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Phylogenetic Systematics

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Introduction

Archaeologists have long used changes in artifact form—in evolutionary terms, changes from one character state to another—to measure the passage of time (Lyman and O'Brien 2006). If evolved character states are ordered correctly, a historical sequence of forms is created, although independent evidence is needed to root the sequence—that is, to determine which end of the sequence is older. Such evidence could come, for example, from chronological dating (e.g., stratigraphy) or historical sources. Over the past several years, archaeologists have grown to appreciate that the methods biologists have developed to reconstruct the evolutionary, or phylogenetic, relationships of species can help them create not only historical sequences of artifact forms—what came before or after what—but sequences based on heritable continuity—what produced what.

One such method is cladistics, the extension of which into the cultural realm is based on the recognition that artifacts—pottery vessels, stone projectile points, and the like—comprise any number of parts that act in concert to produce a functional unit. The kinds of changes that occur over generations of, say, spear-point or ceramic-vessel manufacture are constrained in that new structures and functions usually arise through modification of existing structures and functions—descent with modification—as opposed to arising *de novo*. As with DNA, the history of cultural changes is recorded in the similarities and differences in characters (attributes of phenomena) as they are modified over time by subsequent additions, losses, and transformations (Brown and Lomolino 1998).

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Here we describe the basic cladistic method, focusing first on distinguishing between homologous and analogous characters and, in the case of the former, distinguishing between derived and ancestral characters. We then turn attention to how trees are constructed, dividing the process into four steps: (1) generating a character-state matrix; (2) establishing the direction of evolutionary change in character states; (3) constructing branching diagrams of taxa; and (4) generating an ensemble tree. We then introduce an example of a cladistic analysis, the phylogenetic history of early Paleoindian-period (ca. 13,300–11,900 calendar years before the present [calBP]) projectile points from the southeastern United States. We stress that our discussion of cladistics is not intended to replace standard texts on the subject (for readable accounts see Brooks and McLennan 1991, Kitching et al. 1998, O'Brien and Lyman 2003, Williams and Knapp 2010); rather, it is a brief introduction to the logic behind, and key methodological elements of, cladistics.

Cladistics

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.

For example, Fig. 1 is a cladogram, or phylogenetic tree (we use the terms here interchangeably), that classifies four taxa. It tells us that based on a certain character distribution, taxa C and D are more similar to one another than either is to any other taxon. It also says that taxa B, C, and D are more similar to one another than any of the three is to Taxon A. We know that taxa A–D evolved from one or more ancestral taxa, although at this point we know little or nothing about those ancestors except that with respect to certain characteristics taxa C and D look more like their immediate common ancestor (x) than they do the one (y) that unites them with Taxon B. Likewise taxa B, C, and D look more like their common ancestor (y) than they do the one (z)

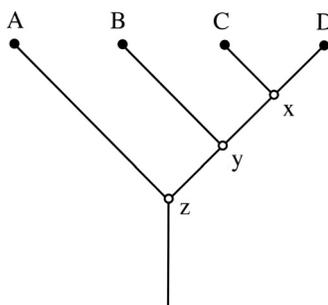


Fig. 1. A phylogenetic tree showing the historical relationship of four taxa (A–D) and three ancestors (x–z). Based on a certain character-state distribution (not shown), taxa C and D are more similar to one another than either is to any other taxon. Also, taxa B, C, and D are more similar to each other than any of the three is to Taxon A. Related taxa and their ancestors form ever-more-inclusive groups, or clades: C + D + x is one clade; B + C + D + y is a second; and A + B + C + D + z is a third.

that unites them with Taxon A. In cladistics, convention is to place *nodes* at the points where branches meet and to refer to the nodes as ancestors that produced the *terminal taxa* (those at the branch tips). In our tree, taxa C + D, together with their hypothetical common ancestor (node x), form a *monophyletic group*, or *clade*. Taxa D + C + B, together with their common ancestor (node y), form another, more inclusive clade, and taxa D + C + B + A, together with their common ancestor (node z), form yet another, and the most inclusive, clade.

