

# Evolutionary Archeology: Current Status and Future Prospects

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Darwinian evolution can be defined minimally as "any net directional change or any cumulative change in the characteristics of . . . populations over many generations—in other words, descent with modification"<sup>1</sup> (p. 5). In archeology the population comprises artifacts, which are conceived of as phenotypic.<sup>2–4</sup> Extension of the human phenotype to include ceramic vessels, projectile points, and the like is based on the notion that artifacts are material expressions of behavior, which itself is phenotypic. Archeology's unique claim within the natural sciences is its access to past phenotypic characters. Thus, historical questions are the most obvious ones archeologists can ask, although admittedly this is hardly a strong warrant for asking them. But if the issue is evolution, then historical questions must be asked. Posing and answering historical questions is the goal of evolutionary archeology.<sup>5</sup>

Any evolutionary investigation is a two-step process. First, lineages are constructed, here artifact lineages; second, explanations are made for the lineages being the way they are.<sup>6,7</sup> The first step is the documentation of descent with modification, meaning that sequent phenomena are related through

transmission. The second step involves the identification of mechanisms that caused changes or periods of stability within a lineage. Accomplishing the first step requires chronological control and documentation of heritability between the archeological manifestations comprising the lineage. Accomplishing the second step requires that hypothesized mechanisms such as natural selection, which result in sorting, be tested during periods of change and that the hypothesized absence of sorting (the presence of stabilizing mechanisms) be tested during periods of stasis. The analytical challenge is to determine which is applicable in any given situation. This challenge demands construction of a set of units for measuring and describing a lineage's fossil record—that is, for writing a historical chronicle. Explaining why a lineage has the appearance it does demands that the uniqueness of historical contingencies and configurations be considered.

The minimum requirements for evolution to occur are variation among individuals (at some scale), inheritance of variant characteristics (requiring transmission), and differential perpetuation of variant charac-

ters (variants are replicated at differing frequencies). The concepts of replicators and interactors are useful for exploring these requirements. Replicators are units that are more or less equivalent to genes; interactors are units more or less equivalent to the phenotype.<sup>8</sup> Replicators and interactors are concepts rather than things, and it is important to be clear about what they comprise. A replicator is an entity that passes on its structure directly through replication. An interactor is an entity that directly interacts as a whole with its environment in such a manner that replication is differential *as a result of selection*.<sup>9</sup> The emphasized phrase is critical because replication may be differential as a result of the vagaries of transmission (the replicators available for transmission, the replicators actually transmitted, how often a replicator is transmitted) rather than as a result of natural selection, in which the differential extinction and proliferation of interactors result in the differential perpetuation of the replicators that produced them.

Selection works directly on interactors and only indirectly on replicators. Evolutionary archeology does not equate evolution precisely with changes in the frequency of classes of replicators—evolutionary processes can result in stasis—but does realize that such changes typically accompany evolution. Evolution can be described as a change—not to preclude stasis—in adaptation and diversity or as a change in relative frequencies of classes of phenomena comprising populations. In evolutionary archeology, the populations are artifacts. Sequent populations of artifacts that comprise lineages, or

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lines of heritable continuity, are termed “traditions” by Americanist archeologists. We prefer “lineage” because of its overtly evolutionary implications.

One major difficulty many archeologists and anthropologists have with using evolutionism to write and explain the history of a cultural lineage resides in a set of interrelated arguments. The operation of cultural transmission is independent of genetic transmission; differential replication of cultural characters has nothing to do with differential biological reproduction of humans; genetic inheritance and cultural inheritance are completely independent of one another; and cultural evolution is faster than biological evolution. These statements are correct in the sense of specifying empirical generalizations derived from the ethnographic record of numerous cultures, including our own, but the fact that such things are possible does not mean they are inevitable.<sup>10</sup>

It has long been observed that cultural transmission is independent of biological transmission,<sup>11,12</sup> but this does not mean that cultural transmission will never be correlated with the degree of genetic relatedness between a transmitter and a receiver. We hazard the guess that in groups whose social organization is founded on kinship rather than on, say, economic status, considerable cultural transmission occurs between close genetic kin, some occurs between remote genetic kin, and little occurs between nongenetic acquaintances. This is an empirical matter that requires further study. The punch line is that the independence of biological and cultural evolution must be treated as a null hypothesis. And although the hypothesis can be tested in an ethnographic setting, a significant problem remains: We want to explain the archeological record. Simpson<sup>13</sup> was the first to grapple with the problem of genetic change being invisible to the paleontologist. The net result of his efforts was the distinction between what today are termed microevolution and macroevolution, the former concerning what a biologist can perceive among living organisms—genetic change—and the latter concern-

ing what a paleontologist can perceive between species and higher taxa—large-scale phenotypic change.

