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Context of Maternal Lineages in the Greater Southwest

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ABSTRACT We present mitochondrial haplogroup characterizations of the prehistoric Anasazi of the United States (US) Southwest. These data are part of a long-term project to characterize ancient Great Basin and US Southwest samples for mitochondrial DNA (mtDNA) diversity.

Three restriction site polymorphisms (RSPs) and one length polymorphism identify four common Native American matrilines (A, B, C, and D). The Anasazi (n = 27) are shown to have a moderate frequency of haplogroup A (22%), a high frequency of haplogroup B (56%), and a low frequency of C (15%). Haplogroup D has not yet been detected among the Anasazi.

In comparison to modern Native American groups from the US Southwest, the Anasazi are shown to have a distribution of haplogroups similar to the frequency pattern exhibited by modern Pueblo groups. A principal component analysis also clusters the Anasazi with some modern (Pueblo) Southwestern populations, and away from other modern (Athapaskan speaking) Southwestern populations. The Anasazi are also shown to have a significantly different distribution of the four haplogroups as compared to the eastern Great Basin Great Salt Lake Fremont (n = 32), although both groups cluster together in a principal component analysis.

The context of our data suggests substantial stability within the US Southwest, even in the face of the serious cultural and biological disruption caused by colonization of the region by European settlers. We conclude that although sample numbers are fairly low, ancient DNA (aDNA) data are useful for assessing long-term populational affinities and for discerning regional population structure. Am J Phys Anthropol 113:85–101, 2000.
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Although the large and ecologically heterogeneous region known as the "Greater Southwest" (Fig. 1) has been inhabited by diverse groups of Native Americans for nearly 12,000 years, it was not until the Formative period (ca. 850 AD; Cordell, 1997) that a number of these groups began to floresce and conglomerate. The archaeological traditions associated with this fluorescence (Anasazi, Hohokam, Fremont, and Mogollon) are well-known, and are generally well-defined.

However, basic quantitative data relating to population structure in the region, and to the amount and patterning of genetic variability among these prehistoric cultures, are

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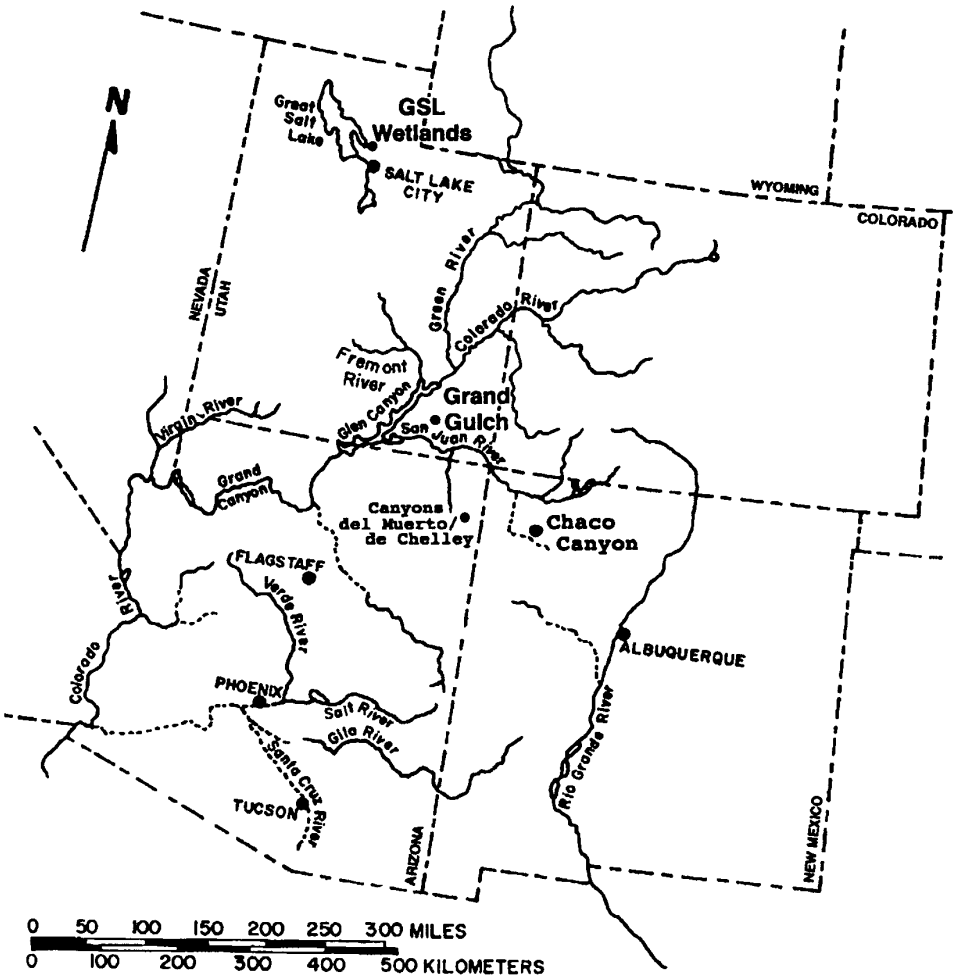

Fig. 1. Map of Greater Southwest. Adapted from Lipe (1983).

lacking (Gumerman and Gell-Mann, 1994; Tainter and Plog, 1994). Further, the context of this genetic variability in antiquity is unclear as compared to modern Southwestern Native American groups now inhabiting the region. To assess such patterning, we contrast molecular genetic data of the ancient Anasazi with the Great Salt Lake (GSL) Fremont, and then compare these data with several modern Southwestern populations.

