# Investigating the peopling of North America through cladistic analyses of Early Paleoindian projectile points

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## Abstract

The initial colonization of North America remains a controversial topic. There is widespread agreement that Clovis and related cultures of the Early Paleoindian period ($\sim$11,500–10,500 BP) represent the first well-documented indications of human occupation, but considerable differences of opinion exist regarding the origins of these cultures. Here, we report the results of a study in which data from a continent-wide sample of Early Paleoindian projectile points were analyzed with cladistic methods in order to assess competing models of colonization as well as several alternative explanations for the variation among the points, including adaptation to local environmental circumstances, cultural diffusion, and site type effects. The analyses suggest that a rapidly migrating population produced the Early Paleoindian projectile point assemblages. They also suggest that the population in question is unlikely to have entered North America from either the Isthmus of Panama or the Midatlantic region. According to the analyses, the Early Paleoindians are more likely to have entered North America via either the ice-free corridor between the Laurentide and Cordilleran ice sheets that is hypothesized to have opened around 12,000 BP, or the Northwest Coast.
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It is widely accepted that Clovis and related cultures of the Early Paleoindian period ($\sim$11,500–10,500 BP) represent the first well-documented indications of human occupation in North America. However, there is considerable debate regarding the origins of these critically important cultures. The most widely accepted hypothesis for the migra-tion of Early Paleoindians into North America is the overland route or ice-free corridor model. In this model, hunter-gatherer groups migrated to North America via Beringia, the landmass between Siberia and Alaska exposed by sea-level reduction during glacial intervals (Haynes, 1964, 1980, 1982, 2005; Hopkins et al., 1982). Once in eastern Beringia, the groups gained entry to the Great Plains via an ice-free corridor between the Laurentide and Cor-dilleran ice sheets that is hypothesized to have opened soon after 12,000 BP (Catto, 1996; Haynes,

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2005; Prest, 1969, 1984; White et al., 1985; but see Arnold, 2002; Mandryk, 2004; Mandryk et al., 2001). Thereafter, according to this model, the Early Paleoindians spread rapidly throughout North and South America, reaching the Patagonian Plateau within just a few centuries (Fiedel, 2000; Haynes, 1964, 1966, 1980, 1982; Kelly and Todd, 1988; Webb and Rindos, 1997; West, 1983, 1996; Wormington, 1957). The speed with which the Early Paleoindian populations colonized the Americas is generally believed to be the result of high population growth (Martin, 1973; Mosimann and Martin, 1975).

While the ice-free corridor route model remains popular, a number of alternative models have been proposed in light of a number of recently discovered putative pre-Clovis sites (see Fiedel, 2000, 2004), in particular the ~12,500-year-old Monte Verde site in southern Chile (Adovasio and Pedler, 1997; Dillehay, 1989, 1997; Meltzer, 1997; Meltzer et al., 1997), and new evidence suggesting that the ice-free corridor may not have been open or feasible to traverse during the latest Pleistocene (Arnold, 2002; Mandryk, 2004; Mandryk et al., 2001). One of the alternative migratory pathways is along the coast of Alaska, British Columbia, and Washington State (Bryan, 1969, 1977, 1978; Dixon, 1993, 1999, 2001; Fladmark, 1978, 1979; Gruhn, 1988, 1994; Mandryk et al., 2001; but see Surovell, 2003). This model, which is usually referred to as the Northwest Coast model, suggests that maritime-adapted groups using boats moved along the ice-free western coast and sometime later moved east into the interior of the continent (Fladmark, 1979; Dixon, 1993, 1999; Gruhn, 1994). Another possibility that has been highlighted recently is that the Early Paleoindians could have rapidly skirted the western coast of North America and established their first substantial colonies in South America (Anderson and Gillam, 2000). Following the colonization of South America, groups could then have moved northward and populated North America via the Isthmus of Panama. Lastly, a trans-Atlantic voyage from Europe has also been proposed as a possible colonization scenario (Bradley and Stanford, 2004; Stanford and Bradley, 2002; but see Sellet, 1998; Straus, 2000; Straus et al., 2005). Bradley and Stanford (2004), the main proponents of this model, suggest that a number of similarities between Clovis and pre-Clovis technology on the one hand and Solutrean technology on the other indicate a historical connection. They suggest that Solutrean people

left what is now northern Spain, traveled along an "ice bridge" between Europe and North America, and entered North America in the Midatlantic region.

Currently it is difficult to test these competing hypotheses. One problem is that evidence pertaining to the Northwest Coast, Isthmus of Panama, and Midatlantic entry models is difficult to obtain because the post-glacial rise in sea level covered the coasts except were uplift occurred at the same time (Fedje and Christenson, 1999; Josenhans et al., 1997). Another problem concerns the radiocarbon dates associated with sites. The recovery of suitable materials for radiocarbon analysis in association with Early Paleoindian assemblages is a rare occurrence and most of the reliable radiocarbon ages that have been assayed are associated with statistical error ranges that overlap significantly (Barton et al., 2004; Bonnichsen and Will, 1999; Haynes, 1993; Haynes et al., 1984; Levine, 1990; Stanford, 1999; Taylor et al., 1996). Thus, it is not yet possible to use radiocarbon dates to map migration routes as has been done for the spread of the Neolithic in Europe (e.g., Ammerman and Cavalli-Sforza, 1984; Gkiasta et al., 2003).

In the study described here, we tackled the problem of testing the hypothesized migration routes of the Early Paleoindians by applying a technique from biology called cladistics to morphological data derived from assemblages of Early Paleoindian projectile points. We did so on the grounds that the route by which a group of conspecific populations colonized a landmass can be inferred from the historical relationships among the populations, and cladistics is designed to reconstruct historical relationships among populations. In addition, we used cladistic methods to test alternative explanations for the variation among the assemblages, including adaptation to local environmental circumstances, cultural diffusion, and site type effects.

## Cladistics

First presented coherently in the 1950s and 1960s (Hennig, 1965, 1966), cladistics is now the dominant method of phylogenetic reconstruction used in zoology, botany, and paleontology (Brooks and McLennan, 1991; Eldredge and Cracraft, 1980; Kitching et al., 1998; Minelli, 1993; Page and Holmes, 1998; Quicke, 1993; Robson-Brown, 1996; Schuh, 2000; Smith, 1994; Strait and Grine, 2004; Wiley et al., 1991). Based on a model of descent with modifica-

tion in which new taxa arise from the bifurcation of existing ones, cladistics defines phylogenetic relationships in terms of relative recency of common ancestry. Two taxa are deemed to be more closely related to one another than either is to a third taxon if they share a common ancestor that is not also shared by the third taxon. The evidence for exclusive common ancestry is evolutionarily novel or "derived" character states. Two taxa are inferred to share a common ancestor to the exclusion of a third taxon if they exhibit derived character states that are not also exhibited by the third taxon.

In its simplest form, cladistic analysis proceeds via four steps. First, a character state data matrix is generated. This shows the states of the characters exhibited by each taxon. Next, the direction of evolutionary change among the states of each character is established. Several methods have been developed to facilitate this, including communality (Eldredge and Cracraft, 1980), ontogenetic analysis (Nelson, 1978), and stratigraphic sequence analysis (Nelson and Platnick, 1981). Currently the favored method is outgroup analysis (Arnold, 1981; Maddison et al., 1984). Outgroup analysis entails examining a close relative of the study group. When a character occurs in two states among the study group, but only one of the states is found in the outgroup, the principle of parsimony is invoked and the state found only in the study group is deemed to be evolutionarily novel with respect to the outgroup state. Having determined the probable direction of change for the character states, the next step in a cladistic analysis is to construct a branching diagram of relationships for each character. This is done by joining the two most derived taxa by two intersecting lines, and then successively connecting each of the other taxa according to how derived they are. Each group of taxa defined by a set of intersecting lines corresponds to a clade, and the diagram is referred to as a cladogram. The final step in a cladistic analysis is to compile an ensemble cladogram from the character cladograms. Ideally, the distribution of the character states among the taxa will be such that the character cladograms imply relationships among the taxa that are congruent with one another. Normally, however, a number of the character cladograms will suggest relationships that are incompatible. This problem is overcome by generating an ensemble cladogram that is consistent with the largest number of characters and therefore requires the smallest number of ad hoc hypotheses of character change or "homoplasies" to account

for the distribution of character states among the taxa. An example of an ensemble cladogram is shown in Fig. 1.

### Anthropological applications of cladistics

Recently, a number of studies have appeared in which cladistic methods have been applied to linguistic and material culture data in order to shed light on events in prehistory (e.g., Collard and Shennan, 2000; Collard et al., 2006; Foley, 1987; Foley



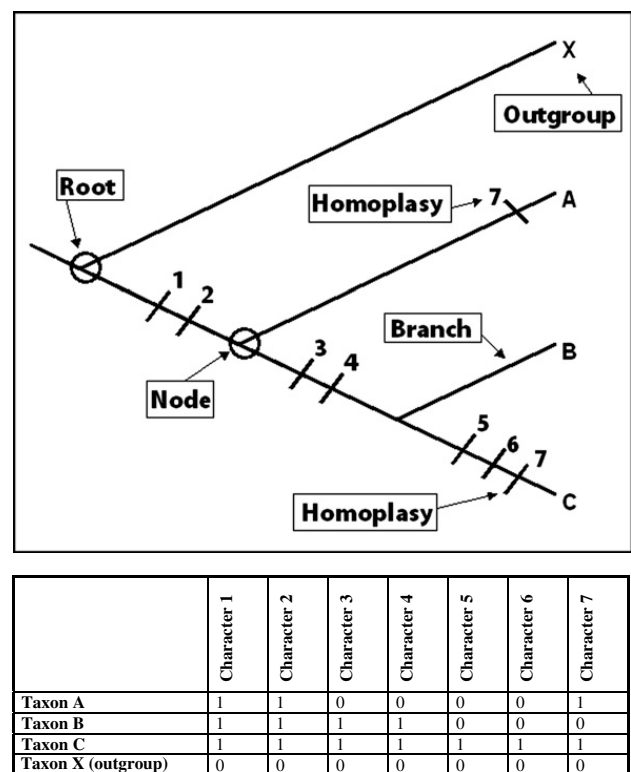| | Character 1 | Character 2 | Character 3 | Character 4 | Character 5 | Character 6 | Character 7 |
|---|---|---|---|---|---|---|---|
| Taxon A | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| Taxon B | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| Taxon C | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Taxon X (outgroup) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Fig. 1. An example of a tree of evolutionary relationships generated via cladistics together with the character state data matrix from which it was derived. Trees of evolutionary relationships generated with cladistics are usually referred to as "cladograms". Cladograms are read from the tips to the root. Thus, the cladogram shown indicates that taxa B and C form a monophyletic group to the exclusion of taxon A based on the shared possession of derived character states for characters 3 and 4. It also suggests that taxa A, B, and C form a monophyletic group based on the shared possession of derived character states for characters 1 and 2. Taxon C is the most derived taxon having derived states for character 5, 6, and 7 in addition to the other derived characters. Character 7 is homoplastic as it is in a derived state in taxa A and C, even though taxa A and C are not directly related through one common ancestor. Two equally parsimonious solutions are available to resolve this character data matrix, in the cladogram shown above taxa B and C are shown more closely related and forming a clade to the exclusion of taxon A. In the second solution taxa A and C form a clade to the exclusion of taxon B.

and Lahr, 1997, 2003; Gray and Jordan, 2000; Holden, 2002; Jordan and Shennan, 2003; O'Brien and Lyman, 2003, 2005; O'Brien et al., 2001, 2002; Rexová et al., 2003; Robson-Brown, 1996; Shennan and Collard, 2005; Tehrani and Collard, 2002). The most significant of these studies for present purposes are those by Gray and Jordan (2000), Holden (2002), O'Brien and colleagues (O'Brien and Lyman, 2003, 2005; O'Brien et al., 2001, 2002), and Jordan and Shennan (2003).