Archeologists will never be able to perceive change in cultural replicators the way an ethnographer might. What archeologists can see is change in artifacts of various scales. Granting that artifacts are likely “polygenic” or, more properly, polyreplicator, archeology typically is forced to study macroevolutionary phenomena. One advantage that cultural transmission has is that transmission is freed from more or less fixed units, meaning that transmitters and receivers both can analyze recipes into constituent parts, or replicators.<sup>14</sup> This conclusion has three significant implications.

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First, because humans can intentionally make choices about how to behave in particular situations based on learned possibilities, they sometimes are considered to be adaptively plastic and thus not subject to the forces of natural selection.<sup>15</sup> Numerous nonhuman taxa, however, are ecophenotypically plastic, but this does not completely shelter them from natural selection and, in fact, sometimes presents selection with variation on which to work. Further, the conclusion that adaptive plasticity shields humans from natural selection is an empirical generalization founded on temporally limited obser-

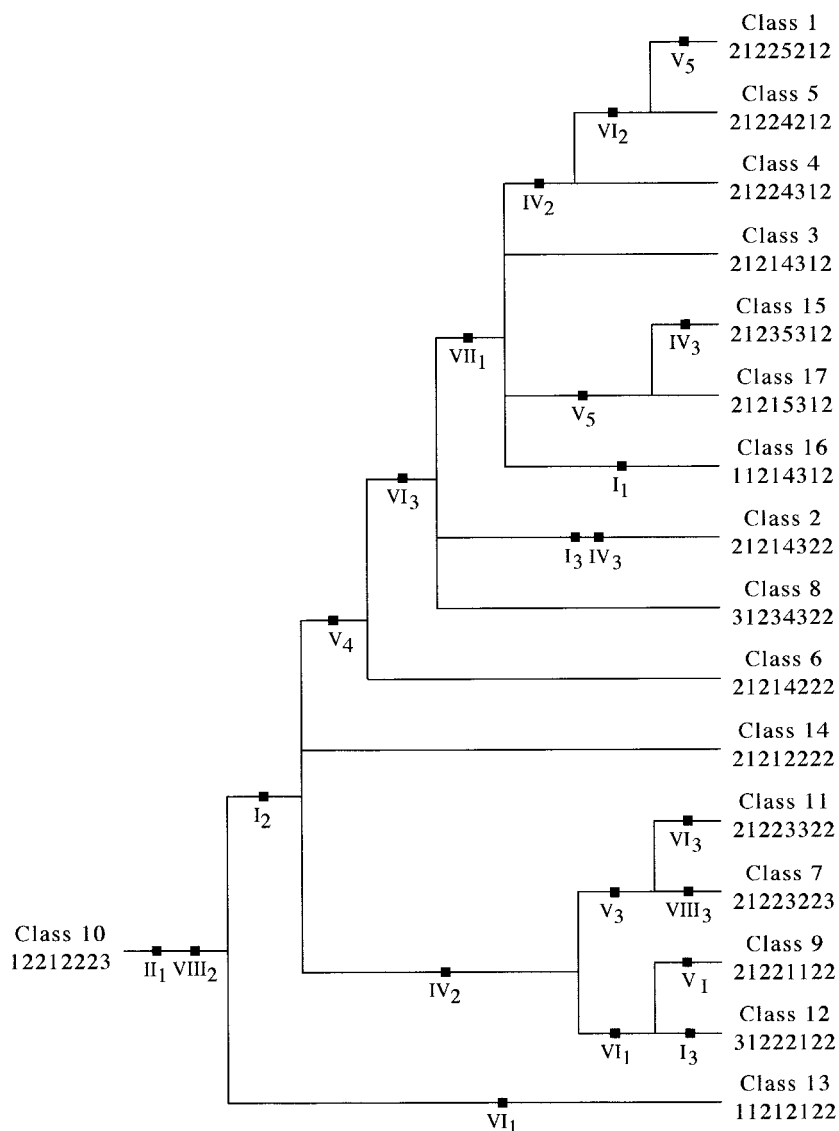
vations of microevolutionary processes. Finally, to suggest that humans can dodge natural selection by making choices regarding behaviors is to suggest that artificial selection and natural selection are separate and distinct; modern biology takes the former to be a special case of the latter.<sup>8</sup> Merely because people can eliminate some possible behaviors from consideration based on knowledge of the possible outcomes of acting out those behaviors in particular situations does not mean they will always choose a behavior that is immune to natural selection.<sup>5</sup>

Second, archeologists regularly consider the long-term effects of cultural change on human reproductive success, largely because of the lack of intragenerational temporal resolution afforded by archeological chronometers.<sup>16</sup> That admission does not deny the importance of intent and decisions regarding change over time in human behaviors. To the contrary, it underscores that as archeologists we must shift from the level of causes that are microevolutionary, proximate, and archeologically invisible to causes such as natural selection that are macroevolutionary, ultimate, and archeologically visible. Our belief that this necessity will eventually produce a workable solution in archeology is predicated on the success of punctuated equilibrium in paleobiology,<sup>17</sup> despite the existence of a chasm between (genetic) microevolution and (intertaxonomic, paleontological) macroevolution.