ANCIENT POPULATIONS OF THE SOUTHWESTERN USA

The Anasazi

The Anasazi are one of four major adaptive traditions in Southwest prehistory, representing the "irreducible minimum of ancestral Puebloan archaeological remains of the Colorado Plateau and Rio Grande Valley" (Dean, 1994, p. 408). The Anasazi are characterized by a long period of archaeo-

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logical continuity (Irwin-Williams, 1973; Haury, 1994a), with sites scattered over five states: Utah, New Mexico, Nevada, Arizona, and Colorado. Anasazi groups are well-known for their commitment to agriculture despite a highly variable and often marginal environment (Gumerman, 1988); corn pollen is ubiquitous at nearly every Anasazi site over the last 2,000 years (Haury, 1994a). In addition to a distinctive pottery style (e.g., Colton, 1958; Hegmon, 1995), the Anasazi archaeological record is typified by complex networks of communication and trade (Toll, 1991; Judge, 1991; Nials, 1983), as well as in domestic (Great Houses) and ceremonial (D-shaped kiva) architecture (Smith, 1990).

The Anasazi are usually identified by site-specific or geographical locale (e.g., "Kayenta Anasazi," "Mesa Verde Anasazi"), but it may also be useful to divide the Anasazi into two general regional variants, the Eastern and Western Anasazi (Cordell, 1979; Plog, 1979; Gumerman and Dean, 1989). This taxonomy mirrors the ethnic division between the modern Eastern and Western Pueblos (Plog, 1979; Eggan, 1950).

Around 1100 AD, the Anasazi began to abandon their large communities (Mesa Verde, Chaco Canyon; Fish et al., 1994; Gumerman and Gell-Mann, 1994; Lekson, 1995; Cordell, 1995), probably dispersing into smaller groups. Archaeological and ethnographic evidence suggests that the modern descendants of the Anasazi are distributed among the various Puebloan groups (Zuni, Jemez, Hopi) who still inhabit the region (e.g., Woodbury, 1979; Sando, 1979).

The Fremont

North of the traditional Anasazi homelands, the US Southwest blends obliquely into the eastern Great Basin, the home of the Fremont. The Fremont have traditionally been defined by contrasting them with the roughly contemporaneous Anasazi cultures further south (Morss, 1931; Steward, 1933; Wormington, 1955; Gunnerson, 1969; Madsen, 1979). Like the Anasazi, Fremont groups practiced maize agriculture, but also relied to a greater degree upon wild foods such as cattail and other locally available resources (Simms, 1986, 1999; Marwitt, 1986). This distinction is tenuous at best, given that most Anasazi groups also heavily exploited local resources (e.g., Sebastian, 1992; Hass and Creamer, 1993).

Fremont groups can be distinguished from the Anasazi by a complex of archaeological traits, including moccasin and pottery style (Fremont "Gray Ware": Madsen, 1977; Jennings, 1978), unique anthropomorphic clay figurines (Morss, 1931; Madsen, 1977), a geographically constrained and drought resistant type of maize ("Fremont Dent": Winter, 1973; Jennings, 1978), and the lack of a formal kiva (Wormington, 1955; Madsen, 1979). The Fremont remained in pit-houses long after Anasazi groups began to live in above-ground structures and probably never developed the complex political and social stratification evidenced at many later Anasazi sites (Frisbie, 1978; Toll, 1991; Sebastian, 1992; Tainter and Plog, 1994).

Based on pottery core areas and a "shared artifact tradition," Fremont groups have been divided into five regional variants (Marwitt, 1970; Jennings, 1978; Madsen, 1979). However, with the exception of one-rod-and-bundle basketry (Adovasio, 1986), there are no traits that are found uniformly across the entire Fremont area (Jennings, 1978). This has led some researchers to doubt that a single "Fremont" cultural entity existed (Madsen, 1979).

The Fremont disappear from the archaeological record at nearly the same time that the Anasazi began to abandon the four corners region (ca. AD 1200–1250: McGuire et al., 1994; Madsen and Simms, 1998). Archaeological and linguistic evidence has been taken to imply that the Fremont were replaced by nomadic Numic speakers (ancestors of modern Ute, Paiute, and Shoshoni) sometime during the mid-fourteenth century (Lamb, 1958; Madsen, 1975; Bettinger and Baumhoff, 1982; Aikens and Witherspoon, 1986). Although the exact nature of the replacement is unclear, it seems unlikely that the historically known populations of the Great Basin are the modern genetic descendants of the Fremont (Marwitt, 1986; Parr, 1998).

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Fremont/Anasazi interaction

Interest in the cultural interaction between the Fremont and Anasazi began as soon as the Fremont culture was described in the early 20th century (Morss, 1931; Steward, 1933). The exact relationship between Anasazi and Fremont populations is obscured by the Mesoamerican cultural influences underlying all Formative Southwest cultures (Irwin-Williams, 1973; Jennings, 1978; Gumerman, 1978; Riley, 1978; Haury, 1994b).

Although Fremont pottery and agricultural technology, for example, are clearly of Southwestern/Mesoamerican derivation (Haury, 1945), few believe that actual Mesoamerican migrants entered central and northern Utah. Aikens (1966) and Reed (1966) observed that ". . . a uniformity of the Fremont physical type [existed] over a large area; [and that] differences from the Southwest physical type argue against any invasion or expansion of a Southwest population into the eastern Basin" (Jennings, 1978, p. 156).

The large number of cultural similarities led many early archaeologists to hypothesize that the Fremont were "splinter" or "northern" Anasazi groups (Morss, 1931; Wormington, 1955; Jennings, 1978). Indeed, the Fremont tradition was most widespread at the time of the Anasazi northward expansion between AD 800–900 (Rohn, 1989; McGuire et al., 1994). The hypothesis that the Fremont are best described as "splinter Anasazi" has yet to be rejected, despite over 60 years of inquiry.

The archaeological boundaries between the cultures have always been unclear. Fremont sites in northern Utah are easily distinguishable from the Anasazi archaeological tradition. However, Fremont sites in southeastern Utah, near the Anasazi/Fremont "border." exhibit striking similarities with Anasazi sites. In some cases the two are nearly indistinguishable (Jennings, 1978; Cordell, 1997; Madsen, 1979).