Gray and Jordan (2000) employed cladistic methods to assess the two main competing models regarding prehistory in the Pacific, the "express train" model and the "entangled bank" model. The former suggests a rapid dispersal of Austronesian speakers from a homeland in Taiwan around 6000 years ago through Island Melanesia and into the Polynesian islands of the remote Pacific, whereas the latter contends that the Polynesian colonizers derived from populations in Island Melanesia that had been there for tens of thousands of years. In the entangled bank model, the cultural and linguistic patterns among Polynesians are the complex result of not just their colonization, but also founder's effects associated with original colonization, and the continued cultural contact between different islands during the subsequent millennia, with genetic, linguistic, and cultural traits transmitted at varying intensities between populations. In the entangled bank model linguistic patterns largely reflect human interaction and continued cultural transmission rather than the phylogenetic history of the language speakers described by the express train model. To test these conflicting models, Gray and Jordan (2000) used cladistics to produce a phylogeny of Pacific languages, onto which they then mapped the prehistoric events suggested by the express train model. Gray and Jordan (2000) found a close fit between the stages of the express train model and the branching pattern of their language phylogeny. Significantly, languages that were closely related in the phylogeny were not necessarily close geographically. Gray and Jordan (2000) concluded that these linguistic patterns have resulted predominantly from the colonizing migrations of the language speakers rather than cultural contact since the time of initial colonization.

Holden (2002) conducted a comparable analysis in which she used cladistic analysis to reconstruct the relationships among 75 Bantu and Bantoid African languages from 92 items of basic vocabulary. As in the Polynesian case, some researchers contend that the Bantu languages evolved rapidly during the Neolithic and Iron Age with the colonization of farmers into sub-Saharan Africa, while others hold that the evolution is mainly the result of diffusion of Bantu words among neighboring speech communities. Holden's (2002) analysis returned a relatively small set of possible cladograms, the consensus of which is consistent with the model for the spread of farming in Sub-Saharan Africa constructed by archaeologists through chronological analysis of pottery. Holden (2002) concluded, therefore, that the dispersal and diversification of the Bantu languages was linked to the expansion of farming during the Neolithic and Iron Age, and that since that time Bantu speaking communities have not moved to any great extent.

O'Brien and colleagues (O'Brien and Lyman, 2003, 2005; O'Brien et al., 2001, 2002) focused on points from the southeastern United States. Because the majority of Paleoindian points from this region are surface finds without associated dates, the temporal relationships among point types remain largely unknown and the ordering of types in the region largely has been developed using temporal sequences from other parts of the country (primarily the Plains and Southwest). With this in mind, the primary goal of the analyses conducted by O'Brien and Lyman was to derive phylogenetic hypotheses that would shed light on the evolution of projectile points in the region. O'Brien et al. (2001) began by recording three qualitative and five quantitative characters on a sample of 621 projectile points representing a range of projectile point types, including the well-known Clovis, Dalton, and Cumberland points. They then subjected the specimens to paradigmatic classification in order to cluster them into classes with unique combinations of character states. This resulted in 491 classes. O'Brien et al. discarded classes with less than four specimens in order to minimize the impact of idiosyncratic behaviors. This reduced the number of classes to 17, and it was these that O'Brien et al. used as taxa in their phylogenetic analyses. Thereafter, O'Brien et al. employed occurrence seriation to select an outgroup. Using a custom computer program to search for the fewest steps (in terms of character state changes) in the alignment of 17 taxa, they found 172 optimal solutions (O'Brien et al., 2002). The solution that most commonly rooted one end of the seriation (58% of least-step seriations) was a taxon containing points traditionally referred to as Clovis, Dalton, and Redstone points. Based on this

analysis, O'Brien et al. (2001) chose the Clovis, Dalton, and Redstone taxon as the outgroup. Subsequently, they used a phylogenetic analysis program to search for the shortest possible cladogram. The program identified a single most-parsimonious cladogram with a length of 22 steps. O'Brien et al. (2001) evaluated the fit between the cladogram and the dataset with the Consistency Index (CI). The CI assesses homoplasy as a fraction of character change in relation to a given cladogram. It ranges between 1.0 and 0.0, with values close to 1 indicating a good fit between the cladogram and the dataset and values close to 0 indicating a poor fit. The cladogram obtained by O'Brien et al. (2001) had a CI of 0.59, which suggests that it is a reasonable depiction of the relationships among the projectile point taxa. Subsequently, O'Brien and Lyman (2003) assessed the reliability of the cladogram by increasing and decreasing the number of taxa in their dataset. They found that many of the clades remained intact when taxa were removed, although in the majority of cases multiple most-parsimonious cladograms were found. O'Brien and Lyman (2003) also examined the geographic distribution of the taxa within the two clades featured in the 36-taxa cladogram using state-level provenience data. Based on this distribution they concluded that a center of point experimentation began in the east and moved west over time.

Jordan and Shennan (2003) used cladistics to examine variation in Californian Indian basketry in relation to linguistic affinity and geographic proximity. They carried out three sets of cladistic analyses. In the first, they used the Permutation Tail Probability (PTP) test to determine whether or not their basketry datasets (coiled baskets, twined baskets, all baskets) contain a phylogenetic signal. The PTP test was originally proposed as a method of determining whether or not a given dataset contains a statistically significant phylogenetic signal (Archie, 1989; Faith, 1990; Faith and Cranston, 1991). However, following criticism (e.g., Carpenter, 1992; Steel et al., 1993), it is now generally considered to be a heuristic device rather than a formal statistical test (Kitching et al., 1998). In the PTP test, a dataset is reshuffled multiple times and the length of the most parsimonious cladogram computed after each permutation. Thereafter, the length of the most parsimonious cladogram obtained from the unpermuted data is compared to the distribution of lengths of the most-parsimonious cladograms

yielded by the permutations. If the original cladogram is shorter than 95% or more of the cladograms derived from the permutations, then the dataset is considered to contain a phylogenetic signal. These analyses suggested that a significant phylogenetic signal is present in all three datasets. In the second set of analyses, Jordan and Shennan (2003) used the CI to assess the fit between the datasets and the bifurcating tree model. These analyses suggested that the phylogenetic signal detected by the PTP test is weak. In the third set of analyses, Jordan and Shennan (2003) used the Kishino–Hasegawa (K–H) test (Kishino and Hasegawa, 1989) to assess the fit between the datasets and trees reflecting linguistic relationships, geographic distance, ecological similarity, and adjacency. In this test, cladogram length, the standard deviation of length values, and the $t$ statistic are used to measure the significance of the difference in cladogram-to-dataset fit between the most-parsimonious cladogram and one or more hypothetical cladograms and, where relevant, the difference of fit among the hypothetical cladograms. If the difference in length between any two cladograms is more than 1.96 times the standard deviation, then they are deemed to be significantly different at $p < 0.05$. The K–H test enabled Jordan and Shennan (2003) to distinguish between two different potential sources of homoplasy—independent invention and blending. In an analysis of the complete sample of baskets, the fit between the dataset and the adjacency tree was considerably better than the fit between the dataset and the other trees. This suggests that horizontal cultural transmission had a bigger impact on the distribution of similarities and differences among the basketry assemblages than vertical cultural transmission or adaptation to local environments. In an analysis of just the coiled baskets, horizontal cultural transmission was also found to play a more significant role than branching or adaptation to local environments. The analysis of the twined baskets contrasted with the preceding analyses in that the language cladogram fitted the dataset better than the other cladograms. This suggests that vertical cultural transmission was more important in generating the twined baskets than horizontal cultural transmission or adaptation to local environments. Jordan and Shennan (2003) concluded on the basis of these results, and the results of a range of multivariate analyses, that the evolution of Californian Indian baskets has been dominated by horizontal cultural transmission.

The work of Gray and Jordan (2000), Holden (2002), O'Brien and colleagues (O'Brien and Lyman, 2003, 2005; O'Brien et al., 2001, 2002), Jordan and Shennan (2003) represents an important foundation for the study presented here. Combining aspects of the approaches employed by these authors, we used cladistic methods to reconstruct the relationships among Early Paleoindian projectile point assemblages from across the continent, and then compared the reconstruction with a series of "explanatory" models.

## Character state data matrix

We employed assemblages as taxa to minimize the complexity of the analysis. Four criteria had to be met in order for the projectile points from an assemblage to be included in the study. First, the assemblage had to be reliably dated to the Early Paleoindian period. An assemblage was deemed to fulfill this criterion if it was associated with radiometric dates in the ~11,500–10,500 BP time range, or if it contained diagnostic artifacts that are radiometrically dated to ~11,500–10,500 BP at another site. Second, the diagnostic artifacts in the assemblage had to be restricted to artifacts that are generally agreed to have been produced only in the Early Paleoindian period. Third, the assemblage's points, or casts of its points, had to be available for measurement. Fourth, the assemblage had to contain at least two complete or near complete projectile points. The first and second criteria were employed to minimize the potential confounding effects of temporal mixing; the third and fourth criteria were dictated by the methods used in the study.

Twenty-five assemblages conformed with the selection criteria. Details of the assemblages are given in Table 1. Their locations are shown in Fig. 2. In terms of regional coverage perhaps the most noteworthy omissions are the Far West (the Great Basin and California) and the Southeast. Both of these regions have projectile points that are thought to date to the Early Paleoindian period (e.g., Clovis and Great Basin Stemmed in the Great Basin [Beck and Jones, 1997; Bryan, 1991; Willig, 1991], and Clovis, Cumberland, Redstone, and Quad in the Southeast [O'Brien et al., 2001]). However, at the time of data collection neither region had an assemblage that met all four criteria. Thus, they could not be included in the study.

A total of 216 projectile points were measured. We included all near-complete points that were available for analysis. Casts were used in lieu of original specimens in approximately 17% of cases. Morphometric comparison of a sample of casts and original points revealed no significant differences in form between the casts and the original points (see Buchanan, 2005).

In order to capture the fine details of form variation among the projectile points we employed a new digitizing method (Buchanan, 2005; see also Buchanan et al., in press). Based on recent work in biology (Bookstein, 1982, 1991; Bookstein et al., 1985; Lele and Richtsmeier, 2001; Reyment, 1991; Richtsmeier et al., 2002; Strauss and Bookstein, 1982), this method entails photographing each specimen with a digital camera, and then using a digitizing pad, computer, and a shareware software package called Thin Plate Spline Digitizing Version 2.02 (Rohlf, 2002) to record a series of landmarks around its edges. Thereafter, Euclidean distances between pairs of landmarks that define what are deemed to be key aspects of projectile point form are computed. We elected to use this method rather the conventional caliper-based approach to measuring projectile points because it is both more precise and more accurate. In addition, the digitizing method allows area and other variables that are difficult to record with mechanical measuring devices (e.g., Dibble and Chase, 1981) to be determined relatively easily.

Minor amounts of missing data for mostly complete points (i.e., points missing a basal ear or with minor edge or tip damage) were estimated from the remainder of the data (see Buchanan, 2005). For points with missing portions, digitized positions were left out and missing coordinate data were estimated using the expectation–maximization method of imputation, which uses information about covariation among variables to predict missing values (Strauss et al., 2003).

Eleven interlandmark distances were computed from the Cartesian coordinates of the landmarks. The characters are listed in Table 2 and depicted in Fig. 3. They were designed to capture aspects of width (TW, BL, MW) and length (EL, TB, ML, OL) as well as basal dimensions (BB, LB, BW, LT). The characters were calculated in Matlab 6.0.

