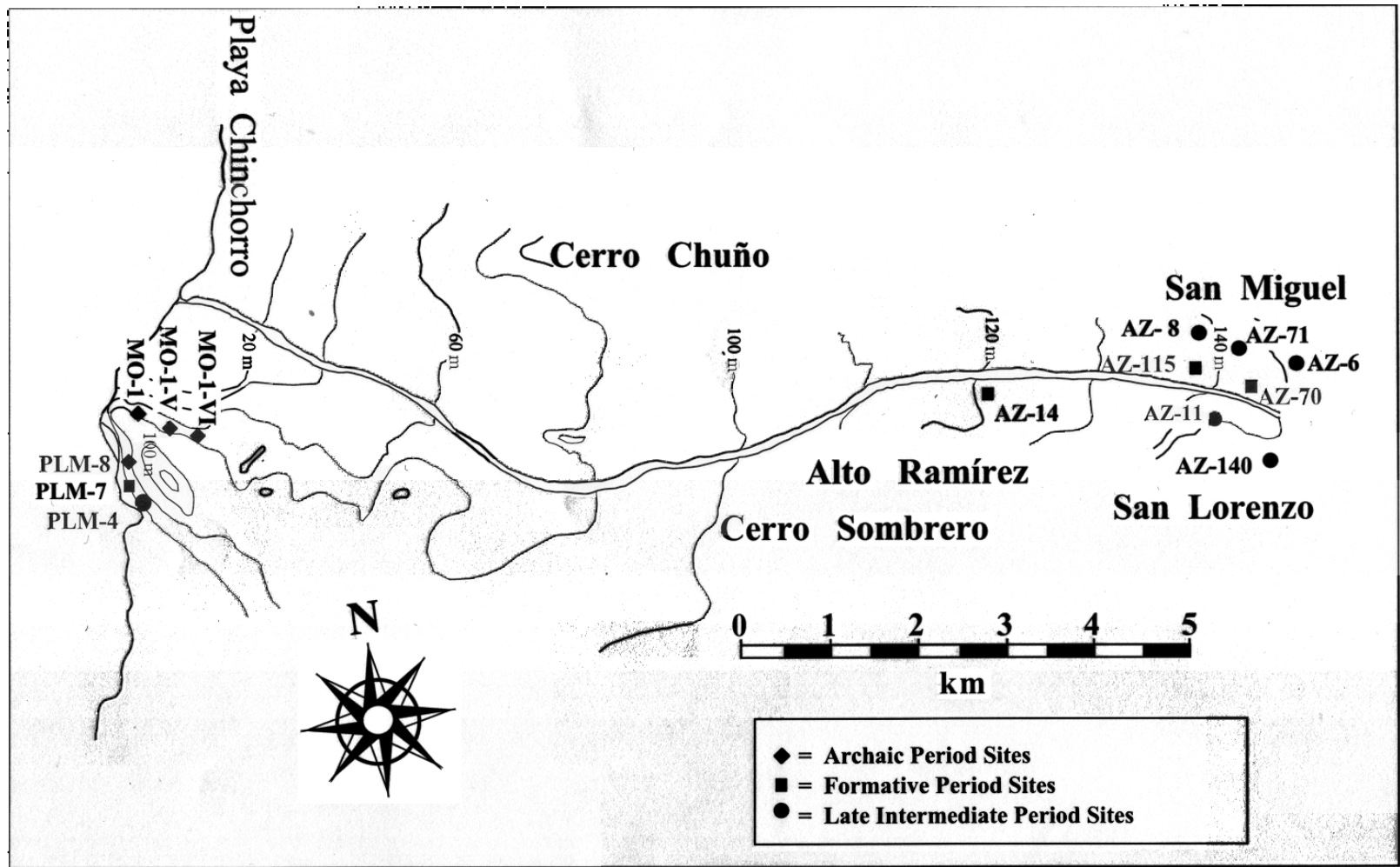


Figure 4. Archaeological sites for the Azapa Valley mentioned in the text (after Sutter 1997a: figure 17, 2000: figure 4; Sutter and Mertz: Figure 2).