Despite their geographical proximity and cultural similarities, the amount of gene flow between the two cultures is hypothesized to be low (McGuire et al., 1994). The only substantial evidence of trade between the two areas is the Anasazi black-on-white pottery which begins to appear in some southern Fremont sites after 1050 AD (Jennings, 1978; Rohn, 1989). However, both groups maintained trading contacts with other, non-Great Basin/Southwest populations (Lister, 1978; Blinman and Wilson, 1992; Mathien, 1992; McGuire et al., 1994; Hughes, 1994).

Evidence that there was cultural "friction" between the Anasazi and Fremont comes from the area where the two cultures came into contact (the Colorado River/Glen Canyon area of southeastern Utah). There is widespread evidence of violence and conflict on both sides of the boundary. On the northern frontiers of the interaction zone, a cluster of Fremont sites in south-central Utah (Nawthis Village, Snake Rock Village, and Backhoe Village) exhibit Anasazi-like patterning of scalping, dismemberment, and fracturing of long bones (Novak and Kollmann, 2000; Turner and Turner, 1999). On the southern side of the boundary, evidence of similar violence is widespread in the Grand Gulch/Colorado River region (e.g., Graham Canyon, Sheiks Canyon: Hurst and Turner, 1993; Turner and Turner, 1999), and in the Kayenta region of northern Arizona (Hass and Creamer, 1993). Whether or not this pattern of violence should be connected with events in, or migration from, Mesoamerica is unclear (Turner and Turner, 1999).

The Greater Southwest was undoubtedly an area of both sedentism and migration (Berry, 1982; Gumerman, 1988; Cameron, 1995). If migration was rare or nonexistent between the Fremont and the Anasazi, then the two contiguous groups could develop and maintain separate ethnic identities (as measured by maternal haplogroups), even if they were founded by the same initial population around 2,000 years ago. Alternatively, if mate exchange was common, initial distinctions in founding populations (if they existed) could be obscured, and ethnic boundaries (as measured by maternal haplogroups) would seem not to exist. At the most basic level, we wish to know: 1) if the Anasazi and Fremont can be distinguished from one another using genetic data, and 2) the context of this genetic data in relation to

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other modern Southwestern groups of North America.

MATERIALS AND METHODS

The analysis of Anasazi mtDNA includes nucleic acids derived from both soft and hard tissue samples from several different archaeological sites (Fig. 1): Canyons del Muerto and de Chelley, northeastern Arizona; the Grand Gulch and Colorado River areas, southeastern Utah; and Chaco Canyon, New Mexico. The samples from Canyons del Muerto and de Chelley are usually aligned with the "Kayenta Anasazi."

Anasazi archaeological sites in the southeastern corner of Utah (Grand Gulch/Colorado River areas) represent the extreme northern extension of Anasazi populations, and are usually associated with the "Mesa Verde Anasazi," but are of special note. Some are from "cave seven," the site of Richard Wetherill's original discovery of the deeply buried Basketmaker culture (McNitt, 1966; Hurst and Turner, 1993). They represent some of the earliest examples of Anasazi culture.

The skeletal series that characterizes the northern Fremont was recovered from wetlands near the eastern margin of the Great Salt Lake (GSL), and is associated with the GSL Fremont archaeological tradition (Marwitt, 1970; Simms et al., 1991). The samples provide a temporally and geographically controlled archaeological sample (Simms et al., 1991; Simms, 1999). The Fremont samples have been individually dated by AMS C^{14}, and span an age range of approximately 540 years BP to 1630 BP (Parr et al., 1996). The molecular genetic characterization of the Fremont was reported by Parr et al. (1996) and Parr (1998).

Maternal haplogroups

Previous studies showed that approximately 97% of modern Native Americans fall into one of at least four maternal haplogroups (A, B, C, or D: Schurr et al., 1990; Horai et al., 1993; Torroni and Wallace, 1995; cf. Merriwether and Ferrell, 1996; Easton et al., 1996). The haplogroups are defined by the joint distribution of restriction site marker status (Table 1). Nucleotide pair (np) designations follow those of Anderson et al. (1981). Samples exhibiting the diagnostic markers for two haplogroups (compound haplogroups) are rare, and probably represent very recent back-mutation events, admixture with Caucasian populations, or contamination of aDNA samples (Ward et al., 1991).

TABLE 1. Definition of Native American haplogroups by RSP

Haplogroup	*Hae*III 663	9-bp deletion, region V	*Hinc*II 13259	*Alu*I 5176
A	+	−	+	+
B	−	+	+	+
C	−	−	−	+
D	−	−	+	−

A *Hae*III restriction site at nucleotide pair (np) 663 is associated with haplogroup A. A 9 base pair (bp) deletion in the COII-$tRNA^{Lys}$ intergenic region defines haplogroup B (Wrischnik et al., 1987). Most European derived sequences have a repeat of the 9-bp sequence, while many Asian and Amerind groups are characterized by a deletion of one copy of the 9-bp repeat (Schurr et al., 1990; Shields et al., 1992; Horai, et al. 1993). The absence of a *Hinc*II restriction site at np 13,259 is associated with haplogroup C, while the absence of an *Alu*I restriction site at np 5176 defines haplogroup D. Primer sets (Wrischnik et al., 1987; Vigilant et al., 1989; Ward et al., 1991) used to amplify each mtDNA region containing these markers are given in Table 2.

Recently, a fifth founding haplogroup has been identified. Haplogroup "X" can be defined by the lack of a *Dde*I site at both np 1,715 and np 10,394 (Bailliet et al., 1994; Brown et al., 1998; Smith et al., 1999). Haplogroup X has been found among both modern (Bianchi and Bailliet, 1997; Smith et al., 1999) and ancient (Stone and Stoneking, 1998) Native Americans. Haplogroup X may also be present among the ancient Fremont and Anasazi, although confirmation of its presence in these samples awaits further analyses of relevant markers and hypervariable sequencing. In this report, we report samples that do not fall into one of the four primary lineages as "other."