One common misconception is that the interior nodes—“ancestors”—are somehow “real”. They are not, and in fact, ancestors play no analytical role in cladistics because we can never be sure exactly what produced what. We know that taxa do not die when they produce offspring—Taxon z in Fig. 1 did not die when it produced Taxon A and Taxon y—so we show the ancestor as a sister taxon. It is simply a matter of convention to circumvent the illogical problem of having parents die when offspring are born (Sober 1988).

Characters and Character States

The key to cladistics lies in the kind of characters and character states that it employs. Two broad kinds of characters and character states occur in the natural world—analogs and homologs. Analogs are functionally similar characters (or character states) that evolve separately in two or more lineages after those lineages diverge. Thus they are of no utility in reconstructing lineages. In contrast, homologs *are* useful for tracking heritable continuity because they are holdovers from a previous time when two lineages were a single lineage. Darwinian theory provides the explanation for homology—descent with modification—but it does not tell us how to identify it. Although “similarity is the factor that compels us to postulate homology” (Cracraft 1981: 25), simple similarity in form is not a particularly useful criterion for homology. The reason for this is clear: Similarity can result from convergence. Thus whereas similarity is factual, homology must remain a hypothesis (Patterson 1988). But if it is a hypothesis, then it is testable (e.g., Brady 1985, Lyman 2001, McKittrick 1994).

Constructing Phylogenetic Trees

In its simplest form, cladistic analysis proceeds via four steps, the end process being the construction of phylogenetic trees that are useful in understanding not only the evolutionary relationships among taxa but also the evolutionary changes in characters that the taxa exhibit.

Step 1: Generating a Character-state Matrix

The data set used in any cladistics analysis is a matrix that lists the taxa and the various states that their characters exhibit. This shows the states of the characters exhibited by each taxon. How do we choose appropriate characters, with appropriateness meaning how well a character performs in allowing us to separate taxa phylogenetically? In other words, how do we know a priori that a particular character will produce a phylogenetic signal? The bottom line is we don't. In reality, character choice is a classic case of trial and error, with a good measure of inductive reasoning thrown in. Archaeologists, like biologists, do not go into phylogenetic reconstruction with *no* prior knowledge of which



characters might be useful. They know from chronological tracking—by means of, for example, radiometric dating, seriation, or superposition—or they strongly suspect, how certain characters change states over time. Other character polarity might not be so obvious in terms of which states are ancestral and which are derived, but even here prior knowledge offers at least a reasonable means of selecting useful characters.

Step 2: Establishing the Direction of Evolutionary Change in Character States

Several methods have been developed to facilitate establishing the direction of evolutionary change in character states, one of which is outgroup analysis (Maddison et al. 1984). Basic to the method is identifying a close relative of the taxa in the study group. The logic is this: When a character occurs in two states among taxa in 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. It is important to make clear that analytical use of the term “parsimony” has nothing to do with whether evolution itself is parsimonious. Rather, it has to do with logical argumentation: It is more parsimonious to make as few ad hoc phylogenetic hypotheses as possible (Sober 1983).

Step 3: Constructing Branching Diagrams of Taxa

After the probable direction of change for the character states has been determined, usually through the use of computer programs designed for that purpose (see below), the third step is to construct a branching diagram that shows phylogenetic relationships of the taxa. 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 they are derived. Again, this is usually done with the assistance of computer programs. Various methods have been used for phylogenetic inference, each based on different models and each having its own strengths and weaknesses (Archibald et al. 2003, Goloboff and Pol 2005, Pol and Siddall 2001, Sober 2004). One, maximum parsimony, is based on a model that seeks to identify the least number of evolutionary steps required to arrange the taxonomic units under study. Parsimony trees are evaluated on the basis of the minimum number of character-state changes required to create them, without assuming a priori a specific distribution of trait changes. Two other commonly used methods, maximum likelihood and Bayesian inference, are probabilistically based, where the criterion for constructing trees is calculated with reference to an explicit evolutionary model from which the data are assumed to be distributed identically (Kolaczkowski and Thornton 2004). Cultural phylogenies that are based on language evolution have relied largely on probabilistic methods (e.g., Currie and Mace 2011, Gray et al. 2009). Those not based on language evolution—archaeological phylogenies, for example, which are more prospective—tend to rely on parsimony (e.g., Buchanan and Collard 2007, 2008, García Rivero and O’Brien 2014, O’Brien et al. 2001, 2012, Tehrani and Collard 2002).