Third, the microevolution–macroevolution scale distinction does not present an insurmountable hurdle to evolutionary archeology. Archeologists can directly monitor the replicative success<sup>18</sup> of cultural characters, a form of differential persistence of variants that can be completely independent of biological reproduction. The replicative success of a particular cultural character may or may not affect the reproductive success of the bearer—this is an empirical matter—which means that characters may be replicated irrespective of whether they confer a selective advantage or disadvantage. Evolution involves the transmission and replication of replicators. There are no agreed-on units

### Box 1. The Use of Cladistics in Archeology

We used cladistics to create a phylogenetic ordering of projectile points from the southeastern United States that ostensibly date to about 9250–8500 B.C.<sup>30</sup> Projectile-point form varied considerably during that period, and although much of the variation undoubtedly was temporally related, there is no agreed-on historical ordering of traditional point types. There also must have been heritable continuity between at least some sequent forms, but this has never been documented. Instead, prevailing wisdom ties changes in form to such mechanisms as diffusion and population displacement. We used characters and character states to create our taxa, or classes, instead of relying on traditional, extensionally derived types. PAUP\* (version 4)<sup>31</sup> was used to generate the tree (interestingly, only a single tree was produced). The tree contains several polytomies. For example, a trichotomous branching produces classes 8, 2, and the clade comprising classes 1 + 5 + 4 + 3 + 15 + 17 + 16. The first characters in our outgroup (class 10, defined as 12212223) to change were character II, base shape, which changed from state 2 (normal curve) to state 1 (arc-shaped) and character VIII, length-width ratio, which changed from state 3 (3.00–3.99) to state 2 (2.00–2.99). This produced an ancestor (11212222), which in turn produced both class 13, after an additional change in character VI from state 2 to state 1, and an ancestor to all the other taxa. The latter ancestor underwent a change in character I, location of maximum blade width, from state 1 (proximal quarter) to state 2 (second-most proximal quarter) and produced an ancestor (21212222). That ancestor produced class 14 (with no modification), the clade comprising



classes 11 + 7 + 9 + 12, and the clade comprising all remaining taxa.

Homoplasy, including functional convergence, is as problematic in reconstructing phylogenetic histories of artifacts as it is in reconstructing the histories of organisms. The tree

shown here has a retention index of 0.7000 and a consistency index of 0.5909. The consistency index is much higher than expected, but still low enough to indicate that considerable homoplasy is present.

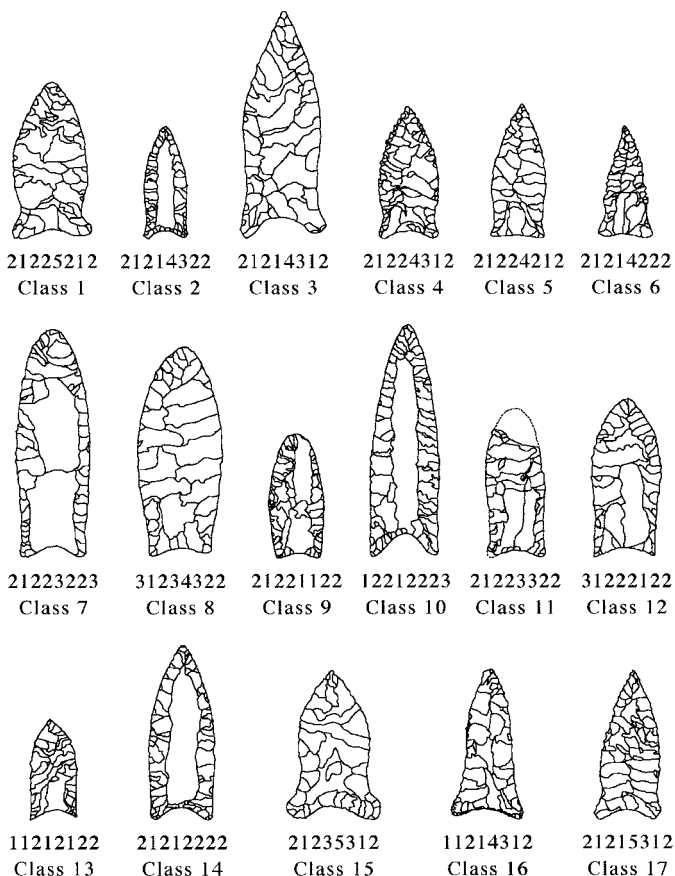
of cultural transmission,<sup>19</sup> but we can define these units theoretically as the largest units of socially transmitted information that reliably and repeatedly withstand transmission with a high degree of fidelity.<sup>20</sup> The fre-

quency of such units of information is a product of transmission, selection, and innovation. The archeologist's artifacts, like a paleontologist's fossils, are the products that result from these processes.