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TABLE 2. Primer designs used in the current study

Marker	Primer	Sequence (5′–3′)
*Hae*III np 663	L611	ACC TCC TCA AAG CAA TAC ACT G
	H743	GTG CTT GAT GCT TGT TCC TTT TG
*Alu*I np 5176	L5120	TAA CTA CTA CCG CAT TCC TA
	H5230	AAA GCC GGT TAG CGG GGG CA
*Hinc*II np 13259	L13232	CGC CCT TAC ACA AAA TGA CAT CAA
	H13393	TCC TAT TTT TCG AAT ATC TTG TTC
9-bp deletion, set 1	L8215	ACA GTT TCA TGC CCA TCG TC
	H8297	ATG CTA AGT TAG CTT TAC AG
9-bp deletion, set 2	L8267	GGG CCC GTA TTT ACC CTA T
	H8332	GGT GTT GGT TCT CTT AAT CTT

Extraction and amplification

Ancient mtDNA was obtained from two sources. Approximately 0.25 g of ancient tissue sample (Anasazi) was cross-linked with ultraviolet irradiation (254 nm for 10 min; Sarkar and Sommer, 1990), and then washed in a phosphate-buffered saline solution (PBS) prior to the extraction. Bone samples (between 0.5–1 g) were gently crushed and then fully immersed in a 10% bleach solution for 10 min. These procedures served to reduce the amount of external DNA contamination (Parr et al., 1996; O'Rourke et al., 1996).

After the PBS wash, dessicated tissue samples were placed directly into the extraction buffer. Bone fragments were rinsed clean of bleach with sterile H_2O, placed in 0.5 M EDTA for decalcification, and gently agitated for 72 hr. The EDTA was replaced with a new solution every 24 hr. Chelated bone was rinsed clean of EDTA with three sterile H_2O washes, and placed in extraction buffer for 24 hr (Parr et al., 1996). Two milliliters of product were cleaned with a standard phenol/chloroform extraction (Sambrook et al., 1989). Two milliliters of product were spun through Centricon-30 concentrators (Amicon, Inc.), cleaned with saturated ammonium acetate, and ethanol-precipitated (Sambrook et al., 1989; Parr et al., 1996). The concentrated DNA pellet was subsequently dissolved in a 25-μl solution of a modified TBE DNA buffer, and diluted to the desired concentration with DNA buffer. The ratio of dilution is variable, but is usually between 1:5 (1 part sample to 5 parts buffer) to 1:25. Five microliters of the dilution were used as template for a polymerase chain reaction (PCR: Mullis and Faloona, 1987; Saiki et al., 1988). A more detailed extraction protocol may be found in Parr et al. (1996), Parr (1998), and O'Rourke et al. (1996, 1999).

We employ standard PCR protocols (Ward et al., 1991) modified to work optimally for our ancient DNA samples (Parr et al., 1996; O'Rourke et al., 1996, 1999). Restriction site polymorphism screening is carried out with commercially available enzymes, and amplified fragments are visualized on 2–4% NuSieve (FMC Bioproducts, Inc.) gels stained with ethidium bromide.

Contamination control

Perhaps the greatest challenge in aDNA research is not to recover prehistoric nucleic acids, but to demonstrate that they are authentic, and not modern contaminating DNA (Pääbo, 1985; Pääbo et al., 1989a,b; Lindahl, 1993; Stoneking, 1995; Richards et al., 1995). Reproducibility of results is of paramount importance, and redundancy of experiments is standard operating procedure. The results reported here were independently confirmed in separate experiments. We approach contamination on two fronts: 1) the use of strict protocols for prevention of contamination in the laboratory, and 2) identification of contamination when it occurs. All materials used in the extraction and PCR setup are autoclaved and exposed to ultraviolet (UV) radiation (cross-linked at 254 nm for 5 min; Sarkar and Sommer, 1990) immediately prior to PCR preparation. Solutions are prepared in small volumes to avoid multiple use. PCR pipettors are dedicated to ancient DNA analyses, and are not used for applications using modern DNA. In fact, no modern samples are analyzed within our laboratory. Filtered, aerosol-resistant "barrier tips" to pre-

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vent sample crossover are always used. Extraction, PCR preparation, and PCR template production are carried out in three separate rooms. PCR preparation is performed in a controlled environment providing continuous positive (filtered) air flow, and UV irradiation. All working surfaces are regularly washed with bleach, and equipment is wiped down with DNA-Off (CPG, Inc.).

Despite these precautions, contamination occasionally occurs. To identify modern contaminants, multiple controls for the extraction and PCR procedures are always employed. Negative controls (i.e., sterile H_2O and the extraction control in lieu of ancient template) test the reagents and procedures used in the extraction and PCR process for the presence of nonancient DNA. To decrease the probability of crossover contamination from modern DNA, the Anasazi material was not amplified in the presence of a "positive" control.

With the possible exception of the "other" haplotypes, it is unlikely that the results reported here are due to modern contamination. None of the authors possess haplogroups A, B, C, or D, as expected for individuals of European ancestry. It is possible that the "other" haplotype represents modern contamination, even though negative controls should have revealed such problems. However, the low frequencies of the "other" haplotype in both the Anasazi and Fremont and the regular detection of haplogroups A, B, C, and D, as well as the fact that no modern Native American DNA (or European DNA) has ever been analyzed in our laboratory, increase our confidence that the data are authentic. We are currently working to clarify the status of the "other" reported samples by analysis of additional relevant markers (Brown et al., 1998; Smith et al., 1999).

Statistical methods

There are obvious problems associated with the assumption that ancient populations represent "breeding populations" in any real sense. Most archaeological populations cannot be considered true breeding populations because of their disparate temporal and geographic distribution. The Fremont samples encompass a fairly restricted time frame, come from a single geographic locale, and belong to a uniform, well-known, material culture (Simms et al., 1991; Simms, 1999). Dividing the Fremont samples by age does not reveal significant disruptions to the overall distribution of haplogroups: the earliest and latest dated Fremont samples are essentially indistinguishable (Parr et al., 1996; Parr, 1998).