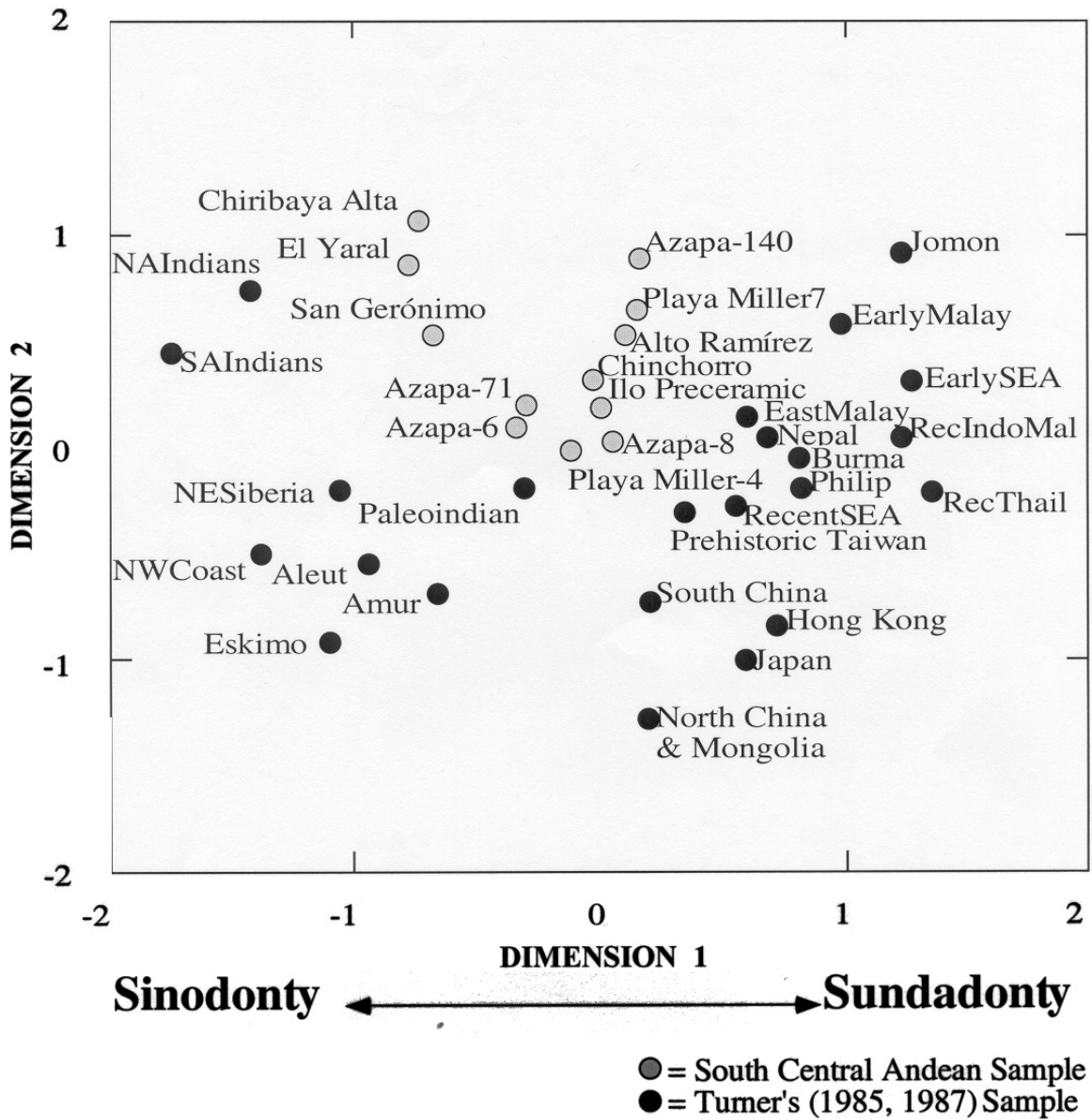


Figure 5. Two-dimensional multidimensional scaling solution of standardized Mean Measure of Distance values for sinodont and sundadont samples. The first dimension discriminates sinodont samples from sundadont samples (from Sutter 1997a: figure 17).