### ISSUES IN MODERN EVOLUTIONARY ARCHEOLOGY

Evolutionary archeology has dealt with myriad issues in its attempt to rewrite evolutionism in archeological

## Box 1. Continued



Character Character state	Character Character state
I. Location of Maximum Blade Width	V. Outer Tang Angle
1. proximal quarter	1. 93°–115°
2. second-most proximal quarter	2. 88°–92°
3. second-most distal quarter	3. 81°–87°
4. distal quarter	4. 66°–80°
II. Base Shape	5. 51°–65°
1. arc-shaped	6. ≤ 50°
2. normal curve	VI. Tang-Tip Shape
3. triangular	1. pointed
4. Folsomoid	2. round
III. Basal Indentation Ratio *	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 †	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

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

† 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.

terms.<sup>21</sup> We have chosen three closely related topics—units and their construction, life-history graphs, and transmission—that are broad enough to allow us to explore briefly several related issues that crosscut them.

## Units and Their Construction

Evolutionary archeologists have spent considerable time examining various units that have been proposed to track phenotypic change.<sup>21–26</sup> In the process, they have emphasized the distinction between empirical (real) units and theoretical (measurement) units, the latter defined as units that have explanatory significance because of, and only because of, their theoretical relevance to the particular problem at hand. Much of the empirical research that has been done in evolutionary archeology has bypassed traditional archeological units and employed a particular kind of theoretical unit, the class, which is a measurement unit that specifies the necessary and sufficient conditions that specimens must display in order for them to be identified as a member of that class. Morphospace is defined by a number of mutually exclusive characters, each with a set of character states; classes are defined by the intersection of character states.<sup>27</sup> The number of characters and character states included in a particular classification is unrestricted. Thus it is unnecessary for all classes to have empirical members. Analytically, empty morphospace is just as important as filled morphospace.

The important point here is not that evolutionary archeology sees no role for traditional units such as named artifact types, some of which are excellent for tracking the passage of time or monitoring cultural transmission. But if our interest is in monitoring small-scale change through time, traditional units are inappropriate for two reasons. First, there often is a lack of redundancy among types in terms of the characters used to define the types: One projectile-point type might be defined in terms of base shape and degree of shouldering, whereas another type might be defined on the basis of base shape and angle of notching. How can we hope to measure change when different characters



are used to create the units that ostensibly are being used to measure it? Second, artifact types in most cases are extensionally defined.<sup>28</sup> The definitions are derived by sorting through a pile of specimens, placing similar specimens together, and using visible properties of the specimens as the basis of the definitions. The problem reduces to this: Extensionally derived units (types) conflate the unit and the specimens in it—a dilemma recognized by biologists<sup>29</sup> with respect to organisms and taxa.

### Life-History Graphs

Evolutionary archeologists use several methods to construct hypotheses of phylogeny and to study phylogenetic histories of artifact lineages, two of which are cladistics and clade-diversity diagrams.

### Cladistics

The logical basis for extending cladistics into archeology is the same as it is in biology: Artifacts are complex systems, comprising any number of replicators. The kinds of changes that occur over generations of tool production are constrained. New structures and functions almost always arise through modification of existing structures and functions as opposed to arising *de novo*. The history of these changes—additions, losses, and transformations—is recorded in the similarities and differences in the complex characteristics of related objects, that is, in objects that have common ancestors (Box 1).

Cladistics is not a method that depends on genetic continuity as a basis for reconstructing phylogeny.<sup>32</sup> It depends solely on heritable continuity, irrespective of the mode of transmission. Proper use of cladistics in archeology recognizes both biological (genetic) and cultural transmission, both of which play a role in the evolution of such things as tool lineages. As in biology, if there is phenotypic change and if, over time, enough variation is generated, cladistics might indeed be able to detect the phylogenetic signal. If so, we can create phylogenetic orderings that have testable implications.<sup>30</sup>

Objections to the applicability of

cladistics to archeological phenomena might take several forms. First, it has been argued that although there might be tool lineages, they are almost impossible to discover archeologically because of the kind of process—cultural evolution—that produced them.<sup>33–35</sup> Under this view, cultural evolution is seen as vastly different from biological evolution, with a faster tempo and often a different mode, reticulation.

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Both of these differences swamp all traces of phylogenetic history and thus reduce the cultural landscape to little more than a blur of interrelated, particularly hybrid, forms. We agree that cultural evolution probably is, in most respects, faster than biological evolution and that cultural evolution might on occasion involve reticula-

tion, but we do not view these aspects as being theoretically problematic. Biological evolution often involves reticulation, especially in the plant kingdom, but this has not precluded phylogenetic analysis. In related fashion, paleobiologists who examine the phylogenetic history of fossils must assume that the units of their analysis, sets of morphometrically similar fossils, termed species, in fact comprise species and thus do not interbreed. In other words, genetic transmission is assumed to occur only within a lineage of some taxonomic scale—species, genera, families, and so on. Phylogenetic analysis of artifact lineages requires the same assumption, that cultural transmission is primarily within either a lineage or a series of closely related lineages rather than between distantly related lineages.