The situation among the Anasazi samples is more complex. The dated Anasazi samples span over 1,500 years, indicating that they are from both the Basketmaker (BM) and Pueblo (P) Anasazi phases. Further, they come from disparate archaeological sites separated by a considerable geographic distance (Fig. 1). Assigning the undated Anasazi samples to a distinct temporal period (such as BMII or PIII) is problematic, as most were collected around the turn of the century, when archaeological standards and record-keeping were often informal. We are currently working to clarify the precise temporal context of each sample.

We analyzed the Anasazi data as a single population not because we are proposing that they are a single population, but rather because this represents the most logical null hypothesis. We recognize the long-standing argument concerning the relationship between the earliest Anasazi (Basketmakers) populations and the more recent (Pueblo) ones. We are also aware of the archaeological and ethnographical evidence indicating a division between the western and eastern Pueblos. As our sample numbers grow, we will be in a better position to either accept or reject the null hypothesis. At this time, then, as a first approximation, treating the Anasazi as a temporal population is both useful and necessary, if somewhat artificial. Any conclusions should be tempered by this realization.

To statistically compare the distribution of the molecular markers under study in multiple samples, we employed Fisher's exact test of homogeneity (Weir, 1990). Unlike a standard chi-square test, Fisher's exact test is less sensitive to problems caused by small sample sizes, or haplogroup values of zero, and does not assume that the distribution of the data follows a chi-square distri-

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TABLE 3. Haplogroup status among the Anasazi

AMNH I.D.	Location	C^{14} date	Haplogroup
H/16403	SE Utah	1,740 ± 60 ybp	B
H/16019	SE Utah	1,010 ± 60 ybp	A
H/16032	SE Utah		C
H/16033	SE Utah		B
99/7362	SE Utah		B
99/7364	SE Utah		Other
99/7336	SE Utah		Other
99/7349	SE Utah		A
99/7712	SE Utah		B
99/9434	SE Utah		A
99/9436	SE Utah		A
99/9437	SE Utah		A
G485	Canyon Del Muerto	1,670 ± 50 ybp	B
99/9600	Canyon Del Muerto		C
99/9608	Canyon Del Muerto		B
99/9610	Canyon Del Muerto		B
99/8476	Canyon Del Muerto		B
99/8477	Canyon Del Muerto		B
99/8478	Canyon Del Muerto		B
99/8480	Canyon Del Muerto		B
99/8483	Canyon Del Muerto		B
H/5805	Chaco Canyon		B
H/15010	Chaco Canyon		C
99/9115	Canyon de Chelley		A
99/9362	Canyon de Chelley		B
99/9368	Canyon de Chelley		C
99/9370	Canyon de Chelley		B

bution (Weir, 1990). The null hypothesis of the Fisher's exact test is that the two subpopulations being compared are from the same (larger) population, or statistical distribution. The test yields the probability (P) that the null hypothesis is correct. Low values of this exact probability imply little chance that the two subpopulations being tested are from the same population, whereas larger values indicate that the two subpopulations are essentially the same.

A principal component analysis was performed using standard methods (Harpending and Jenkins, 1973). The matrix was created using the joint distribution of the frequencies of four haplogroup categories: A, B, C, and D. The principal coordinates were derived from the first two eigenvalues and eigenvectors, using SPSS 5.1, without any additional rotation. The first two principal components explain 72% of the variance observed among the samples.

TABLE 4. Haplogroup vs. marker frequencies among the Anasazi

Haplogroup	Haplogroup %	Marker %
A	22	19
B	56	38
C	15	15
D	0	0
"Other"	7	

RESULTS

Anasazi and Fremont

A total of 27 Anasazi samples can be placed into haplogroups (Table 3), yielding the following haplogroup frequencies: A = 22%, B = 56%, C = 15%, D = 0%, and "other" = 7%. Of 47 Fremont skeltons examined, 32 samples provided sufficient molecular data to make provisional haplogroup assignments. The distribution of the four molecular markers examined in these samples was reported as follows: A = 0%, B = 75%, C = 13%, D = 6%, and "other" = 6% (Parr, 1998).

These frequencies are slightly different from those originally reported (Parr et al., 1996), due to the subsequent clarification of haplogroup status of some Fremont samples. We suspect that the estimated frequency for the B haplogroup is inflated for both populations. If we estimate the frequency of the B haplogroup among the Anasazi, for example, using the total number of samples typed for that single marker site (i.e., the "marker frequency;" data not shown, n = 40), we would estimate the B haplogroup at only 38%. The estimates of the other haplogroups using "marker frequency" are largely unchanged (Table 4). We elected to use "haplogroup frequencies" which are based only on samples for which a haplogroup could be unambiguously assigned. This is the standard way that such data are reported (e.g., Lorenz and Smith, 1996; Torroni et al., 1992), and this approach makes our ancient samples directly comparable to other reported populations.

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TABLE 5. Comparatory populations

Population	N	A	B	C	D	Other	Reference(s)
Western Great Basin[1]	42	7%	33%	2%	52%	5%	Kaestle, 1998
Oneota[1]	108	32%	12%	43%	8%	6%	Stone and Stoneking, 1998
Navajo	58	52%	41%	3%	0%	3%	Lorenz and Smith, 1996; Torroni et al., 1992
Apache	29	62%	17%	14%	7%	0%	Torroni et al., 1993; Lorenz and Smith, 1996
Pima	37	5%	57%	38%	0%	0%	Torroni et al., 1992; Lorenz and Smith, 1996
Zuni	22	18%	64%	9%	0%	9%	Lorenz and Smith, 1996
Quechan/Cocopa	23	0%	65%	30%	0%	4%	Lorenz and Smith, 1996
Jemez	36	0%	86%	3%	3%	8%	Lorenz and Smith, 1996
Fremont[1]	32	0%	75%	13%	6%	6%	Parr, 1998
Anasazi[1]	27	22%	56%	15%	0%	7%	Present study
Northern Paiute/Shoshoni	33	0%	39%	21%	39%	0%	Kaestle, 1998
Washo	28	0%	54%	36%	11%	0%	Lorenz and Smith, 1996

[1] Ancient populations.