Each group of taxa defined by a set of intersecting lines corresponds to a clade. Ideally, the distribution of character states among the taxa will be such that all the character-state relationships are congruent, but we have never witnessed such a happy event. Far more likely, a tree will contain multiple character states that show up in lines not related directly through one common ancestor. These are referred to as *homoplasies*. One kind of homoplasy results from character-state reversals—meaning, for example,

that character state A changed to state A' and then at some later point in the lineage reverted to state A. We view this kind of homoplasy more as a classification problem, meaning that rarely if ever will precisely the same character state reemerge after it disappears. More likely, the classification system being used makes it *appear* as if the new character state is a homoplasy. Another kind of homoplasy results from parallelism or convergence—organisms, perhaps because of anatomical and/or environmental constraints (the first the result of common history, the second because of similar environments), independently evolve the same character state.

Step 4: Generating an Ensemble Tree

The fourth step is to generate an ensemble tree that is consistent with the largest number of characters and therefore requires the smallest number of homoplasies to account for the distribution of character states among the taxa. There are several ways of generating such a “consensus” tree, one of which is to construct a majority-rule consensus tree, which places taxa in their most common positions across the sample of trees (Swofford 1991). The percentage of trees in which the taxa must occur in the same positions can be varied between 50 percent and 100 percent. An example of a 50-percent majority-rule consensus tree is shown in Fig. 2. Notice that the G + H + I clade has the same arrangement in two out of the three trees; thus that arrangement is the one shown in the consensus tree. The same is true for the E + F clade. It also holds true for the other four taxa, although it is not as readily apparent. Note also that the middle tree just happens to have the same arrangement of taxa as the consensus tree.

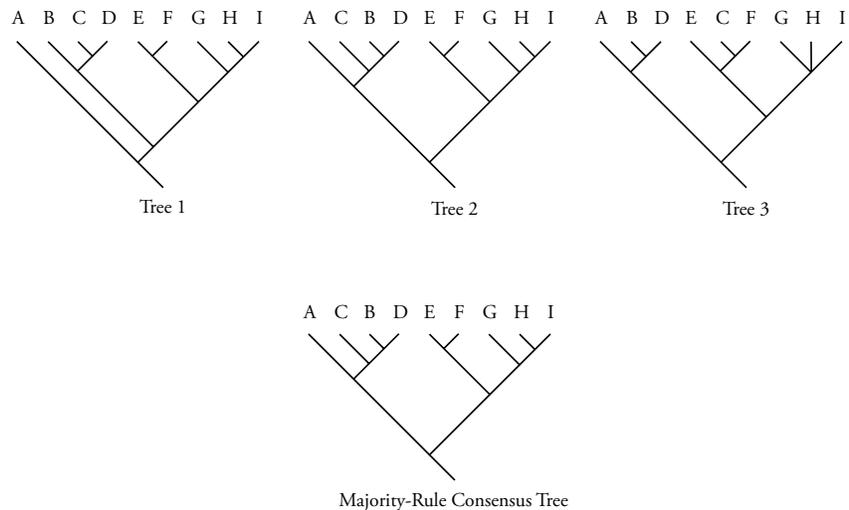


Fig. 2. Fifty-percent majority-rule consensus tree based on three trees of equal length.

Computers and Cladistics

As the number of taxa and/or the number of characters and character states increases, constructing trees and resolving them becomes impossible to do by hand. There are

numerous programs available to perform all kinds of calculations and tree building. By far the best resource for perusing the various programs and finding out what they can do is on the Web at <http://evolution.genetics.washington.edu/phylip/software.html>. The site is maintained by Joseph Felsenstein of the Department of Genome Sciences at the University of Washington. At the time of this writing, June 2014, Felsenstein had listed almost 400 phylogeny packages and 54 free Web servers.