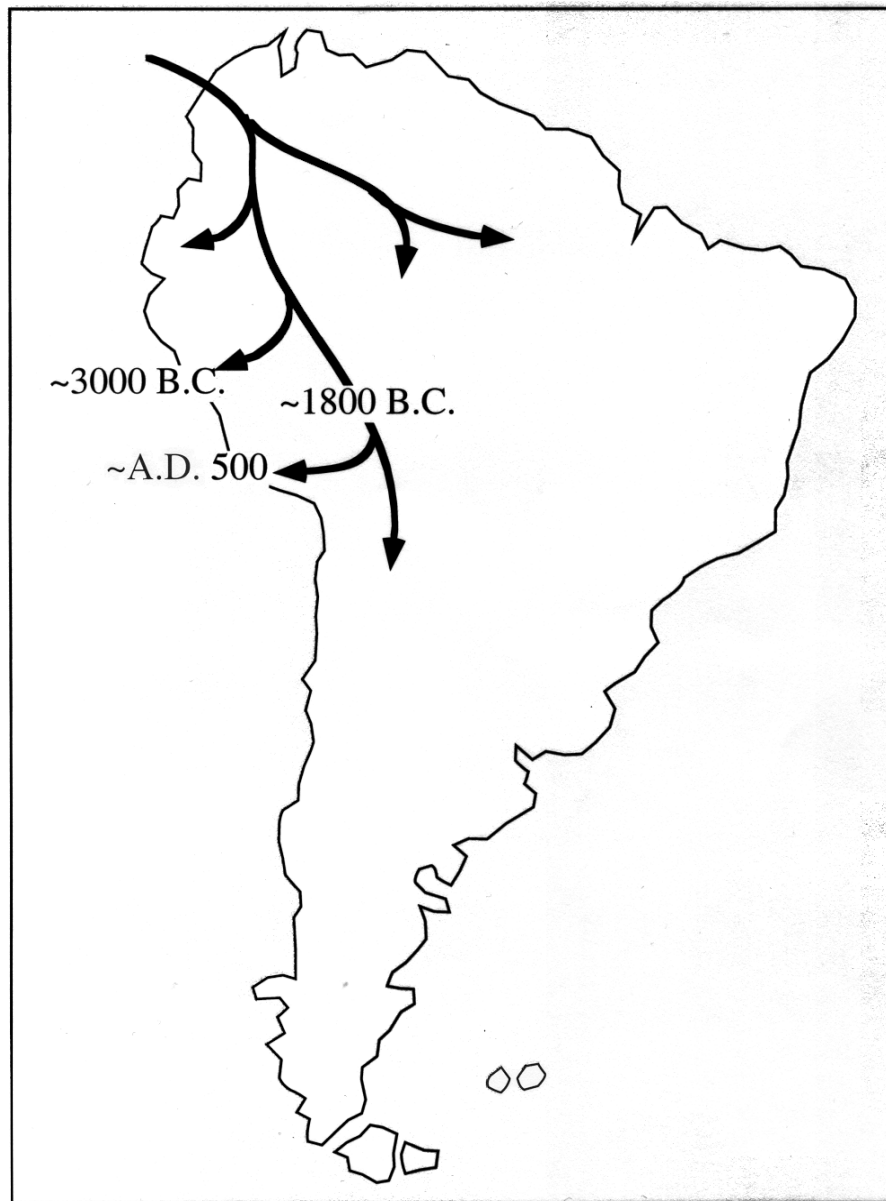


Figure 6. The distribution of four mtDNA haplotypes among extant South Americans (from Merriwether et al. 1995 and Nichols 1995). In general, northern and central Andean populations exhibit high frequencies of haplotypes A and B and low frequencies of haplotypes C and D, whereas southern coastal and Amazonian populations exhibit relatively high frequencies of haplotypes C and D and low frequencies of haplotypes A and B (from Sutter 1997a: figure 20).