Other populations

To provide a context for our ancient samples, we used several ancient and modern Great Basin and Southwest groups for whom comparatory data exist (Table 5). Recently, Kaestle (1998) reported results from two ancient groups which inhabited the Western Great Basin: the Stillwater Marsh and Pyramid Lake samples. The samples range over a similar time frame, ca. 350–2,500 ybp, and come from roughly the same geographic region. The distribution of the haplogroup data between these two western US groups was not significantly different at the $P = 0.05$ level (chi-square test for homogeneity, with Yates' correction; Kaestle, 1998). This, combined with the observation of a similar temporal and geographical distribution, led the author to combine the data to create an ancient "Western Great Basin" group, and we have done the same for our principal component analysis. The sample size of this group is n = 42, with the following frequencies: A = 7%, B = 33%, C = 2%, D = 52%, and "other" = 5% (Kaestle, 1998).

Modern Greater Southwestern groups included for comparison in our principal component analysis span several cultures and languages. Most modern Southwestern Native Americans speak a Southern Athapaskan language, and these are represented by the Apache and Navajo (Swanton, 1969). Numic is the most northerly branch of the Uto-Aztecan language family, and is primarily spoken by Native Americans living in the historical Great Basin (Miller, 1986). Numic speakers are represented here by the Northern Paiute and Shoshoni (Swanton, 1969). The Pima also speak a Uto-Aztecan language (Upper Piman: Miller, 1986). The Quechan (Yuma) speak a Hokan language (Bee, 1983), and while the linguistic classification of the Washo is unclear, they too probably speak a Hokan-related language (Swanton, 1969).

Tribes that the Spanish called "Pueblo" speak several different languages, and they are also represented in the principal component analysis. The Jemez speak Towa, a largely extinct Tanoan language (Sando, 1979), while the Zuni speak a distinct language (Zuni) that has no close correlates (Hale and Harris, 1979; Woodbury, 1979).

As an ancient "outgroup," we utilize the report of Stone and Stoneking (1998) on the Oneota, a pre-Columbian population in central Illinois living approximately 700 years ago. With a sample size of n = 108; they reported the following haplogroup frequencies: A = 32%, B = 12%, C = 43%, D = 8%, and "other" = 6%.

DISCUSSION

The Anasazi samples show a haplogroup distribution that appears to be very similar to that of the Fremont (Fig. 2). They both have high frequencies of B (56% and 75%, respectively); low frequencies of C (15% and 13%, respectively), low to moderate frequencies of A (22% and 0% respectively), and low frequencies of D (0% and 6%, respectively). This distribution places both populations squarely within the "Southwest pattern": modern (Pueblo) populations of the Southwest can be characterized by an absence or

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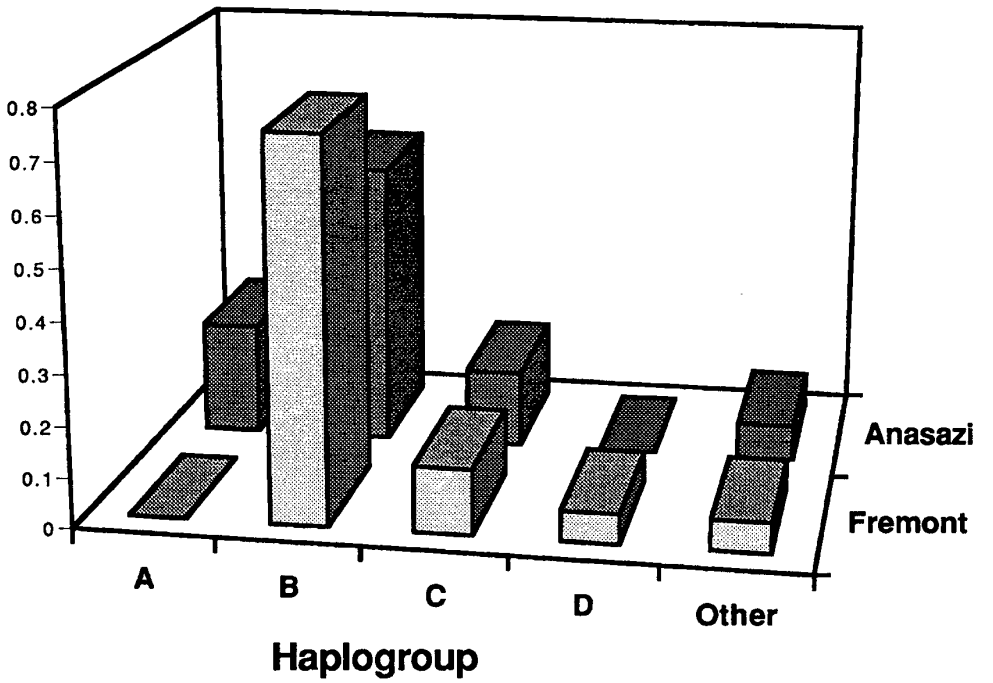

Fig. 2. Anasazi vs. Fremont haplogroup frequencies.

very low frequency of haplogroup A, moderate to high frequencies of haplogroup B, low to moderate frequencies of haplogroup C, and the effective absence of haplogroup D (Lorenz and Smith, 1996).

In a principal component analysis (Fig. 3), both the Fremont and Anasazi cluster near modern Pueblo Southwestern groups, and apart from Athapaskan-speaking groups. Despite these apparent similarities, the overall distribution of haplogroups between the two cultures is significantly different ($P = 0.0264$). This heterogeneity is partially reflected in the fact that the Anasazi and Fremont lack different haplogroups (the *Hae*III RSP defining lineage A is absent in the Fremont, while the *Alu*I marker defining lineage D has so far not been observed among the Anasazi). Another contributing factor is the nearly 20% difference in the frequency of the B haplogroup between the two groups.