Not all researchers accept the use of morphometric characters in cladistic analyses. Before morphometric data are analyzed cladistically, they must be adjusted to minimize the potentially confounding effects of size (e.g., size-related character correlation, allometric convergence), and then converted

Table 1
Projectile point assemblages from Early Paleoindian sites included in the analysis by state or province, region, the number of complete or mostly complete points analyzed in each assemblage, and references

| Site | State or Province | Region[a] | # of points in analysis | References |
|---|---|---|---|---|
| Anzick | MT | NP | 6 | Jones and Bonnichsen, 1994; Lahren and Bonnichsen, 1974; Owsley and Hunt, 2001; Wilke et al., 1991 |
| Blackwater Draw | NM | SP | 24 | Boldurian and Cotter, 1999; Cotter, 1937, 1938; Green, 1963; Haynes, 1995; Hester, 1972; Howard 1935; Montgomery and Dickenson, 1992; Warnica, 1966 |
| Bull Brook | MA | NE | 39 | Byers, 1954, 1955; Grimes, 1979 |
| Bull Brook II | MA | NE | 2 | Grimes et al., 1984 |
| Butler | MI | GL | 4 | Simons, 1997 |
| Cactus Hill | VA | MA | 6 | McAvoy and McAvoy, 1997 |
| Colby | WY | NP | 4 | Frison and Todd, 1986 |
| Debert | NS | NE | 6 | MacDonald, 1966, 1968 |
| Dent | CO | NP | 2 | Brunswig and Fisher, 1993; Figgins, 1933; Haynes et al., 1998 |
| Domebo | OK | SP | 4 | Leonhardy, 1966 |
| Drake | CO | NP | 13 | Stanford and Jodry, 1988 |
| East Wenatchee | WA | NW | 11 | Gramly, 1993; Lyman et al., 1998 |
| Gainey | MI | GL | 11 | Simons et al., 1984, 1987; Simons, 1997 |
| Gault | TX | SP | 2 | Collins and Lohse, 2004; Collins et al., 1992; Hester et al., 1992 |
| Kimmswick | MO | MC | 3 | Graham, 1986; Graham and Kay, 1988; Graham et al., 1981 |
| Lamb | NY | GL | 5 | Gramly, 1999 |
| Lehner | AZ | SW | 10 | Haury et al., 1959; Saunders, 1977 |
| Miami | TX | SP | 3 | Sellards, 1938, 1952; Holliday et al., 1991, 1994 |
| Murray Springs | AZ | SW | 6 | Haynes and Hemmings, 1968; Hemmings, 1970; Huckell, 2007 |
| Naco | AZ | SW | 8 | Haury, 1953 |
| Rummells Maske | IA | MC | 10 | Anderson and Tiffany, 1972; Morrow and Morrow, 2002 |
| Shoop | PA | MA | 14 | Witthoft, 1952; Cox, 1986 |
| Simon | ID | NW | 5 | Butler, 1963; Butler and Fitzwater, 1965; Titmus and Woods, 1991; Woods and Titmus, 1985 |
| Vail | ME | NE | 16 | Gramly and Rutledge, 1981; Gramly, 1982, 1984 |
| Whipple | NH | NE | 2 | Curran, 1984, 1987, 1994 |

[a] Regional abbreviations: GL, Great Lakes; MA, Midatlantic; MC, Midcontinent; NE, Northeast; NP, Northern Plains; NW, Northwest; SP, Southern Plains; SW, Southwest.

into discrete character states with the aid of a coding method (e.g., Chamberlain and Wood, 1987; Collard and Wood, 2000). Opponents of the use of morphometric data in cladistics (e.g., Cranston and Humphries, 1988; Crisp and Weston, 1987; Crowe, 1994; Disotell, 1994; Moore, 1994; Pimentel and Riggins, 1987) argue that measurements are unsuitable for cladistic analysis, and that cladistic analyses based on measurement data are no more than "thinly-disguised" phenetic analyses. They also argue that the coding methods break the spectrum of measurements into artificial character states. However, we contend that these objections are not valid. As Maddison et al. (1984), Felsenstein (1988), Swofford and Olson (1990), Thiele (1993), Lieberman (1995) and, most recently, Rae (1998) have pointed out, there is no intrinsic difference between qualitative and morphometric characters as far as cladistics is concerned. The only criterion a character must fulfill for use in a cladistic analysis

is that its states are homologous, and morphometric characters can meet this criterion as well as qualitative characters (Rae, 1998). The artificiality argument can also be easily refuted, for coding is no more artificial than is the decision to break up into discontinuous states what is, with few exceptions, continuously distributed morphology. Lastly, it is difficult to understand the argument that cladistic analyses based on morphometric data are just phenetic analyses in disguise, because unlike phenetic analysis, morphometrics-based cladistics does not group taxa on the basis of overall similarity. In cladistic analyses of morphometric data, as in cladistic analyses of qualitative data, only those parts of the phenotype that are inferred to be shared derived are used to group taxa into clades.

The 11 characters were transformed to "size-free" residuals by regressing each character on the first principal component derived from all the characters (Reis et al., 1990; Strauss, 1985). The first

Fig. 2. Distribution of Early Paleoindian sites with projectile point assemblages used in the cladistic analysis.

principal component is a metavariable that expresses the multidimensional quality of size (Bookstein, 1982; Rohlf and Bookstein, 1987) and, therefore, is used as the generalized size estimate in the regression (Reis et al., 1990; Strauss, 1985). Although ratio-based size-adjustment methods (e.g., dividing each character by the geometric mean of all the characters) are commonly used in biological anthropology (e.g., Collard and Wood, 2000; Jungers et al., 1995; Lycett and Collard, 2005; Smith, 2005), these methods do not account for allometric (size related shape) differences. An earlier study indicated that the projectile point data exhibit considerable allometric variation (Buchanan, 2005). Thus, the regression-based method was deemed to be more appropriate than the ratio-based methods.

The size-corrected data were converted into discrete character states with Thiele's (1993) gap-weighting method. This method uses the following formula to compute range-standardized data:

$$xs = (x - \min / \max - \min) * n$$

where $x$ is the assemblage mean for a character and $n$ is the maximum number of ordered states allowable in the cladistic analysis program. The gap-weighting method retains the rank order of states and the sizes of gaps between states when characters are treated as multistate and ordered for analysis. Twenty-six possible character states were employed since this is the maximum allowed by the programs used in the study, PAUP* 4.0 (Swofford, 1998) and Mesquite 1.06 (Maddison and Maddison, 2005).

In addition to the 11 morphometric characters, we included four qualitative characters deemed important by O'Brien et al. (2001) to describe Early Paleoindian projectile point variation:

*Overall base shape.* A qualitative assessment of the shape of the basal indentation. Character states: 1 = Arc-shaped, 2 = Normal curve, 3 = Triangular, 4 = Folsomoid, 5 = Square.

*Outer tang angle.* The degree of tang (or basal ear) expansion from the short axis of a specimen. Character states: 1 = 116–135+°, 2 = 93–115°, 3 = 88–92°, 4 = 81–87°, 5 = 66–80°, 6 = 51–65°, and 7 = <50°.

*Tang-tip shape.* The shape of the tip ends of tangs (or basal ears). Character states: 1 = Pointed, 2 = Round, and 3 = Blunt.

*Fluting.* The removal of one or more large flakes (≥1 cm long) from the base of a specimen and

Table 2
Characters used in morphometric analyses of projectile points

| Characters | Description |
| --- | --- |
| EL | Average of right and left edge boundary lengths. Edge boundary length is calculated as the sum of interlandmark distances along the 13 landmarks that define each edge |
| TB | Average of the right and left distances from the tip landmark to each of the basal landmarks |
| TW | Average of the right and left distances between the tip landmark to basal landmark segments (character TB) to the position of the maximum edge inflection along each projectile point edge |
| BL | Average of the right and left distances between the position of the maximum edge inflection and the tip landmark |
| MW | Average of the right and left distances between the positions of the maximum edge inflections to the midline (character ML) |
| BB | Base boundary length. Calculated as the sum of the interlandmark distances along the nine landmarks that define the basal concavity situated between the two basal landmarks |
| LB | Base linear length. Calculated as the distance between the two basal landmarks |
| ML | Midline length. Calculated as the distance from the tip landmark to the midpoint of the basal concavity (character BB) |
| OL | Overall length. Calculated as the distance from the tip landmark to the midpoint of the segment between the basal landmarks (character LB) |
| BW | Basal width at one-third the total length above the basal landmarks |
| LT | Average of the right and left distances from basal landmarks to the position at one-third the total length along the opposite edge boundaries |
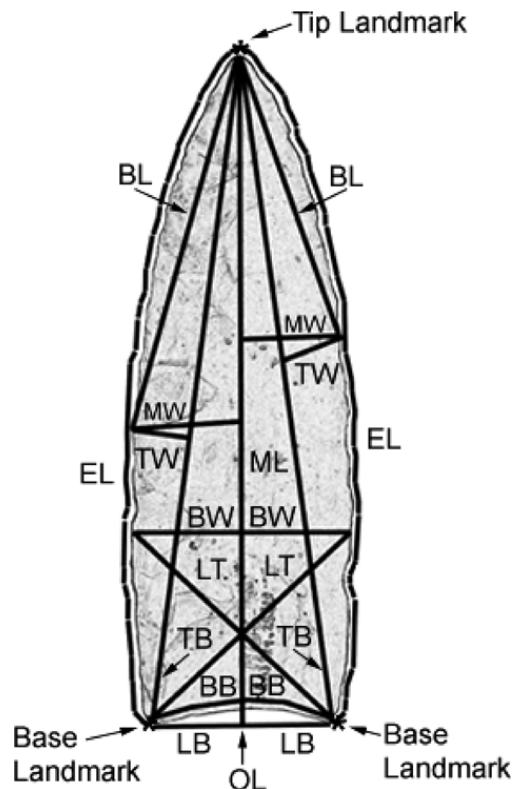
Fig. 3. Image of Clovis point showing approximate location where 11 interlandmark characters are measured and the location of the three landmarks. Character initials: EL, edge boundary length; TB, tip landmark to base landmark; TW, width of tip to base length to maximum inflection position; BL, blade length; MW, maximum width; BB, base boundary length; LB, linear measure of base; ML, midline length; OL, overall length; BW, basal width across first third of point; LT, length from base to 1/3 along opposite edge.

parallel to its long axis. Character states: 1 = Absent and 2 = Present.

For the character "overall base shape" we added a fifth state (square base), and for the character "outer tang angle" we added an extra bin (116−135+°) in order to encompass the variation in our sample of points. Because our analysis focused on assemblages, we coded characters as polymorphic when two or more states were represented for a given qualitative character within an assemblage. For example, the base shape character was coded as polymorphic for the Anzick assemblage because the assemblage contains points with arc-shaped, normal curve, triangular, and square bases.

## Analyses

Once the character state data matrix was compiled, it was subjected to a parsimony analysis in order to identify the cladogram or set of cladograms that fits it most parsimoniously. We treated the 11 morphometric characters as linearly ordered and freely reversing (Chamberlain and Wood, 1987; Collard and Wood, 2000; Thiele, 1993). We also treated one of the qualitative characters, outer tang angle, in the same manner. Ordered characters are only allowed to change in single steps forward or backward along the character transformation series (Kitching et al., 1998). Thus, for example, a change from state 1 to state 2 entails only one step, whereas a change from state 1 to state 6 involves five steps. We dealt with the 11 morphometric characters and outer tang angle in this way because it is likely that in order for each of them to have changed from small to large, or vice versa, they would have passed through medium-sized (cf. Collard and Wood, 2000). We treated three of the four qualitative characters (base shape, tang-tip shape, and presence of fluting) as unordered (transformation between any two states entails the same cost). Our approach to outgroup selection differed from the approach employed by O'Brien et al. (2001). Rather than using occurrence seriation, we selected an outgroup based on the published radiocarbon assays associated with the assemblages. Considerations of the reliability of the dates (e.g., Bonnichsen and Will, 1999; Haynes et al., 1984; Levine, 1990; Taylor et al., 1996) suggest that, when error ranges are taken into account, the assemblage from Blackwater Draw, New Mexico has the oldest reliable age of the assemblages. It should be noted that the use of Blackwater Draw as an outgroup does not imply that this site represents the initial source of a colonizing population for the Americas. It simply implies that, because of its early age, Blackwater Draw retains the most ancestral character states of the assemblages in the study. The branch-and-bound search routine of PAUP* 4.0 was used to analyze the character state data matrix. The branch-and-bound search routine is one of several approaches to parsimony analysis that PAUP* 4.0 offers; it is guaranteed to find the most parsimonious cladogram(s).