Reticulation is a red herring that deflects attention from what really goes on most of the time in cultural traditions. Individual characters or character states can originate inside a tool lineage, just as they can originate outside a lineage and, through transmission, be grafted onto preexisting forms within that lineage. But why should this be equated with hybridization? The answer is that it should not, given the marked difference in scale. That a single individual of a species occasionally breeds with an individual of another, closely related species, even though the two species otherwise interbreed only internally, does not destroy the phylogenetic signal of either. The addition of those extramural characters or states might interfere with the phylogenetic signal we are trying to detect, but this is simply an analytical hurdle, not a reason to abandon cladistics. Goodenough<sup>36</sup> makes an excellent point with respect to language: “Contact between Japan and the United States has resulted in considerable borrowing in language and culture by Japan and some reverse borrowing by the United States, but their languages and cultures retain their respectively distinct phylogenetic identities” (p. 178).

The second objection that might be raised against the use of cladistics in archeology is the same one that has been raised in biology with respect to intraspecific applications of phyloge-

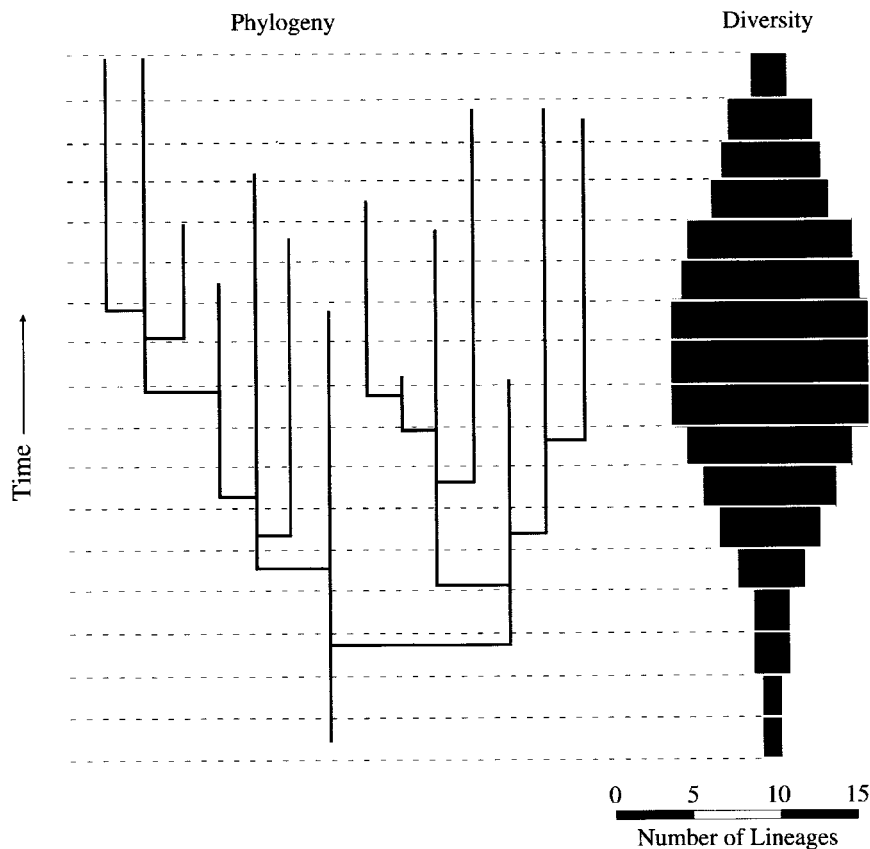


Figure 1. A model for producing a clade-diversity diagram. The phylogenetic history of taxa is shown on the left, and the resulting clade-diversity diagram is shown on the right. Once the phylogenetic history of related taxa has been worked out, including placement of their starting and ending points, the data are summarized as at the right, which shows the waxing and waning of the number of taxa (after Raup and coworkers<sup>40</sup>).

netic methods: Are we even dealing with a nested hierarchy to begin with? In other words, are the terminals in question themselves related hierarchically? We argue that in archeology we are dealing with nested hierarchies, irrespective of whether characters or character states are “borrowed” from outside a lineage. Cultural phenomena reside in a series of nested hierarchies that comprise traditions, or lineages, at ever more inclusive scales and are held together by cultural as well as genetic transmission. We agree that in practice the lines between nested hierarchies and reticulating (not hybridizing) networks are sometimes blurred, just as we agree that without a boundary around the reticulating networks there can be no nested hierarchy, and hence no monophyly.<sup>37</sup> Such boundaries are fuzzy at best, and often are difficult to de-

limit, but they are by no means beyond our power to determine archeologically, as several studies have indicated.<sup>24,38,39</sup>

### Clade-Diversity Diagrams

Once an artifact lineage has been constructed, the next task is to explain why that lineage has the appearance that it does. New artifact forms may replace old ones if the former have higher selective values than the latter, or new forms may be added to a particular lineage. Paleobiologists construct graphs showing the frequency of lower-level taxa within a particular higher-level taxon in order to display the history of life. Many of these graphs comprise what are referred to as clade-diversity diagrams, which display the fluctuating absolute frequency of taxonomic richness within monophyletic lineages over time.