These observations should be tempered by the realization that in samples of this size, and spanning these temporal ranges, this dearth may be the result of inadequate sampling. However, with the data presently available, it would appear highly unlikely that the GSL Fremont and Anasazi belonged to the same "Greater Southwest" population. This does not necessarily reject the hypothesis that the Fremont are "northern" or "splinter" Anasazi. It may be that all Anasazi subpopulations or divisions are genetically distinct from one another—but such a conclusion must await further testing of Anasazi subpopulations.

When all populations under study (Table 5) are considered in the principal component analysis (Fig. 3), three general groupings emerge: a Western Great Basin/Northern Paiute/Shoshoni group; an Athapaskan-speaking Southwestern group; and a Pueblo Southwestern group (including the Fremont and Anasazi). The Navajo and Apache data emphasize these populations' origins outside of the US Southwest. As relatively recent Athapaskan speaking migrants to the

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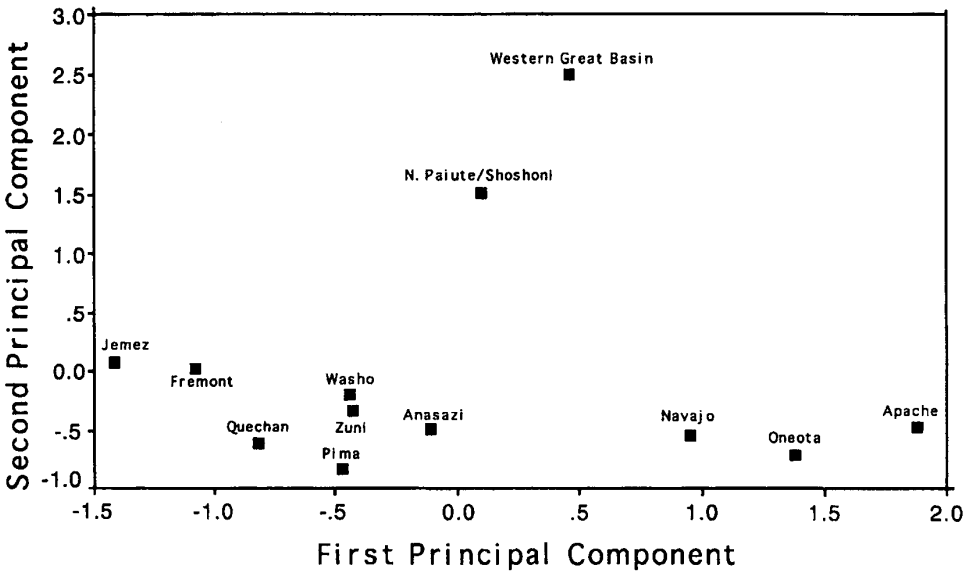

Fig. 3. Principal component analysis.

region (Wilcox, 1981; Towner and Dean, 1996), both the Navajo and Apache are characterized by high frequencies of haplogroup A (52% and 62%, respectively; Torroni et al., 1993; Lorenz and Smith, 1996). The high frequency of this lineage in Southern Athapaskans is hardly surprising, since most Northern Athapasakan groups are nearly fixed for this haplogroup (Torroni et al., 1992).

Lorenz and Smith (1994, 1996) demonstrated that the average frequency of the B lineage is highest among modern Southwestern Amerindian groups, with the frequency typically exceeding 40% (Lorenz and Smith, 1996). Both the Pima (n = 37) and the Zuni (n = 22) have high frequencies of haplogroup B (57% and 64%, respectively; Torroni et al., 1992; Lorenz and Smith, 1996), and this contrasts with the low frequency of the B matriline among modern Athapaskan-speaking groups (Lorenz and Smith, 1996). The deletion is only present at a frequency of 17% among 29 Apache (Torroni et al., 1993; Lorenz and Smith, 1996).

The Anasazi also have a high frequency of haplogroup B (56%), aligning them with modern (Pueblo) populations (Parr, 1998). That the Anasazi share closer genetic affinity with Pueblo and not Athapaskan groups is demonstrated by not only the principal component analysis, but also by tests of statistical significance on the distribution of all four haplogroups combined. For example, the distribution of haplogroups among the Anasazi are significantly different from the Apache (P = 0.0017) and Navajo (P = 0.0213), but much more similar to the Zuni (P = 0.903).

There is evidence of genetic heterogeneity within the ancient Great Basin. The Fremont, an eastern Great Basin group, and the western Great Basin group represented by the Stillwater and Pyramid Lake regions of Nevada, have distinctly different haplogroup distributions (Fisher's exact test, P = 0.0; Fig. 4). This is perhaps surprising, given that both groups inhabited the prehistoric Great Basin at around the same time. However, the principal component analysis (Fig. 3) also clusters the Fremont away from the western Great Basin groups, and nearer to modern Southwest (Pueblo) groups.

Historically, large portions of the Great Basin were inhabited by the Northern Paiute and Shoshoni, including the area around the modern Great Salt Lake. Yet the Fremont are significantly different from