In order to assess the fit between the most parsimonious cladograms and the projectile point dataset, three analyses were carried out. The first employed the PTP test. The test was carried out in PAUP* 4.0, and the dataset was reshuffled 10,000 times. The second employed the Retention Index (RI). The RI measures the number of similarities in a dataset that are retained as homologies in

relation to a given cladogram. The RI is insensitive to the presence of derived character states that are present in only a single taxon, or "autapomorphies". The RI is also insensitive to the number of characters or taxa employed, and therefore can be compared among studies (Hauser and Boyajian, 1997; Sanderson and Donoghue, 1989). Accordingly, RIs for the most parsimonious cladograms were calculated and compared to RIs for 21 biological and 21 cultural datasets reported by Collard et al. (2006). The third fit-assessment analysis focused on the CI. Sanderson and Donoghue (1989) and Hauser and Boyajian (1997) have shown that there is a significant inverse relationship between the CI and the number of taxa included in an analysis. This means that it is not possible to simply compare CIs among studies, and that the significance of the CI for a given cladogram has to be assessed relative to the CI that is expected for a cladogram with the same number of taxa (Sanderson and Donoghue, 1989). Accordingly, the CI for the most-parsimonious projectile point cladograms was compared to the expected CI for a 25-taxa dataset. The expected CI was computed with the aid of a regression equation that Sanderson and Donoghue (1989) derived from a taxonomically diverse set of datasets.

In order to evaluate the robustness of support for the branches of the cladograms yielded by the parsimony analysis we employed a technique called bootstrapping. In phylogenetics, bootstrapping was originally developed as a way of estimating the statistical likelihood of a given clade being real (Felsenstein, 1985). However, following several recent critiques (e.g., Carpenter, 1992; Kluge and Wolf, 1993), it is now considered by many researchers to be a heuristic tool rather than a statistical test (Kitching et al., 1998; but see Sanderson, 1995). In bootstrapping, a large number of subsets of data (normally 1000–10,000) are randomly sampled with replacement from the character state dataset, with the character state assignments being retained in each sample. Minimum length cladograms are then computed from these subsets of the data, and a list of the clades that comprise the cladograms compiled. Thereafter the percentage of the resampled cladograms in which each clade was found is calculated. Datasets that fit the bifurcating model with little conflicting signal will return high bootstrap support percentages, and vice versa. The bootstrap analysis was carried out in PAUP* 4.0. One thousand iterations were conducted, and the consensus cladogram was computed using a confidence region of 50% (cf. Holden, 2002).

Next, following Jordan and Shennan (2003), the K–H test was used to evaluate several hypotheses that potentially account for the morphological variation among the projectile point assemblages (see above for a description of the K–H test). The site type hypothesis avers that variation in the primary activities carried out at the sites from which the projectile point assemblages are derived is the dominant influence on interassemblage variation in point shape. Three site types are represented among the assemblages. Anzick, East Wenatchee, Drake, Lamb, Rummells Maske, and Simon are caches, while Blackwater Draw, Colby, Dent, Domebo, Kimmswick, Lehner, Miami, Murray Springs, and Naco are inferred to be kill sites, and Bull Brook I and II, Butler, Cactus Hill, Debert, Gainey, Gault, Shoop, Vail, and Whipple are considered to be habitation sites. Accordingly, an "explanatory" cladogram was constructed that had three clades, each of which comprised all the assemblages of a given site type (Fig. 4).

The cultural diffusion hypothesis posits that technological attributes horizontally transmitted among neighboring groups will result in a correlation of projectile point shape with geographic distance (Guglielmino et al., 1995; Jordan and Shennan, 2003; Shennan and Collard, 2005). Accordingly, cladograms representing the cultural diffusion hypothesis were constructed on the basis of geographic proximity using straight-line distances between sites measured in ArcView GIS 3.2a and on the basis of inter-site great-circle arcs (the shortest distance between two sites on the surface of the earth) (Buchanan, 2005). The latter were calculated from the latitude and longitude coordinates for each site. The ArcView distances and great-circle arcs produced an identical cladogram topology (Fig. 5).

The environmental adaptation hypothesis predicts that point assemblages within particular environments will contain similarly shaped projectile points because hunters within each region will tend to adapt their points to the size, shape, and habits of the fauna within each region. Three "explanatory" cladograms were constructed to test the environmental adaptation hypothesis. First, assemblages were grouped by environmental region (Table 3). These regions were defined on the basis of Adams and Faure's (1997) and Steele et al.'s (1998) reconstructions of North American vegetation during the Late Pleistocene. This "explanatory" cladogram
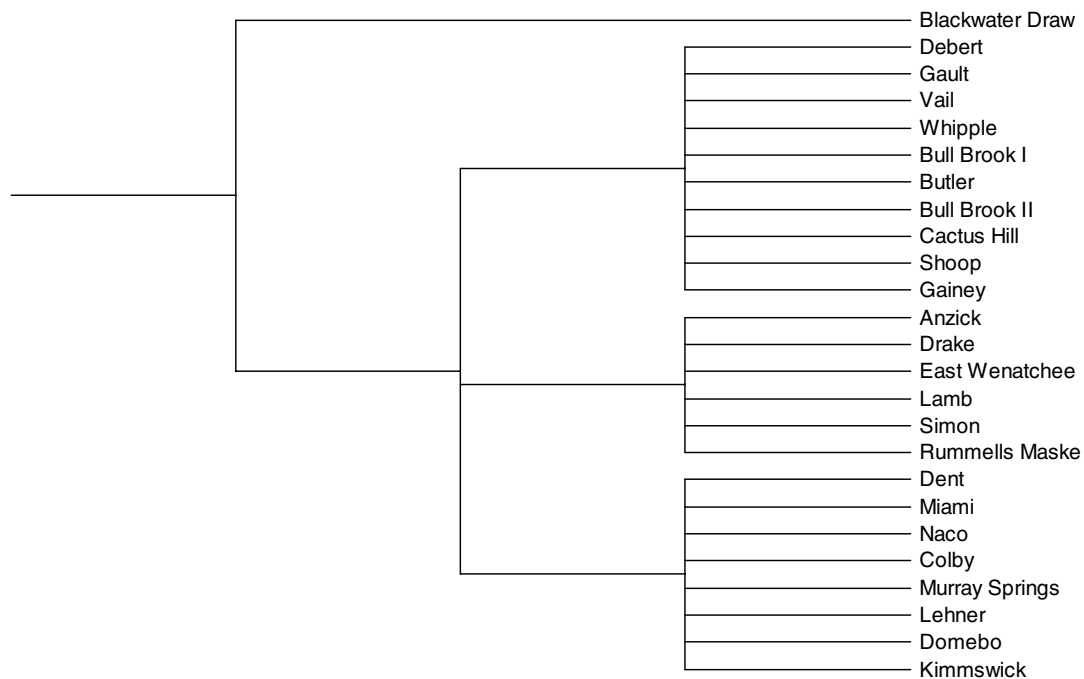
Fig. 4. Hypothetical cladogram representing the general site types (habitation, cache, and kill) associated with the assemblages.

is shown in Fig. 6. Second, the paleovegetation data were used to estimate net primary production (nPP) for each region based on modern estimates (Melillo et al., 1993). Annual nPP is the net amount of carbon captured by land plants through photosynthesis each year and is commonly used in ecology to estimate the energetic productivity, and therefore energetic availability within an environment (Rickleffs and Miller, 1999). A distance matrix of differences in regional nPP estimates was used to build the second cladogram representing the environmental adaptation hypothesis using the nearest-neighbor joining method (Fig. 7; Saitou and Nei, 1987; see also Studier and Kepler, 1988; Kuhner and Felsenstein, 1994). Third, data on the mammalian fauna recovered from Early Paleoindian archaeological sites were used to determine inter-regional differences in species. The data were taken from Cannon and Meltzer's (2004) tabulations of Early Paleoindian faunal assemblages within each region (including sites not in our analysis). Only 37 genera (excluding small rodents, lagomorphs, and insectivores with body sizes less than 100 g) of the total 77 genera reported by Cannon and Meltzer (2004): Table 2) were included in the construction of a distance matrix. The distance matrix was used to build the third cladogram representing the environmental adaptation hypothesis using the nearest-neighbor joining method (Fig. 8).

"Explanatory" cladograms were also created to reflect four colonization models—entry via the ice-free corridor, entry via the Northwest Coast, entry via the Isthmus of Panama, and entry via the Mid-atlantic region. The cladograms were created with the aid of the results of a GIS-based analysis carried out by Anderson and Gillam (2000). These authors used continental scale elevation data, combined with approximations of Late Glacial locations of ice sheets and pluvial lake boundaries, to determine the least-cost migration routes that could have been used by Early Paleoindians following entry into North America via the ice-free corridor, the Northwest coast, or the Isthmus of Panama. The three entry models discussed by Anderson and Gillam (2000) were transformed into cladograms using the primary and regional least-cost routes to derive the sequence of events for each entry model (cf. Gray and Jordan, 2000). In cases where particular sites used in the analysis are not connected by pathways shown in the Anderson and Gillam (2000) models, the relationships within each region were estimated according to the location of the site relative to the least-cost pathways. The Midatlantic model was created in a similar manner. It should be noted that, since no pre-Clovis points were analyzed, the key assumption of the latter model for present purposes is that the Midatlantic was occupied first and for the longest period of time. This
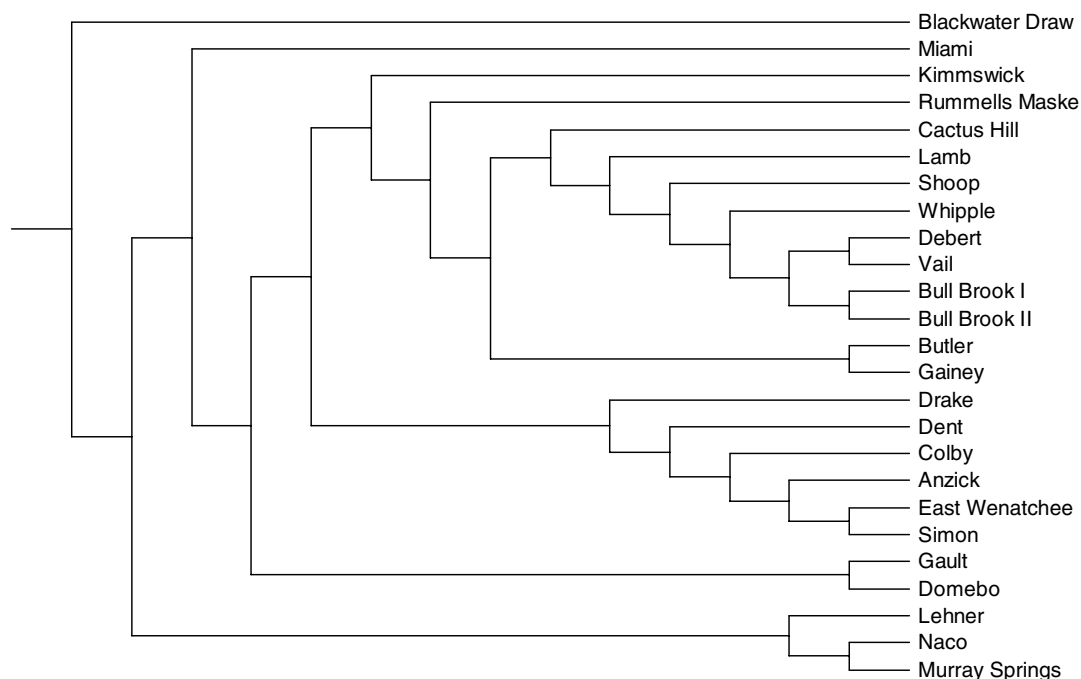
Fig. 5. Hypothetical cladogram representing the nearest-neighbor distances of the geographic separation among assemblages.