What is graphed is the number of taxa within a higher taxon—the number of orders within a class, the number of families within an order, and so on. A monophyletic lineage, or clade, comprises one or more lineages having a common ancestor. New lineages arise only by cladogenesis, and each clade contains only and all those taxa deriving from a common ancestor plus the common ancestor. Because a clade-diversity diagram shows change in the number of extant lineages over time, it comprises a history of the origination and extinction of taxa within a clade, as shown on the left in Figure 1.

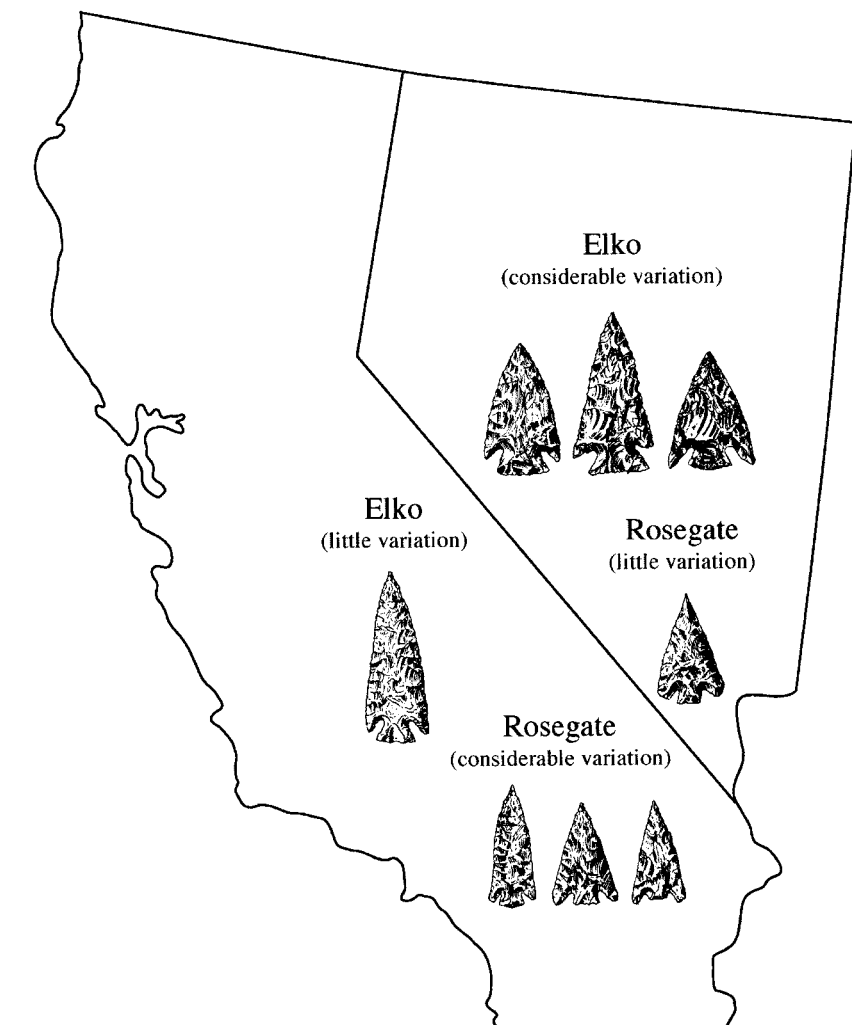
Once an artifact lineage has been constructed, included artifacts can be reclassified into functional units. Changes in the richness or heterogeneity of functional classes within an artifact clade over time would, we suspect, reveal much about adaptive history, such as the question of whether the bow and arrow replaced the atlatl in the overall weapon delivery system in the western United States or, as we believe, was simply an addition to that system.<sup>21,41</sup> Such evolutionary trends are at the macroevolutionary scale—here, within a clade—and are explicable in macroevolutionary terms. Similarly, studies of variation in functional characters, if arrayed against time,<sup>42</sup> might reveal much about the history of particular tool traditions.

Clade-diversity analyses could conceivably yield insights into adaptive plasticity. It might be reasonable to conclude that we are dealing with plasticity if a set of functional classes were to change from, say, manifestation A to manifestation B and then back to manifestation A, in concert with changes in the selective environment. Such a conclusion might involve demonstrating that changes in prey population took place coincident with functional changes in artifact assemblages. Archeologists employing foraging theory as a part of behavioral ecology have shown such changes in prey populations,<sup>43–45</sup> but correlations with changes in artifacts have rarely accompanied these studies. A caution must be noted, however, because even with apparent stability in the composition of artifact assemblages rendered in traditional functional terms (for example, knives,