Perhaps the most widely used series of programs, and certainly one of the more user-friendly, is PAUP* (Phylogenetic Analysis Using Parsimony [and Other Methods]), written by David Swofford (1998) of the Department of Biological Science and the School of Computational Science and Information Technology at Florida State University. It currently is in version 4.0 (beta) and is a cross-platform program, running on Macintosh, Windows, and UNIX machines. Because the Macintosh version offers pull-down menus for all commands and settings, it is by far the simplest to use. However, the current GUI-based version is compatible only with MacOS 9 and earlier. Users with access only to MacOS 10 and later machines are restricted to the command-line UNIX version of PAUP. Originally, PAUP implemented only parsimony, but starting with version 4.0 (when the program became known as PAUP*) it also supports distance matrix and likelihood methods.

PAUP* and other tree-building programs can use several search methods to generate the shortest possible trees. There are two main kinds of searches: exact methods and heuristic methods. Which method should one use? That depends in large part on the amount of time available for analysis. Tree building is not a rapid process, especially with a large number of taxa. Lipscomb (1998: 40) summed up the bottom line beautifully: “Balancing the need for precision in finding the shortest tree against a reasonable amount of computation time is one of the most difficult computational problems for systematists.”

Exact methods are guaranteed to find all shortest trees—if one has the time and computational equipment. The exhaustive search sorts through every possible tree until it finds the shortest one(s). The branch-and-bound search works by checking only those trees that are likely to be shorter than the shortest tree already found. It first creates a tree—any tree—and begins creating other trees to compare against it. As soon as it finds a tree of shorter length, that tree becomes the one against which to compare new trees. If a certain partial arrangement of taxa looks as if the trees it will produce are going to be longer than the comparative tree, the program doesn’t waste time continuing to build trees in that direction. It abandons that direction and takes off in another one. Once it finds a partial solution that looks promising, it continues building in that direction until it finds a shorter solution or decides it’s moving toward a longer tree and abandons that search vector.

If the data set is small, exact searches might be feasible, but for large data sets we might have to turn to heuristic methods. In heuristic searches there are no guarantees that even one shortest possible tree will be found, but we might get close. One heuristic method is branch swapping, of which there are two kinds. In local swapping, adjacent branches of a tree are systematically swapped until a shorter length is found. The routine continues swapping branches until no shorter trees are found (or until the operator terminates the search). In global swapping, the program slices the trees into “subtrees” and then rearranges the various “subtrees” into new trees and calculates their length.

An Archaeological Example

The earliest well-documented human occupation of North America is marked by the occurrence of bifacially chipped and fluted projectile points (Fig. 3) that date roughly 13,300–11,900 calBP (Faught 2008, Hamilton and Buchanan 2007)—a time period referred to as the Early Paleoindian period. Despite the fact that it is marked by the presence of fluted points, the Early Paleoindian period encompassed a range of spatial and temporal variation in such things as settlement pattern, diet, and technology (Haynes 2002, Meltzer 1993). The picture that has emerged for the first several hundred years of the Early Paleoindian period is one of hunters who targeted a wide range of large game animals, including mammoth, mastodon, bison, and, in the eastern woodlands, caribou (Cannon and Meltzer 2004, Robinson et al. 2009, Surovell and Waguespack 2009).

The most widely accepted hypothesis for the origin of Paleoindian peoples is that hunter-gatherer groups migrated by way of Beringia, the landmass between Siberia and North America that was exposed by sea-level reduction during glacial intervals (Haynes 2005). Once in eastern Beringia, the groups gained entry to the interior of the continent, specifically the Great Plains, by way of an ice-free corridor between two ice sheets that is hypothesized to have opened around 14,000 calBP (Catto 1996). Thereafter, Early Paleoindians spread rapidly throughout North and South America, reaching the Patagonian Plateau within just a few centuries (Fiedel 2000).

Much of our work over the last 15 years has focused on flaked-stone weaponry from the Early Paleoindian period (Buchanan and Collard 2007, 2008, Buchanan and