Table 3
Paleoenvironmental regions defined for the analysis

| Region | Biome | nPP | Sites |
|---|---|---|---|
| Midcontinent | Prairie | 335 | Kimmswick, Rummells, Maske |
| Northeast | Parkland to tundra | 147 | Bull Brook I & II, Debert, Vail, Whipple |
| Midatlantic | Spruce forest | 238 | Cactus Hill, Shoop |
| Great Lakes | Spruce forest | 173 | Butler, Gainey, Lamb |
| Northwest | Semi-desert and mountain mosaic | 230 | East Wenatchee, Simon |
| Northern Plains | Dry steppe | 214 | Anzick, Colby, Dent, Drake |
| Southern Plains | Dry steppe | 214 | Blackwater Draw, Domebo, Gault, Miami |
| Southwest | Semi-desert | 129 | Lehner, Murray Springs, Naco |

Paleoenvironmental biomes, net primary production (nPP), and sites listed for each region.

is in keeping with Stanford and Bradley's (2002) proposal that the pre-Clovis levels of Cactus Hill may represent an initial migration of Solutrean groups from Europe arriving via a trans-Atlantic maritime voyage. The four colonization "explanatory" cladograms are shown in Figs. 9–12.

**Results**

The parsimony analysis returned four most-parsimonious cladograms (Fig. 13). The cladograms disagreed regarding the relationships of the Debert and Vail assemblages. In cladogram A, Debert is the sister taxon of a clade comprising Colby, East Wenatchee, Gault, Murray Springs, Vail, and Whipple, and Vail is positioned as the sister taxon of a clade consisting of Colby, East Wenatchee, Gault, Murray Springs, and Whipple. Within the latter clade, East Wenatchee and Whipple form a clade that is the sister taxon of a clade comprising Colby, Gault, and Murray Springs, and Murray Springs is the sister taxon of a clade consisting of Colby and Gault. In cladogram B, Debert and Vail form a clade that is the sister taxon of a clade comprising Colby, East Wenatchee, Gault, Murray Springs, and Whipple, and East Wenatchee and Whipple form a clade that is the sister taxon of a clade consisting of Colby, Gault, and Murray Springs. Within the latter clade, Murray Springs is located as the sister taxon of a clade comprising Colby and Gault. In cladogram C, Vail is the sister taxon of a clade comprising Colby, Debert, East
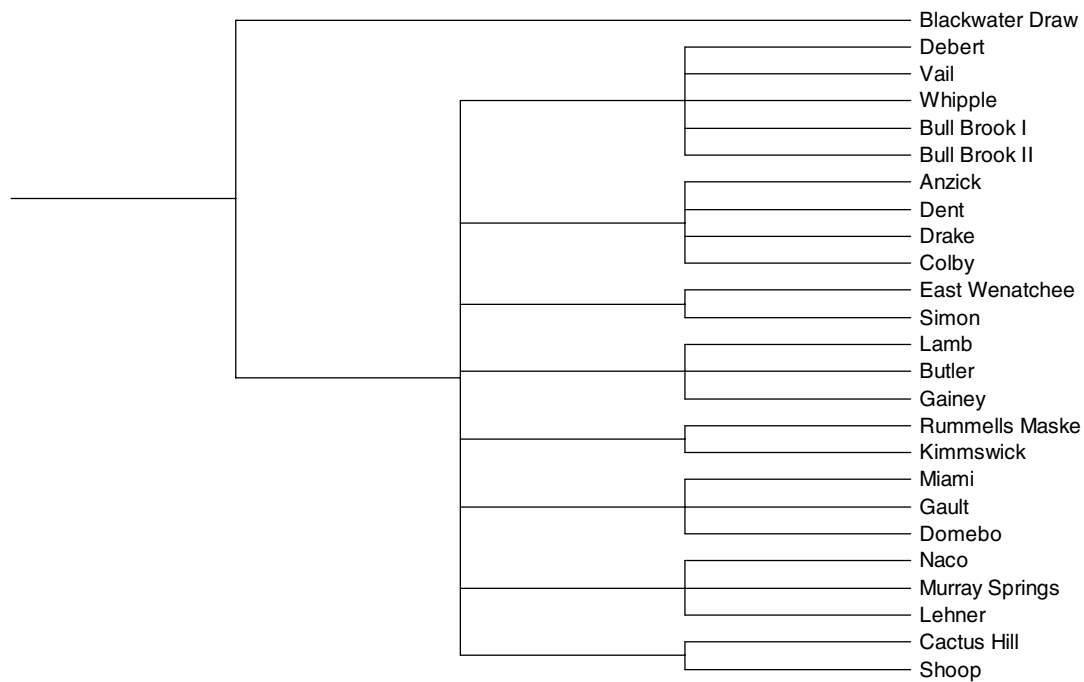
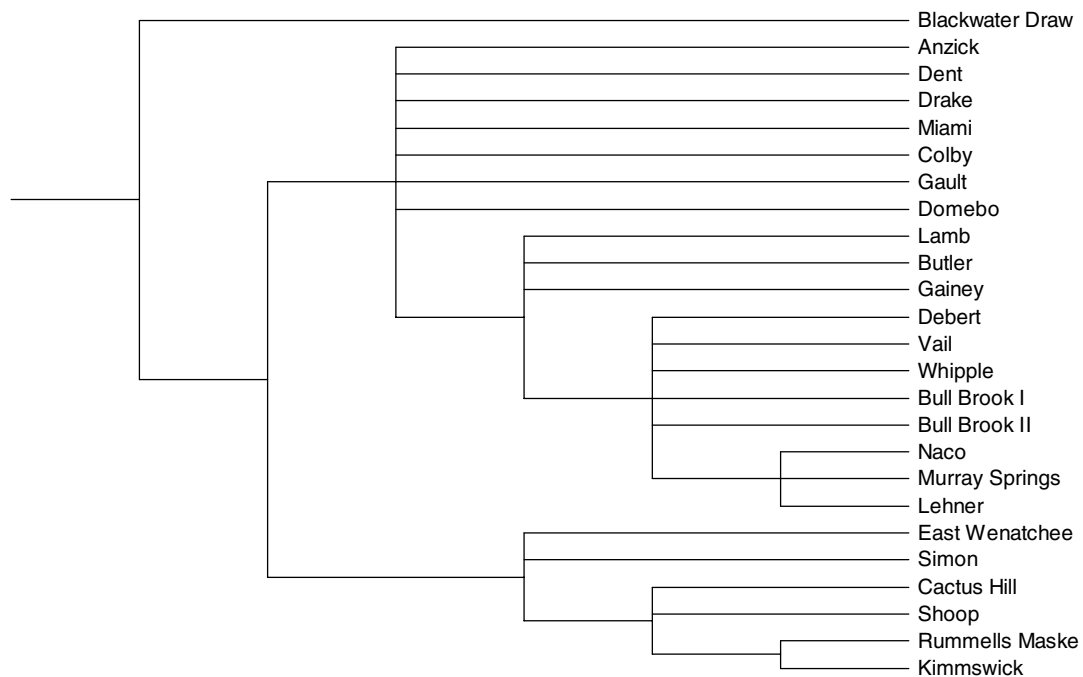Fig. 6. Hypothetical cladogram grouping assemblages by environmental region.

Fig. 7. Hypothetical cladogram representing the nearest-neighbor distances of paleoenvironmental net primary production estimates among regions.

Wenatchee, Gault, Murray Springs, and Whipple, and Debert is positioned as the sister taxon of a clade consisting of Colby, East Wenatchee, Gault, Murray Springs, and Whipple. Within the latter clade, East Wenatchee and Whipple form a clade that is the sister taxon of a clade comprising Colby,

Gault, and Murray Springs, and Murray Springs is the sister taxon of a clade consisting of Colby and Gault. In cladogram D, Debert, East Wenatchee, Vail, and Whipple form one clade, and Colby, Gault, and Murray Springs form a second. Within the clade comprising Debert, East Wenatchee, Vail,
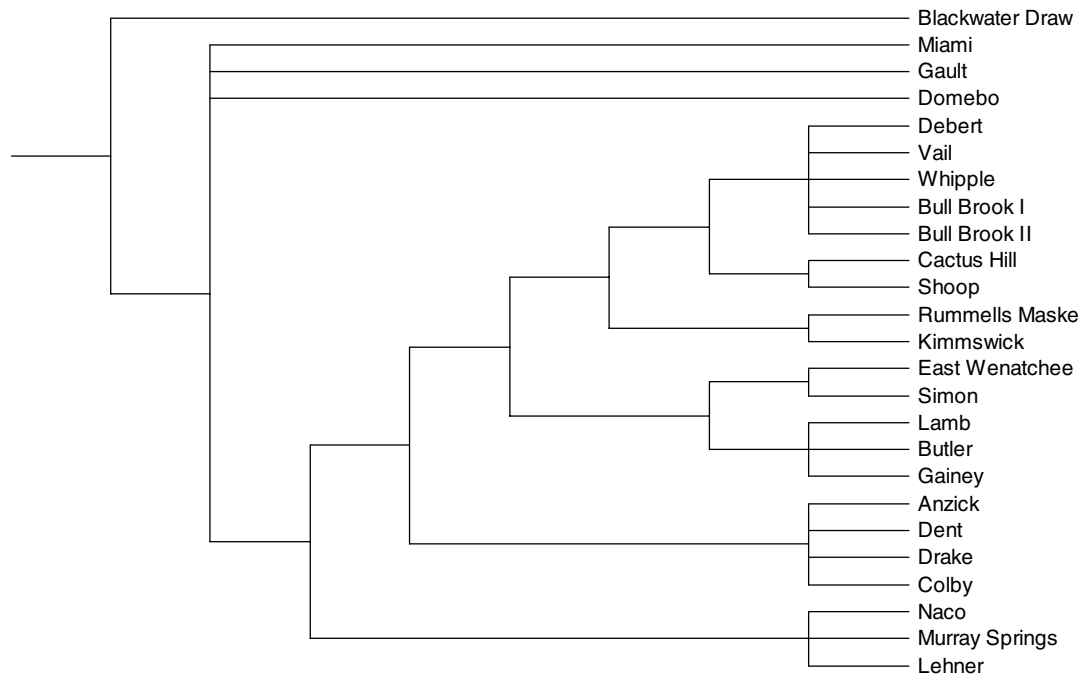
Fig. 8. Hypothetical cladogram representing the nearest-neighbor distances of regional mammalian fauna recovered from Early Paleoindian sites.
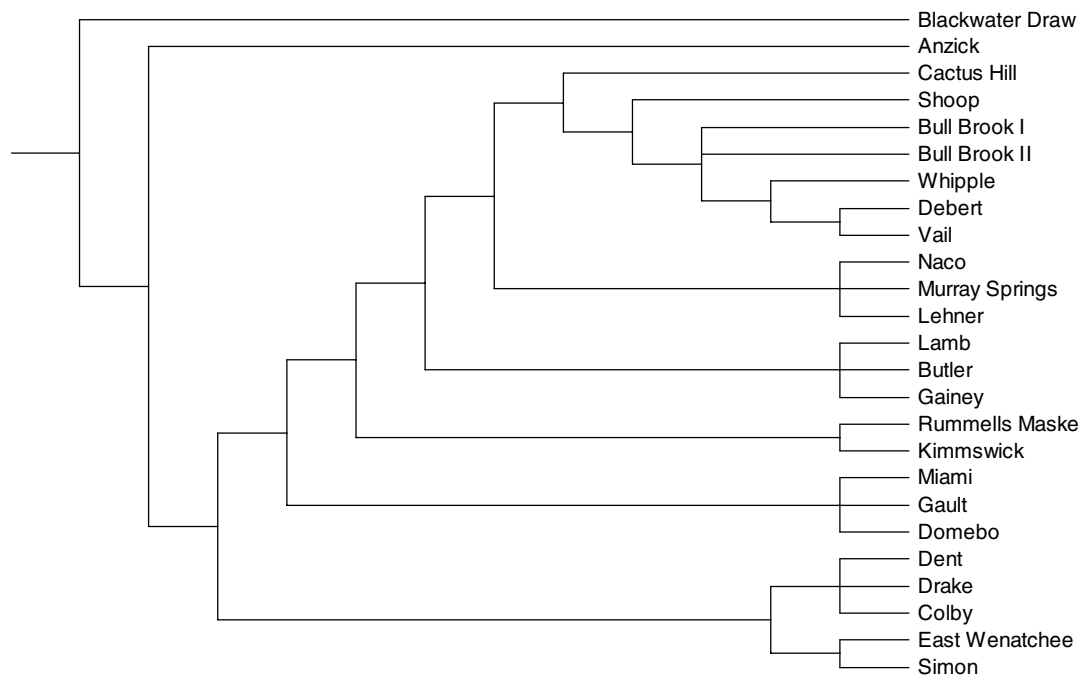


Fig. 9. Hypothetical cladogram representing the ice-free corridor entry route.

and Whipple, Vail is positioned as the sister taxon of the other three assemblages, and Debert is located as the sister taxon of Whipple and East Wenatchee. Within the clade comprising Murray Springs, Colby, and Gault, Murray Springs is positioned as the sister taxon of Colby and Gault.