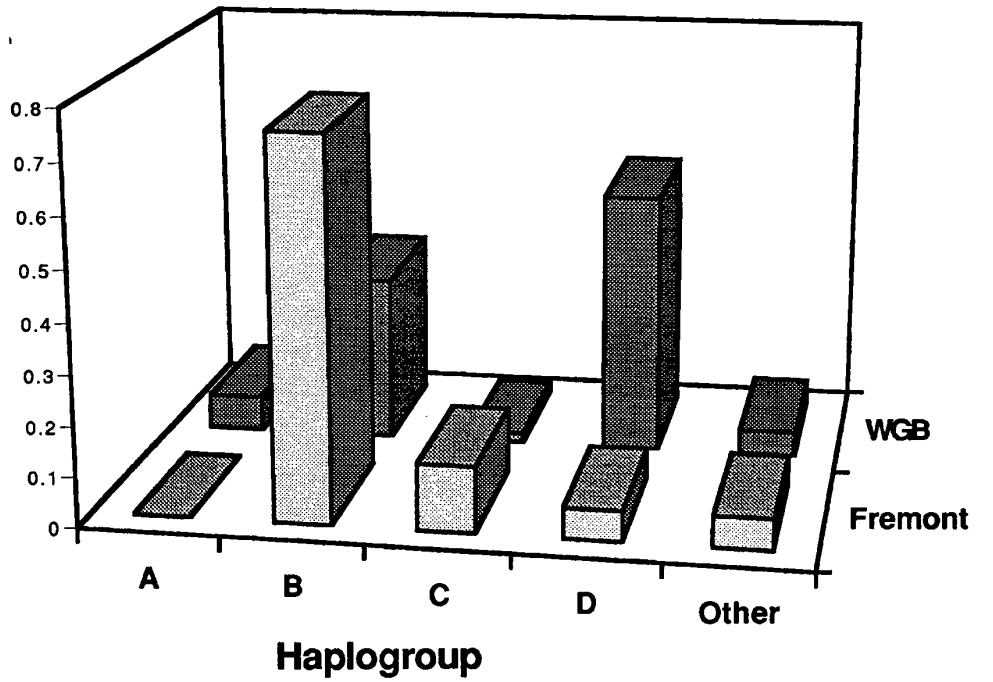

Fig. 4. Western Great Basin vs. Fremont haplogroup frequencies.

these populations (P = 0.0013). This suggests that the skepticism drawn from the ethnographic and archaeological evidence regarding close genetic and cultural affinity between the Fremont and later Numic-speaking populations is well-grounded (Parr, 1998).

Data from the modern Navajo illustrate the usefulness of understanding both the ancient and historical context of the region. The Navajo (n = 58) exhibit the deletion at a frequency of 41% (Lorenz and Smith, 1996). This relatively high frequency of the B matriline is atypical of other Athapaskan groups, but makes sense in light of the historical and ethnographic evidence. The data likely reflect the result of matrilineal gene flow into the Navajo population following nearly 600 years of intermarriage and cultural fusion in the Southwest (Towner and Dean, 1996).

Another interesting aspect of the mtDNA data is the apparent effect of genetic drift. Very few ancient samples possess all four haplogroups. The Anasazi are missing haplogroup D, the Fremont are missing haplogroup A (Parr, 1998), and a fairly large number of South American samples from the Tierra del Fuego/Patagonia region (Fox, 1996) lack both lineages A and B. Haplogroup C is absent from the prehistoric Stillwater Marsh region of the Great Basin (Kaestle, 1998). Lineage extinction, or inadequate sampling through time, seems the norm in these aDNA investigations, although a number of contemporary samples (with much larger sample sizes) also lack one or more haplogroups (Avise et al., 1984; Merriwether et al., 1995). This suggests that the lack of certain haplogroups among our ancient samples may not be due to inadequate sampling alone.

CONCLUSIONS

Handt et al. (1994) suggested that one benchmark for confirming the reliability of aDNA analyses is that the results make phylogenetic sense. The results presented

here for the Anasazi indicate that this criterion has been met. Like modern Southwestern Puebloan groups, the Anasazi show high frequencies of haplogroup B, in combination with low to moderate frequencies of haplogroup A, and the absence of D. This fits well with the vast amounts of ethnographic and archaeological evidence suggesting that the modern Pueblo tribes are the direct genetic descendants of at least some of those Anasazi populations.

The Fremont, whose descendants are unknown, fit this same basic Southwest pattern (Parr, 1998), yet also appear to be fairly unique. The various Numic-speaking groups considered here do not appear to be the descendants of the GSL Fremont, again, a result clearly consistent with traditional historical, ethnographic, and archaeological evidence.

As to the relationship between the Anasazi and Fremont, conclusions must necessarily be tempered by the small sample number and disparate geographic and temporal distribution of Anasazi samples so far analyzed. The data do distinguish the GSL Fremont from the Anasazi. The fact that the Anasazi and Fremont are missing different matrilines may indicate that the effects of local lineage extinction were not eliminated by subsequent gene flow after the proposed founding population(s) settled in their respective areas, a hypothesis also supported by the archaeological evidence (McGuire et al., 1994). One possible scenario is that the Fremont and Anasazi shared a common (perhaps Mesoamerican) ancestral population (Jennings, 1978), but subsequently diverged during the last 2,000 years due to random genetic drift caused by a lack of gene flow between the Great Salt Lake region and Anasazi territory. Data from other Fremont and Anasazi groups, as well as from ancient Mesoamerican samples, are especially needed in order to more fully understand the context of these maternal lineages within the Greater US Southwest.

It should be emphasized that random deviations in both marker and haplogroup frequencies are not unexpected in small populations, as those in the prehistoric United States are likely to have been (Avise et al., 1984). In ancient samples this effect might also be the result of sampling error due to the small number of remains which have yielded amplifiable aDNA. However, many modern North American populations (with larger samples) are also missing one or more haplogroups (e.g., Lorenz and Smith, 1996). It is therefore imperative to increase not only the number of individuals sampled in aDNA studies, but also to increase the number and variety of molecular markers used to infer population history and historical dynamics.

These results begin to define the biological characteristics of ancient populations in the Greater Southwest, and lay the foundation for future tests of archaeological hypotheses. Clearly, patterns of genetic variation in modern populations have been affected by a variety of historical processes (e.g., population decline postcontact, forced population relocations; Crawford, 1998). However, the analyses presented here indicate that over the longer time-frame of the last 2,000 years, regional patterns of genetic variation are identifiable, and appear to be fairly stable in the Southwestern US: the molecular characterization of archaeologically derived skeletal samples are concordant with geographic patterns of genetic variation in modern populations. This demonstrates the utility of aDNA analyses for clarifying issues in population history and evolution.

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