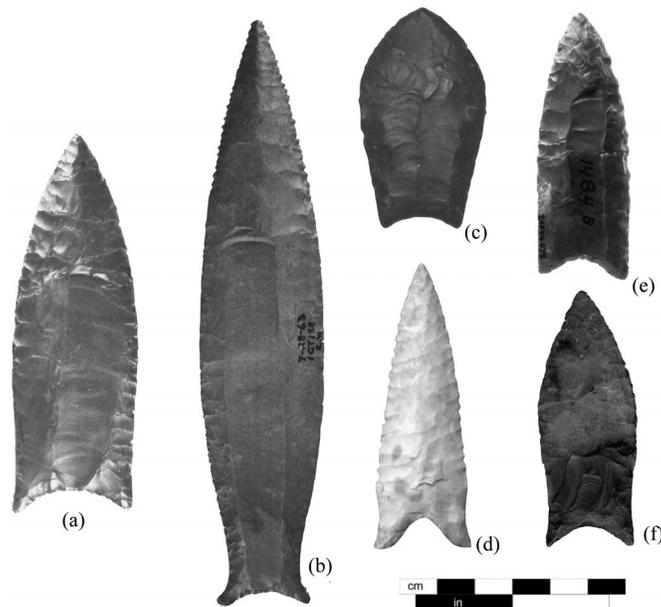


Fig. 3. Examples of Paleoindian fluted projectile points from North America: (a) Clovis (Logan Co., Kentucky); (b) Cumberland (Colbert Co., Alabama); (c) Crowfield (Addison Co., Vermont); (d) Dalton (Lyon Co., Kentucky); (e) Gainey/Bull Brook (Essex Co., Massachusetts); (f) Suwannee (Santa Fe River, Florida).

Color image of this figure appears in the color plate section at the end of the book.

Hamilton 2009, Buchanan, Kilby, Huckell et al. 2012, Buchanan, O'Brien, Kilby et al. 2012, Buchanan et al. 2011, 2014, Collard et al. 2010, Eren et al. 2013, Hamilton and Buchanan 2007, 2009, O'Brien, Boulanger, Buchanan et al. 2014, O'Brien, Boulanger, Collard et al. 2014, O'Brien et al. 2001, 2002, 2012). At the center of analysis is the Clovis point—an elongated symmetrical form that exhibits a concave base and a series of flake-removal scars on one or both faces that extend distally (toward the pointed end) (Fig. 3a). Despite the fact that a single type name, Clovis, is applied to many of these projectile points, considerable regional variation is evident across North America (Buchanan et al. 2013). For example, there are significant differences between points from the East and the West and among points from some subregions, the conclusion being that Clovis people modified their points to suit the characteristics of local prey and/or the habitats in which they hunted. Sometimes other projectile-point type names are given to regional variants (Fig. 3b–f).

One set of analyses was geared to understanding the evolution of points in the southeastern United States (O'Brien et al. 2001, 2002). The first problem encountered was with the taxa that could be used. Although types are commonly used to classify points from eastern North America, there are two major problems with this approach. One is a lack of redundancy in the characters used to create types. In the case of projectile points, one point type may be defined primarily by blade length and curvature, whereas another point type may be defined by basal shape and curvature. The other problem is that types are extensionally defined (Dunnell 1986, Lyman and O'Brien 2000, 2002), meaning that definitions are derived from the sorting of specimens into groups based on overall similarity and then describing the average properties of each group of specimens. Extensionally defined types are often fuzzy amalgams of character states because such units (types) conflate the taxa and the specimens in them (Lyman and O'Brien 2002, O'Brien and Lyman 2002).

To circumvent the problems of using established types, O'Brien and colleagues (2001, 2002) turned to paradigmatic classification (Dunnell 1971) in order to create classes (taxa).¹ Each class comprises eight unweighted characters, each of which has a variable number of character states (Table 1). The characters are defined as follows; locations of the characters are shown in Fig. 4:

- I. Height of maximum blade width—the quarter section of a specimen in which the widest point of the blade occurs.
- II. Overall base shape—qualitative assessment of the shape of the basal indentation.
- III. Basal indentation ratio—the ratio between the medial length of a specimen and its maximum length; the smaller the ratio, the deeper the indentation.
- IV. Constriction ratio—the ratio between the minimum blade width (proximal to the point of maximum blade width) and the maximum blade width; the smaller the ratio, the higher the amount of constriction.
- V. Outer tang angle—the degree of tang expansion from the long axis of a specimen; the lower the angle, the greater the expansion.
- VI. Tang-tip shape—the shape of the tip ends of tangs.
- VII. Fluting—the removal of one or more large flakes (> 1 cm long) from the base of a specimen and parallel to its long axis; subsequent flake removal may obliterate earlier flake scars.
- VIII. Length/width ratio—the maximum length of a specimen divided by its maximum width.