The results of the three fit-assessment analyses were consistent. The PTP test indicated that the most parsimonious cladograms were significantly shorter than any of the 10,000 permuted cladograms ($p = 0.0001$). In the RI comparison, the RI associated with the most parsimonious projectile point
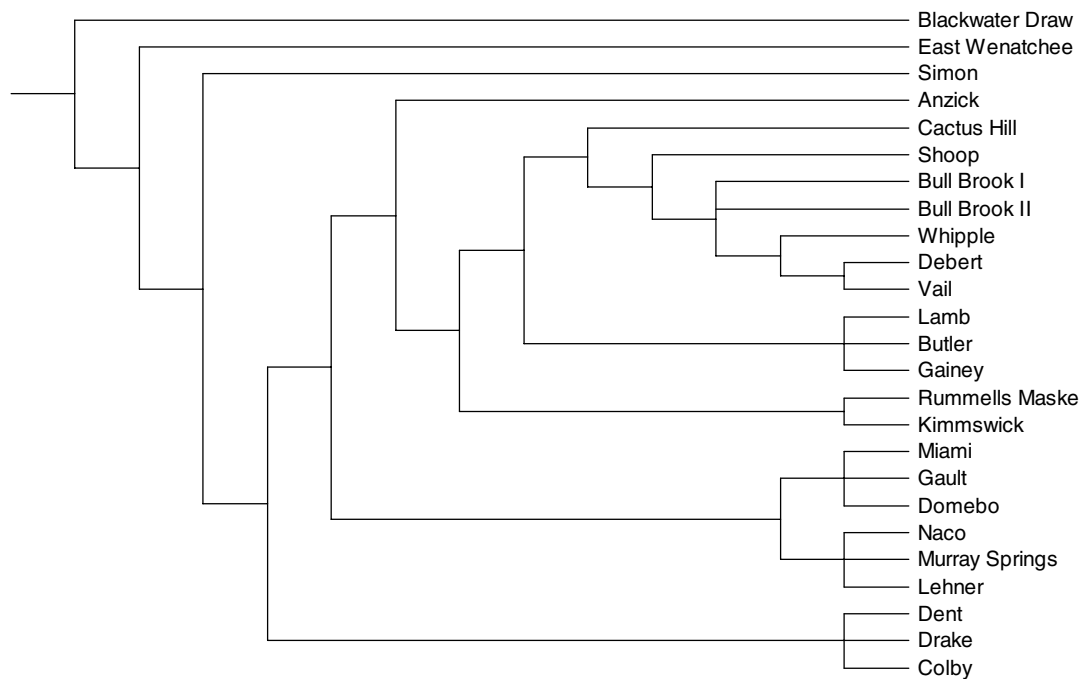
Fig. 10. Hypothetical cladogram representing the Northwest coast entry route.
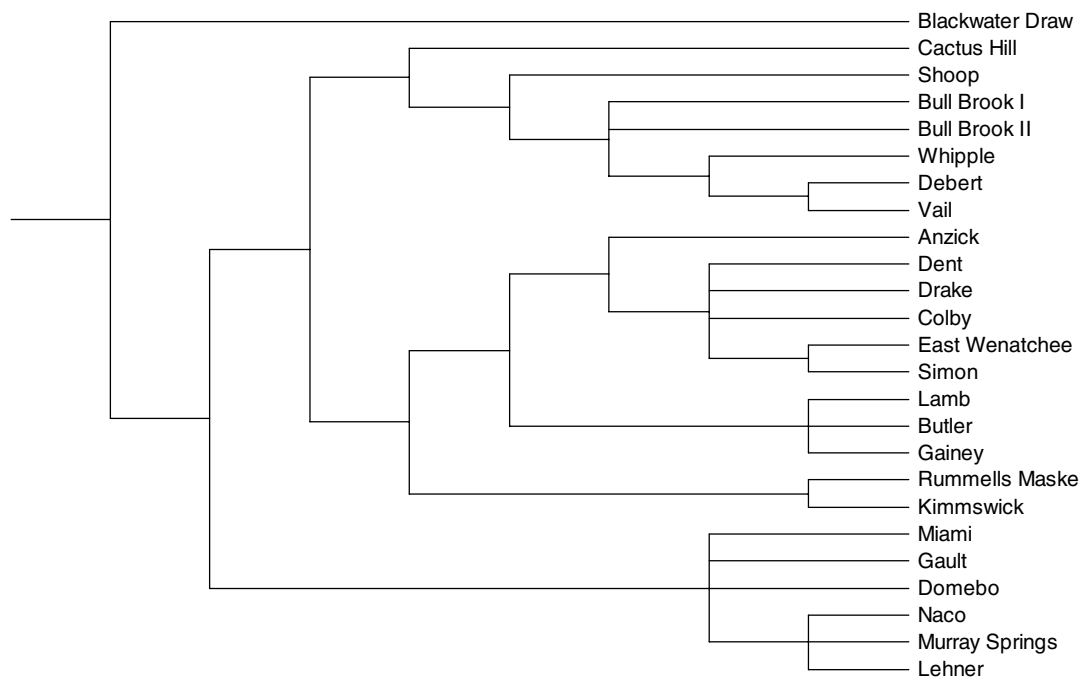
Fig. 11. Hypothetical cladogram representing the Isthmus of Panama entry route.

cladograms was 0.69. This compares favorably with the mean RI of 0.59 returned by Collard et al.'s (2006) cultural datasets. It is also higher than the mean RI of 0.61 returned by their biological datasets. In the CI comparison, the CI for the most parsimonious projectile point cladograms was 0.45. Using Sanderson and Donoghue's (1989) regression formula, the CI of 0.45 derived from the projectile point data is not statistically different from the expected value of 0.48 for 25 taxa. Thus, the results of the PTP test and the RI and CI comparisons suggest that fit between the most parsimonious cladograms and the projectile point dataset is good.
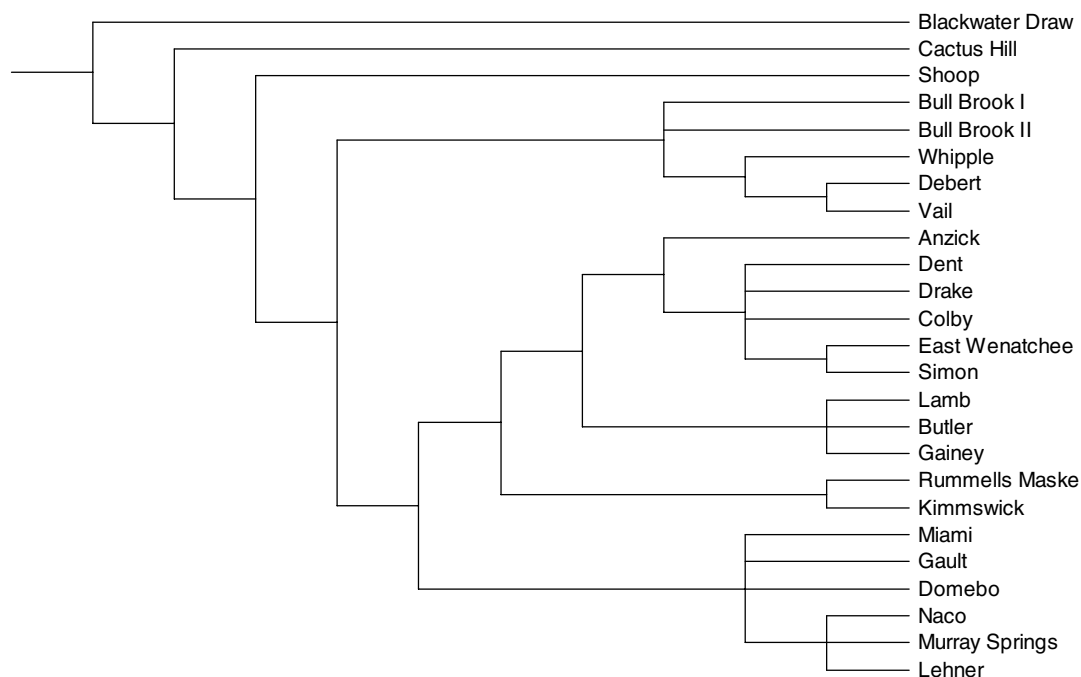
Fig. 12. Hypothetical cladogram representing the Midatlantic entry route.

The bootstrap analysis supported the general structure of the most parsimonious cladograms (Fig. 14). The bootstrap cladogram contains a basal polytomy involving a 13-assemblage clade, a three-assemblage clade, and eight individual assemblages. The 13-assemblage clade is supported by 84% of the bootstrap replicates, and comprises Bull Brook I, Cactus Hill, Colby, Debert, East Wenatchee, Gault, Lamb, Lehner, Rummells Maske, Murray Springs, Shoop, Vail, and Whipple. Within this clade, Colby, Debert, East Wenatchee, Gault, Murray Springs, Vail, and Whipple form a clade that appeared in 59% of the replicates. Within the (Colby, Debert, East Wenatchee, Gault, Murray Springs, Vail, Whipple) clade there is a clade comprising East Wenatchee and Whipple, and a clade consisting of Colby, Gault and Murray Springs. The (East Wenatchee, Whipple) clade is supported by 71% of the replicates, and the (Colby, Gault, Murray Springs) by 55%. Within the (Colby, Gault, Murray Springs) clade, Colby and Gault form a clade to the exclusion of Murray Springs. This clade is supported by 52%. The three-assemblage clade appears in 61% of the replicates and consists of Gainey, Kimmswick and Miami. Within the (Gainey, Kimmswick, Miami) clade, Miami and Gainey form a clade to the exclusion of Kimmswick.

The K–H test in which Blackwater Draw was employed as the outgroup indicated that all of the "explanatory" cladograms are significantly different from the four most-parsimonious cladograms (Table 4). While none of the "explanatory" cladograms fits the data matrix as well as the most parsimonious cladograms, there are marked differences among them in terms of how well they fit the data matrix. The ice-free corridor cladogram is 218 steps longer than the most parsimonious cladograms, and the Northwest Coast cladogram is 222 steps longer. The Isthmus of Panama, cultural diffusion, Midatlantic, environmental regions, regional fauna, and paleoenvironmental nPP cladograms are 229, 237, 240, 260, 260, and 285 steps longer than the most parsimonious cladograms, respectively. The site type cladogram is 302 steps longer than the most-parsimonious cladograms. Thus, the ice-free corridor cladogram is the "explanatory" cladogram that best fits the character state data matrix. The Northwest Coast cladogram has the next best fit, followed by the Isthmus of Panama cladogram, the cultural diffusion cladogram, the Midatlantic cladogram, and the environmental adaptation hypothesis cladograms. The site type cladogram has the poorest fit to the data matrix.