## Box 2. Social Transmission Theory and Great Basin Projectile Points

Decades of work in the Great Basin of the western United States have demonstrated that the bow and arrow replaced the atlatl as the primary hunting weapon between about A.D. 300 and A.D. 600, a replacement that is documented by a reduction in the size of stone projectile points.<sup>50</sup> Many of the points manufactured across the Great Basin after A.D. 600, referred to as Rosegate series points, resemble the older forms, referred to as Elko corner-notched points. cursory examination of samples of both types of points might lead one to infer that Rosegate points are simply miniaturized versions of Elko points and, in a way, this is correct (see the drawing). However, that generalization obscures significant morphological variation among specimens of both types with respect to geographic location. Although all Elko points have a similar base shape—the primary character used to place specimens in the type—specimens from central Nevada vary considerably in weight and length, often being light and stubby, whereas those from eastern California are uniformly heavy and long relative to their width. Conversely, Rosegate points from central Nevada vary little in weight and basal width, whereas specimens from eastern California exhibit significant variation in those two characters. Bettinger and Eerkens<sup>38</sup> suggest that excessive resharpening drove the highly variable weight and length of Elko specimens from central Nevada. The lack of resharpening seen on specimens from eastern California is perhaps explained by the abundance of high-quality obsidian sources present. Elko points were simply discarded rather than resharpened. Resharpening, however, cannot explain why Rosegate points are more variable in basal width in eastern California than in central Nevada.

Bettinger and Eerkens proposed that the variation in Rosegate points is attributable to differences in how the inhabitants of the two regions obtained and subsequently modified bow-related technology. They framed their argument in terms of



two contrasting modes of cultural transmission, guided variation and indirect bias.<sup>11</sup> Under indirect bias, individuals acquire complex behaviors by opting for a single model on the basis of a particular trait identified as an index of the worth of the behavior. Under guided variation, individuals acquire new behaviors by copying existing behaviors and then modifying those behaviors through trial and error to suit their own needs. The social phase of this process tends to level differences between preexisting models and thus reduces variation at the population level. Subsequent experimentation, however, generates new behaviors and thus increases population-level variation.<sup>51</sup>

Neither transmission process is directly visible in the archeological record, but the statistical signatures of both should be clear. Traits acquired through guided variation should be much less strongly correlated with one another than are traits acquired through indirect bias. Following that logic, Bettinger and Eerkens proposed that in eastern California, where the weight and basal width of Rosegate points are poorly correlated, bow-and-arrow technology was both maintained and perhaps spread initially through guided variation. Conversely, in central Nevada, where the same traits are strongly correlated, bow-and-arrow technology was maintained and spread initially through indirect bias.

### Box 2. (Continued)

From an engineering standpoint there is no reason to suspect that the weight and basal width of a projectile point should be correlated. One might argue that a wider base adds to the overall weight of a point, but that gain is insignificant with respect to the trends observed in the Great Basin archeological record. Also there clearly is no significant correlation between the weight and basal width of the points from eastern California, whereas there is in the points from central Nevada. Thus, something other than mechanical constraint drives the disparity. That “something” could be differences in mode of social transmission. In central Nevada, Rosegate-point manufacturers acquired the multiple characters of arrow-point design as a complete package, not as piecemeal and independent acquisitions. In eastern California, manufacturers copied, eval-

uated, and modified existing designs independently.

Why the difference in adoption modes? Bettinger and Eerkens admit the answer is far from clear, but they hypothesize that eastern California groups might have acquired the bow and arrow from groups they interacted with only minimally—perhaps a different linguistic unit. That the eastern California groups’ knowledge of bow-and-arrow technology was limited in the beginning perhaps explains the unusually large number of broken arrow points that occur in eastern California. Of considerably more importance than the question of origin is the result that the forms of transmission have on the evolution of the social group. In cases where cultural transmission is through guided variation (and other modes involving substantial learning and experimentation), human behavior will tend to optimize

fitness in accordance with the predictions of the genetic model. Individual fitness is the index of success, with little opportunity for the evolution of group-beneficial behaviors.<sup>11</sup> In instances where transmission is through indirect bias, which tends to produce behaviorally homogeneous local populations, conditions may be right for the evolution and persistence of group-beneficial behaviors. Supporting this argument is evidence that Numic speakers who occupied the Great Basin in historical times spread rapidly out of eastern California at about A.D. 950.<sup>52</sup> The success of their rapid “colonization” of the basin was based on the competitive advantages of their adaptive strategies relative to those of pre-Numic peoples and the latter’s failure to readapt to competition, a failure caused in part by indirectly biased social transmission.

scrapers, and projectile points), how artifacts were used may have changed,<sup>46</sup> with no apparent change in functional classes. In such cases, classification according to manifestations of use-wear, a different way of measuring function, might or might not reveal variation coincident with changes in prey.