Table 1. System Used to Classify Projectile Points from the Southeast

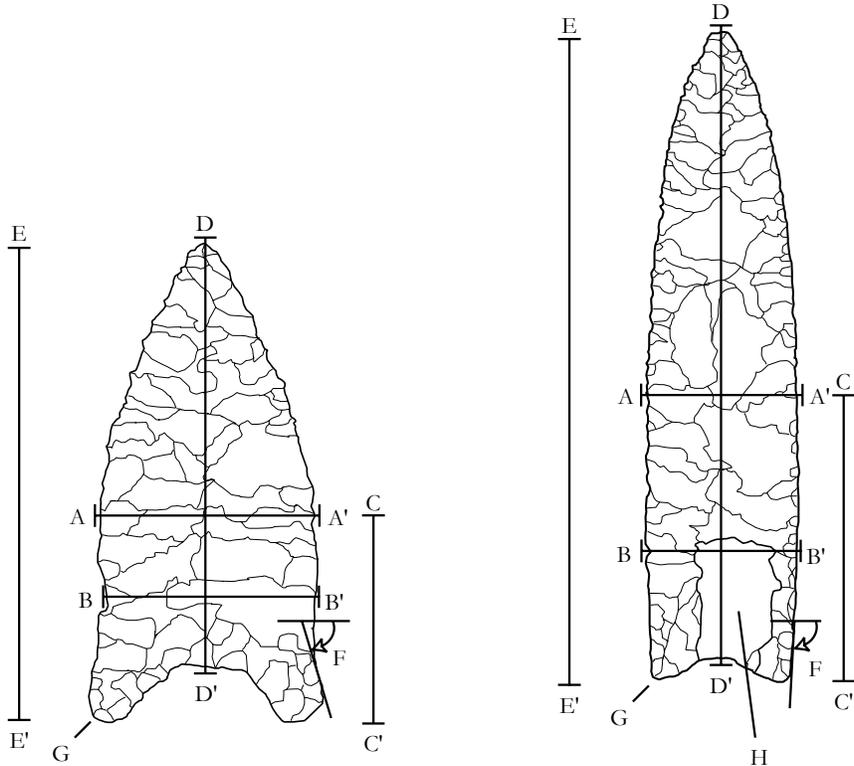
Character Character State	Character Character State
I. Location of Maximum Blade Width	V. Outer Tang Angle
1. proximal quarter	1. 93°–115°
2. secondmost proximal quarter	2. 88°–92°
3. secondmost distal quarter	3. 81°–87°
4. distal quarter	4. 66°–80°
II. Base Shape	5. 51°–65°
1. arc-shaped	6. $\leq 50^\circ$
2. normal curve	VI. Tang-Tip Shape
3. triangular	1. pointed
4. Folsomoid	2. round
III. Basal-Indentation Ratio ^a	3. blunt
1. no basal indentation	VII. Fluting
2. 0.90–0.99 (shallow)	1. absent
3. 0.80–0.89 (deep)	2. present
IV. Constriction Ratio ^b	VIII. Length/Width Ratio
1. 1.00	1. 1.00–1.99
2. 0.90–0.99	2. 2.00–2.99
3. 0.80–0.89	3. 3.00–3.99
4. 0.70–0.79	4. 4.00–4.99
5. 0.60–0.69	5. 5.00–5.99
6. 0.50–0.59	6. ≥ 6.00

^a The ratio between the medial length of a specimen and its total length; the smaller the ratio, the deeper the indentation.

^b The ratio between the minimum blade width (proximal to the point of maximum blade width) and the maximum blade width as a measure of "waistedness"; the smaller the ratio, the higher the amount of constriction.