### Sensitivity testing

In order to assess the validity of the results, we repeated the parsimony analysis and K–H tests after altering key parameters.
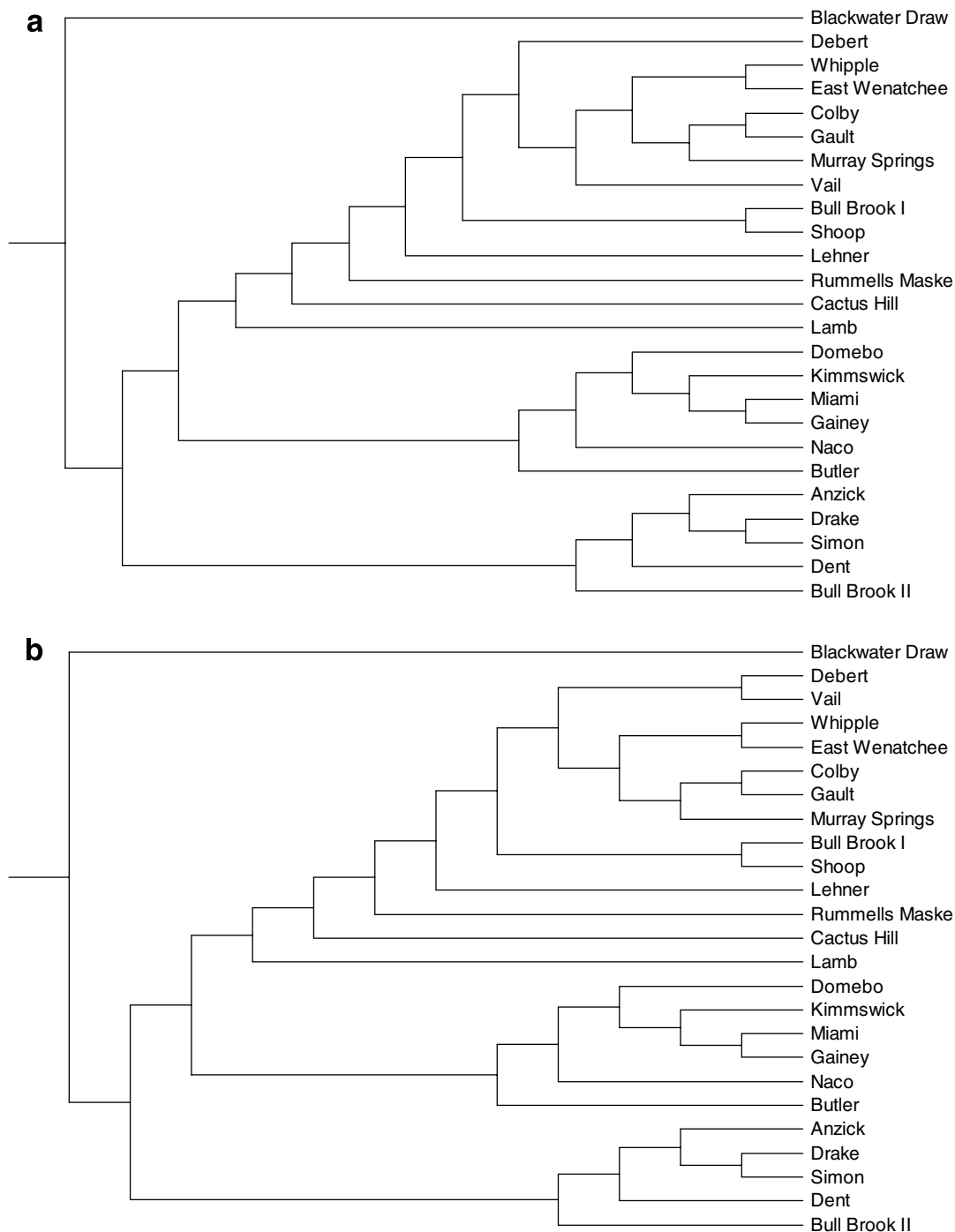
Fig. 13. Maximum-parsimony cladograms a, b, c, and d inferred using the branch-and-bound search algorithm in PAUP* 4.0 of the Early Paleoindian projectile point data (cladogram lengths = 285; CI = 0.45; RI = 0.69).

We ran two analyses to determine if removing assemblages with small sample sizes affected the results. In the first of these analyses we removed assemblages with only two projectile points (Bull Brook II, Dent, Gault, and Whipple) and then re-ran the parsimony analysis and K–H test using the remaining 21 assemblages (see Table 1). In the second, we re-ran the parsimony analysis and K–H test after removing the nine assemblages with less than five projectile points (Bull Brook II, Butler, Colby, Dent, Domebo, Gault, Kimmswick, Miami, and Whipple).

These analyses indicated that small sample size effects do not influence the results. Removing assemblages with only two projectile points produced six equally parsimonious cladograms with
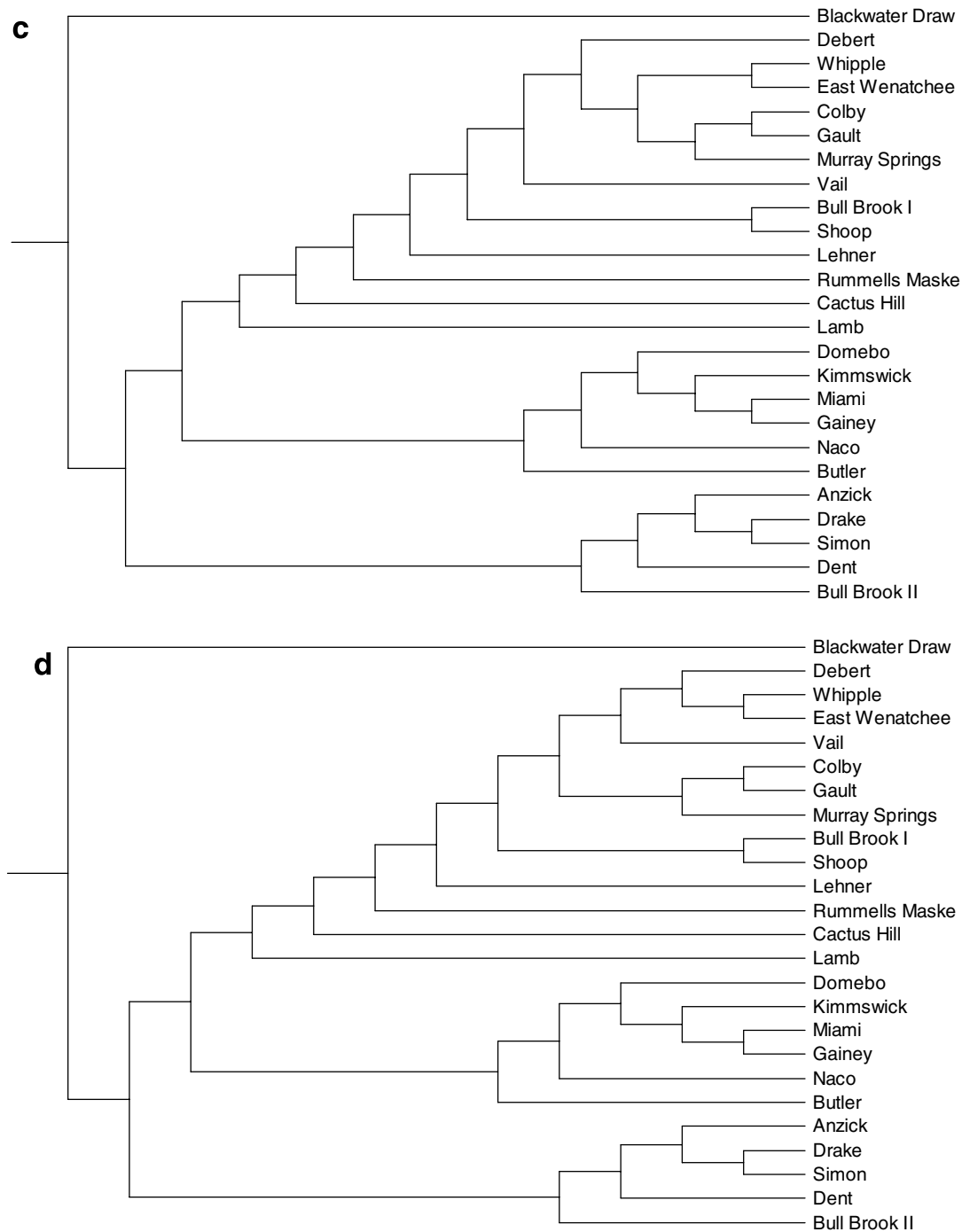
Fig. 13. (*continued*)

lengths of 253 steps and a CI of 0.48 and an RI of 0.67. The removal of the assemblages with only two points did not substantially affect the K–H results. The ice-free corridor entry model had the shortest cladogram length in comparison to the observed trees. In the last analysis, assemblages containing less than five points were removed producing four cladograms with lengths of 194 (CI = 0.57, RI = 0.64). The removal of the assem-

blages with less than five points also did not markedly affect the K–H results. Again, the ice-free corridor model was found to be the best-fitting model.

We also ran two analyses to determine if altering the number of allowable character states in the gap-weighting coding method affected the results. In the first of these analyses, we re-coded the size-corrected data using 16 character states instead of the maximum allowable 26 character states and then
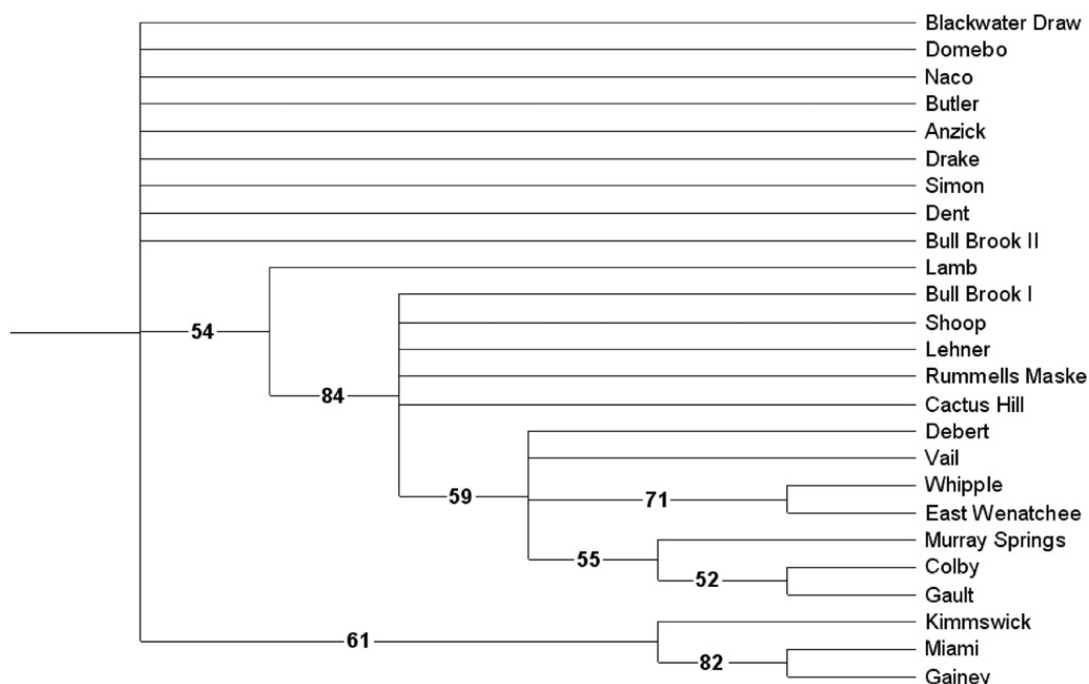
Fig. 14. Bootstrap 50% majority-rule cladogram of the Early Paleoindian projectile point data.