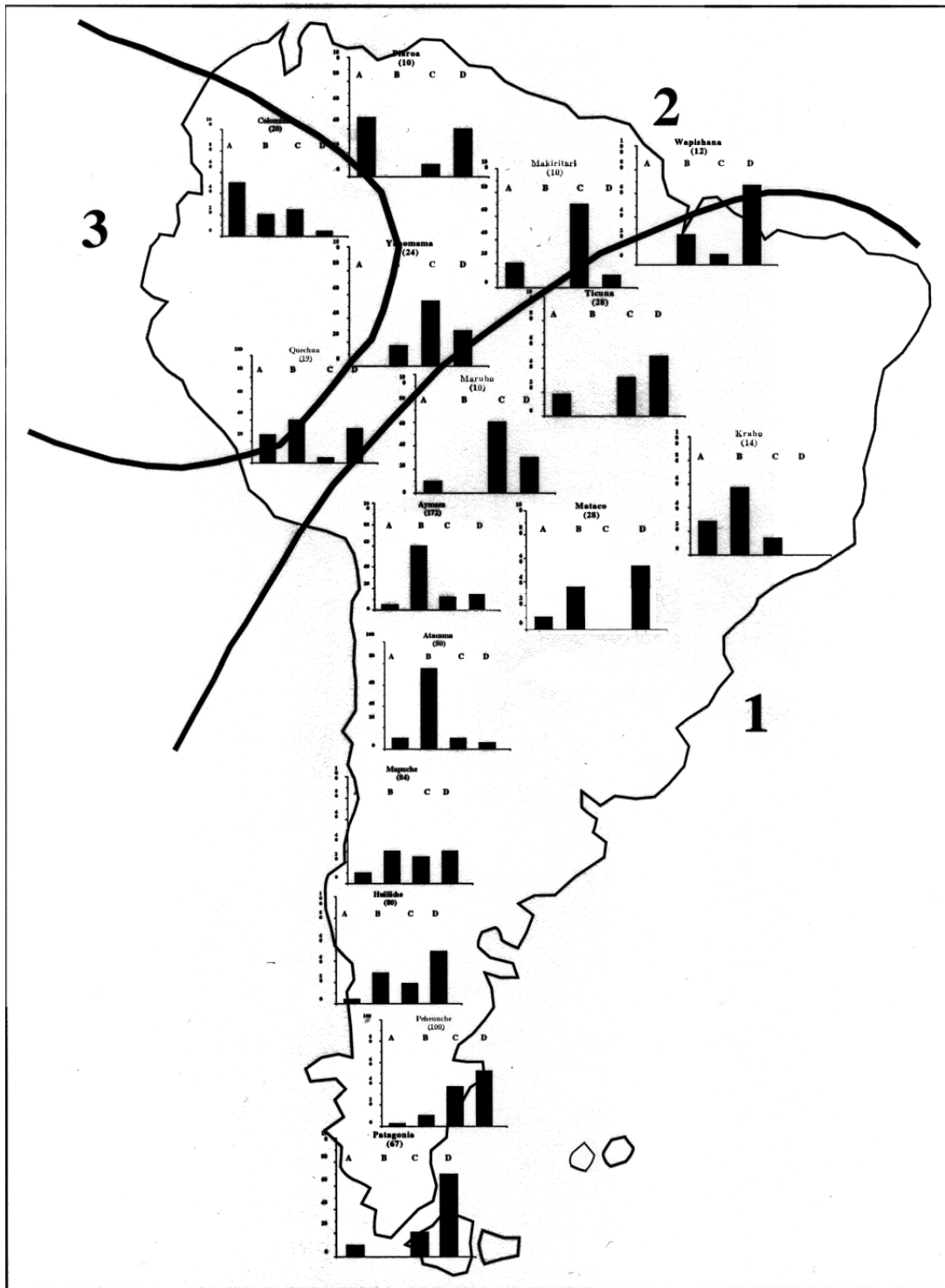


Figure 7. The hypothesized direction of the second demic expansion into South America. According to this scenario, the first migration into South America is represented by the Paleoindians and their descendants. The second demic expansion represents sinodont populations who arrived in northwestern South America through Central America. After arriving in northwestern South America, these sinodont populations expanded from north to south along the Andes through increased fertility and gene flow that accompanied their adoption of agriculture. This hypothesized expansion proceeded from the highlands to the coast and may also have occurred into the tropical lowlands (from Sutter 1997a: Figure 23).