Seventeen classes had a minimum of four specimens each (83 specimens total), and they were the ones used in the analysis. The resulting tree—and, interestingly, there was only one most parsimonious tree—is shown in Fig. 5. It has a length of 22, a retention index (RI) of 0.70, and a CI of 0.59.² The RI and CI values are high enough to offer encouragement that the tree is fairly representative of the true phylogeny, but there are still some problematic features. Notice that the tree contains several *polytomies*, or points at which the program cannot make a simple dichotomous split. For example, there is a polytomy in the form of a trichotomous branching that produces KC, CU, and the ancestor of the clade comprising BQDU + DUCold + DCQUBSow + DAQS + QC + QUDG + QDG. Phylogenetic analysis often assumes that diversification occurs only by a series of bifurcations, but this assumption is unnecessary and may obscure reality (Hoelzer and Melnick 1994). In fact, cultural transmission may result more often in polytomies than in simple bifurcation. Alternatively, in reality there may be a bifurcation, but the phylogenetic signal is too weak for the program to resolve the pattern. Thus it treats it as a polytomy.

Character-state changes—there are 22 of them, hence the tree length of 22—are represented by the small boxes in Fig. 5. Each box has two numbers associated with



Landmark Characters

- A-A' = maximum blade width
- B-B' = minimum blade width
- C-C' = height of maximum blade width
- D-D' = medial length
- E-E' = maximum length
- F = outer tang angle
- G = tang tip
- H = flute

Base Shapes

- arc-shaped 
- normal curve 
- triangular 
- Folsomoid 

Fig. 4. Locations of characters used in the analysis of projectile points (see Table 1 for character states). Character states for base shape are shown at the lower right.

reverted to an ancestral state. For example, character VI began in KDR, the outgroup, as state 2; it later changed to state 3 and then changed back to state 2 in the line that produced BQDU + DUCold.

Conclusion

As we have noted previously (O'Brien et al. 2012), the growing interest in cultural phylogenetics evident over the last two decades marks a return to the questions on which the founding of much of anthropology rests—a return that is important to the growth and continued health of anthropology. Why? Because, as Linder and Rieseberg (2004), point out, a reconstructed phylogeny helps guide interpretation of the evolution of traits by providing hypotheses about the lineages in which those traits arose and under what circumstances. Thus, it plays a vital role in studies of adaptation and evolutionary constraints.

Archaeology is a historical science, and its sole claim to unique status within the human sciences is its access to portions of past phenotypes—something that ethnographers, sociologists, psychologists, historians, and others who study humans do not have. Only archaeologists have access to the entire time span of culture, however it is defined. Historical questions are the most obvious ones archaeologists can ask, although this is hardly a strong warrant for asking them (Eldredge 1989). However, we believe archaeologists should ask historical questions not only because they have access to data that provide a direct test of historical hypotheses but also because answers to historical questions are critical to gaining a complete understanding of cultural manifestations occupying particular positions in time and space. To understand the operation of historical processes means that we not only have the units upon which the processes act in correct historical sequence but that we have them in a sequence that is correct from the standpoint of heredity. Cladistics is a method that allows us to do that.

Acknowledgments

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Note

1. We have also employed other methods of capturing shape, including creating a series of landmarks and then computing interlandmark distances for each specimen (Buchanan and Hamilton 2009; Hamilton and Buchanan 2009) and using geometric morphometric methods, in which shape is defined as the geometric properties of an object that are invariant to location, scale, and orientation (e.g., Buchanan et al. 2011, 2013). All have their strengths and weaknesses, but where our interests are in phylogenetic relationships and plotting spatially various character states, we have found paradigmatic classification to produce superior results (e.g., O'Brien, Boulanger, Buchanan et al. 2014).

2. How robust are the trees we generate? That is, how well do they approximate the one true phylogeny we assume exists? One calculation is the consistency index (CI), which measures the amount of homoplasy in a data set (Farris 1989b, Goloboff 1991). The index ranges from 0 (complete homoplasy) to 1.0 (no homoplasy) and is calculated by dividing the number of characters in the data matrix by the number of characters on the tree. There are several potential drawbacks to the consistency index, one of which is that the CI value is not independent of the number of taxa. When the number of taxa increases, the CI value will decrease. To overcome some of the problems, Farris (1989a, 1989b) developed the rescaled consistency index and the retention index (RI), the latter of which measures the fit of characters to a cladogram (the ratio of apparent synapomorphy to actual synapomorphy). The RI is calculated as

$$\frac{\text{Max. steps in matrix} - \text{No. of characters on tree}}{\text{Max. steps in matrix} - \text{No. of characters in matrix}}$$

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