Table 4
Results of the Kishino–Hasegawa tests comparing the four equally-parsimonious projectile point cladograms to "explanatory" cladograms

| Cladogram | Length | Difference | s.d. (diff) | $t$ | $p$ |
|---|---|---|---|---|---|
| Observed 1 | 285 | (best) | | | |
| Observed 2 | 285 | 0 | 5.28 | 0.00 | 1.0000 |
| Observed 3 | 285 | 0 | 3.87 | 0.00 | 1.0000 |
| Observed 4 | 285 | 0 | 5.07 | 0.00 | 1.0000 |
| Ice-free corridor, NP entry | 503 | 218 | 61.64 | 3.54 | 0.0033[a] |
| Northwest coast entry | 507 | 222 | 62.21 | 3.57 | 0.0031[a] |
| Isthmus of Panama entry | 514 | 229 | 60.10 | 3.81 | 0.0019[a] |
| Geographic proximity | 522 | 237 | 63.17 | 3.75 | 0.0021[a] |
| Midatlantic entry | 525 | 240 | 61.08 | 3.93 | 0.0015[a] |
| Environmental regions | 545 | 260 | 68.31 | 3.81 | 0.0019[a] |
| Regional fauna | 545 | 260 | 66.21 | 3.93 | 0.0015[a] |
| Paleoenvironmental nPP | 570 | 285 | 61.90 | 4.60 | 0.0004[a] |
| Site type | 587 | 302 | 67.95 | 4.44 | 0.0006[a] |

[a] Significantly different from the observed best point size-free cladograms.

repeated the parsimony analysis and K–H test. In the second we repeated the parsimony analysis and K–H test after recoding the size-corrected data using six character states.

These analyses indicated that altering the parameters of the gap-weighting coding method did not affect the results of the K–H tests. Reducing the number of allowable character states to 16 in the gap-weighting coding produced 28 equally parsimonious cladograms (CI = 0.46, RI = 0.69). Reducing the number of character states to six produced

22,351 equally parsimonious cladograms. Although many more cladograms were produced, the CI (0.52) and RI (0.74) were improved. K–H analyses using the re-coded datasets with 16 and 6 character states indicated that all of the "explanatory" cladograms were significantly different from the observed cladograms, but in both analyses the ice-free corridor entry model was the best fit based on cladogram length.

Lastly, additional K–H analyses were conducted to evaluate potential error associated with the use of

Blackwater Draw as the outgroup. Because reliable radiocarbon assays are not associated with all of the assemblages in our analysis (only 11 of the 25 assemblages have reliable radiocarbon assays), it is possible that Blackwater Draw may not be the oldest taxon in the sample. If this is the case, then the interpretation of the most parsimonious, consensus and bootstrap cladograms may be incorrect, as may the results of the K–H tests. In order to evaluate this possibility, we carried out parsimony analyses using each of the 14 assemblages without associated radiocarbon ages or with unreliable dates as outgroups, and examined the differences between the resulting cladograms and the original most-parsimonious cladograms. The poorly dated/undated assemblages are Bull Brook I and II, Butler, Drake, East Wenatchee, Gainey, Gault, Kimmswick, Lamb, Miami, Naco, Rummells Maske, Shoop, and Simon. We also evaluated which of the "explanatory" cladograms fits the dataset best when the alternative outgroups are employed. These analyses suggested that employing Blackwater Draw as the outgroup did not bias the results. No matter which of the poorly dated/undated assemblages was used as the outgroup, the "explanatory" cladograms were significantly longer than the most-parsimonious cladograms, and the cladogram representing the ice-free corridor hypothesis fitted the character state data matrix better than any of the other "explanatory" cladograms.

Thus, the three sets of analyses carried out to assess the validity of the results suggest that they are robust.

## Discussion and conclusions

The good fit between the most-parsimonious cladograms and the character state data matrix revealed by the PTP test, the RI and CI comparisons and the bootstrap analysis suggests that the interassemblage variation in projectile point shape is best explained by a colonization process that was both rapid and involved the repeated fissioning of populations. This is because rapid, population fissioning-based colonization can be expected to give rise to historical relationships among populations that are consistent with the model of descent with modification that biologists use to represent the relationships among species and that, as we noted earlier, the cladistic methodology is based on. The results of the K–H tests are consistent with this interpretation since three of the four "explana-

Table 5
Results of analysis using Maddison and Slatkin's (1991) method

| "Explanatory" cladogram | Minimum | Maximum |
| --- | --- | --- |
| Ice-free corridor | 439[a] | 499[a] |
| Northwest coast entry | 586 | 671 |
| Isthmus of Panama entry | 936 | 1013 |
| Geographic proximity | 1476 | 1595 |
| Midatlantic entry | 1718 | 1866 |
| Environmental regions | 4125 | 4397 |
| Regional fauna | 4125 | 4397 |
| Paleoenvironmental nPP | 7970 | 8106 |
| Site type | 9551 | 9629 |

In this analysis, the lengths of the "explanatory" cladograms were compared 20 times with the lengths of 10,000 randomly generated cladograms to evaluate the significance of the fit between the "explanatory" cladograms and the dataset. The second and third columns of the table show the minimum and maximum numbers of randomly generated cladograms with lengths less than or equal to the length of the "explanatory" cladograms derived from the 20 iterations, respectively. Only "explanatory" cladograms within 5% of the lower tail of the distributions are considered significantly different from random.
[a] Significantly different from random.

tory" cladograms representing colonization models were found to fit the dataset markedly better than the "explanatory" cladograms representing cultural diffusion, different models of environmental adaptation, and site type effects. Thus, collectively, the results of the analyses strongly support the idea that a migrating population produced Clovis and the other Early Paleoindian assemblages.

The analyses are less clear-cut with regard to the colonization model that is most compatible with the projectile point dataset. This is because the differences in goodness of fit between some of the "explanatory" cladograms representing colonization models are relatively small. As noted above, when the "explanatory" cladograms are ranked according to length, the ice-free corridor model is the colonization model that best fits the projectile point dataset. This result appears relatively robust given that the phylogenetic bootstrap and sensitivity analyses exploring the coding method used and assemblage sample size all indicated that the ice-free corridor model was the best-fitting model. The Northwest Coast model is the next best, followed by the Isthmus of Panama model, and then the Midatlantic model. However, while the "explanatory" cladogram representing the ice-free corridor model is markedly shorter than those representing the Isthmus of Panama and Midatlantic models, it is only three steps shorter than the cladogram representing

the Northwest Coast model. Thus, the ice-free corridor model is a more parsimonious explanation of the data than the other three models, but it is only marginally more parsimonious than the Northwest Coast model.

In an effort to better discriminate among the ''explanatory'' cladograms we turned to a nonparametric technique developed by Maddison and Slatkin (1991) to assess whether or not the fit between a dataset and an ''explanatory'' cladogram is significantly different from random. Using PAUP* 4.0 we generated 20 distributions of 10,000 random (equiprobable) cladograms based on the parameters of the observed cladograms (15 characters and 25 taxa), and recorded cladogram length for each of the randomly generated cladograms. We then determined where the lengths of the ''explanatory'' cladograms fell in the distribution of random cladograms. ''Explanatory'' cladograms with lengths less than or equal to 5% of the randomly generated cladograms in the lower tail were deemed to be significantly shorter than random.

Comparison of the lengths of the ''explanatory'' cladograms to the null distributions revealed that less than 5% of the randomly generated cladograms in each of the 20 trials had lengths shorter than the ice-free corridor model (Table 5). The lengths of the other ''explanatory'' cladograms were found to be longer than the shortest 5% of the randomly generated cladograms in the lower tail. Thus, the ice-free corridor model is the only ''explanatory'' cladogram for which the fit with the dataset is significantly better than random. The other colonization cladograms as well as the cultural diffusion cladogram, the environmental adaptation cladograms, and site type cladogram are not significantly different from random ($p$-values range from 0.586 to 0.187).

Together, the K–H test and the analysis in which Maddison and Slatkin's (1991) method was employed indicate that Anderson and Gillam's (2000) Isthmus of Panama entry model and Stanford and Bradley's (2002) Solutrean colonization model are unlikely to be correct. Distinguishing between the other two colonization models that have been proposed—the ice-free corridor and Northwest Coast model—is more difficult. Given that the ice-free corridor model is the only model to fit the dataset better than random, there are grounds for arguing that it is a better explanation than the Northwest Coast model. However, the difference between the two models is sufficiently small

that it is probably sensible to conclude that they are essentially equally likely.

While the analyses suggest that the ice-free corridor and Northwest Coast models are much more likely to be correct than the Isthmus of Panama entry and the Solutrean colonization models, it is also the case that neither the ice-free corridor model nor the Northwest Coast model fits the dataset especially well. To reiterate, all of the ''explanatory'' cladograms are substantially longer than the four most-parsimonious cladograms. The latter were all 285 steps long, while the shortest of the ''explanatory'' cladograms, the one representing the ice-free corridor model, was 503 steps in length. Thus, the ''explanatory'' cladograms are all markedly longer than the most-parsimonious cladograms.

How do we account for this difference in length? One possibility is that the ice-free colonization model and the Northwest Coast model are both wrong, and the most parsimonious cladograms reflect the actual route taken by the Early Paleoindians. This explanation is not particularly convincing. The reason for this is that interpreting some of the clades of the most-parsimonious cladograms in terms of colonization is problematic. The most striking example of this is the clade that links the assemblages from East Wenatchee and Whipple to the exclusion of the other assemblages. The East Wenatchee site is located in Washington State, while the Whipple site is located in New Hampshire. Thus, the clade in question groups together assemblages from different sides of North America. The other prominent example is the clade that exclusively links the assemblage from the site of Miami, which is in Texas, with the assemblage from site of Gainey, which is in Michigan. The presence of these clades in the most parsimonious cladograms makes it difficult to argue that the cladograms reflect the actual route taken by the Early Paleoindians.

The other possibility is that one or other of the models is correct, but processes other than colonization added a substantial amount of ''noise'' to the dataset. The processes that are widely thought to be most likely to create ''noise'' in a dataset like the one used in the study are cultural diffusion and adaptation to local ecological circumstances (Collard et al., 2006; Guglielmino et al., 1995; Jordan and Shennan, 2003; Shennan and Collard, 2005; Tehrani and Collard, 2002). A third possibility is that the ''noise'' in the dataset is a consequence of there being only a limited number of ways in

which a lanceolate shape projectile point can be produced. A constraint of this type would greatly increase the probability of similarities developing among assemblages as a result of chance alone, which in turn would markedly increase the probability of geographically and ecologically disparate assemblages being grouped together in the same clade. Based on the results of the K–H tests and the analyses in which Maddison and Slatkin's (1991) method was employed, there is little reason to think that cultural diffusion and ecological adaptation produced the "noise". Both processes were found to be considerably worse explanations of the dataset than the ice-free corridor model and the Northwest Coast model. Indeed, the analyses in which Maddison and Slatkin's (1991) method was used suggested that the cultural diffusion and environmental adaptation "explanatory" cladograms fit the dataset no better than randomly generated cladograms. Thus, it would seem that the "noise" in the dataset is most likely a consequence of there being a constraint on projectile point shape.

In sum, then, the analyses reported here suggest that a rapidly migrating population produced the Early Paleoindian projectile point assemblages. They also suggest that the population in question is unlikely to have entered North America from either the Isthmus of Panama or the Midatlantic region. According to the analyses, the Early Paleoindians are more likely to have entered North America via either the ice-free corridor that is hypothesized to have opened around 12,000 BP or the Northwest Coast.

With respect to future work, the obvious next step is to assess the impact of excluding projectile points from the Far West (California and the Great Basin) and the Southeast from our sample. To reiterate both of these regions have projectile points that are thought to date to the Early Paleoindian period (Beck and Jones, 1997; Bryan, 1991; O'Brien et al., 2001; Willig, 1991), but the points in question are either isolated finds or from temporally mixed sites. Thus, the challenge is to find a way of testing the four colonization hypotheses using individual points. It is possible that the paradigmatic classification-based method outlined by (O'Brien et al., 2001; see also O'Brien and Lyman, 2003) could be of assistance in this regard, since it employs individual points. However, it will require some adjustment because the phylogenies it produces do not readily lend themselves to testing hypotheses regarding human population movements.

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