### Transmission

A necessary component of Darwinian evolutionism is heritability: A population of organisms can exhibit any amount of variation possible, both genetically and phenotypically, but if there is no means of passing on replicators to succeeding generations there can be no evolution. Modes of transmission and the way that various modes bias what is transmitted play a large role in evolutionary biology. The situation is no different in archeology. Here we are speaking of cultural transmission as opposed to genetic transmission, which opens the question of whether or not the former has any bearing on the fitness of culture-

bearing organisms. We believe it does, as do Bettinger and Eerkens<sup>38</sup>:

It seems clear to us that cultural transmission must affect Darwinian fitness—how could it be otherwise? And Darwinian fitness must also bear on cultural transmission. Again, how could that not be true? At minimum, humans must have the biological, hence, genetically transmitted, ability for the cultural transmission of behaviors that certainly affect Darwinian fitness. It is obvious, at the same time, that cultural transmission differs in fundamental ways from any form of genetic transmission . . . Again, this is what we would expect . . . [A]s with sexual reproduction, the human use of cultural transmission is simply the exploiting of an evolutionary opportunity. To deny that would imply that the culturally mediated evolutionary success of anatomically modern hu-

mans is merely serendipitous happenstance (p. 239).

Strictly in terms of transmission, whether the kind of character being transmitted is functional (shaped by selection) or selectively neutral is unimportant. What is important is whether a particular character gets transmitted at all and, if so, the form in which it is transmitted. Is the character that shows up in the recipient a faithful copy—a clone—of the character in the transmitter or is it different in form or structure? If the latter, is the variation so slight that it makes no difference in terms of the recipient’s fitness? In other words, are the two states of the character neutral? Of more importance, what effect might that variation, even if slight, have on much later generations? Slight variations, when coupled with succeeding slight variations, can have cascading effects on organisms that generationally are far removed from the time when a particular variant first appeared.

Despite the advances archeologists



have made in understanding the transmission process, from an evolutionary standpoint the most significant insights have come from nonarcheologists.<sup>11,12,47,48</sup> This collective work is often referred to as dual-inheritance theory. Although significant differences exist among the various authors in terms of the ways in which they view the transmission process,<sup>49</sup> enough similarities exist for those views to be considered here as complementary. Dual-inheritance theory posits that genes and culture provide separate but linked systems of inheritance, variation, and evolutionary change. The spread of cultural information is seen as being influenced by numerous processes, including natural selection, decision making, and the strengths of the transmitters and receivers. Several studies by behavioral ecologists have applied Boyd and Richerson's<sup>11</sup> models of cultural transmission to the archeological record. One of the most interesting of these studies is that by Bettinger and Eerkens,<sup>38</sup> who examined differences in projectile-point morphology in two locales in the Great Basin (Box 2).

### EVOLUTIONARY ARCHEOLOGY AND HUMAN BEHAVIORAL ECOLOGY: COMPLEMENTARY APPROACHES

In several respects, evolutionary archeology and human behavioral ecology are complementary approaches, although that complementarity has seldom been appreciated. Both view behaviors as phenotypic characters, just as they view behavioral by-products—pots, projectile points, and the like—as phenotypic characters. But there is a lack of consensus between the approaches on how best to examine past behavior.<sup>5,15</sup> Evolutionary archeology is a more macroevolutionary approach, whereas behavioral ecology is geared more toward examination of microevolutionary processes. Our view is based on the historical development of the approaches and the kinds of phenomena that have been the purview of each. As the approaches mature and a synthesis emerges from their unification, lines dividing them will blur. This is reminiscent of how things were in evolu-

tionary biology in the days of the Modern Synthesis in the late 1930s and early 1940s, when there was not only methodological disparity but also deep theoretical division among geneticists, neontologists, and paleontologists.<sup>53</sup>

A key area of emphasis in evolutionary archeology is the reconstruction of artifact lineages—that is, the demonstration of heritable continuity rather than simply historical continuity between archeological manifestations under study. This step, the demonstration of ancestor–descendant relationships, is fundamental to any evolutionary study. Once such a relationship has been demonstrated, attention can shift to macroevolutionary issues such as the tempo and

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**A key area of emphasis in evolutionary archeology is the reconstruction of artifact lineages; that is, the demonstration of heritable continuity rather than simply historical continuity between archeological manifestations under study.**

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mode of change. Evolutionary archeologists, at least those with a paleobiological bent, have begun to assemble the methods and techniques needed to examine such issues and to rewrite the relevant parts of the theory in archeological terms.<sup>21,41</sup>

For its part, human behavioral ecology brings to the table diverse interests ranging from social-transmission theory to foraging theory. In archeology the latter has been used to study how prehistoric human predators responded to changes in available prey,<sup>43,45</sup> as well as to monitor change in human population size.<sup>44</sup> But Grayson and Cannon<sup>46</sup> found that the most rigorous archeological applications of

foraging theory are problematic, even though they provide important insights into subsistence change and the relationships between human impacts on environments and human responses to those environments. Because foraging theory derives from observations of living organisms, the hypotheses derived from that theory are written in the equivalent of ethnographic terms and at the scale of ecological time. That is, the hypotheses are written at microevolutionary scales when the temporal dimension of the archeological record typically provides primarily a macroevolutionary scale of resolution.

Human behavioral ecologists are not unaware of the disparity between ecological and evolutionary time, nor are they unaware that behavior evolves. Their response would be that foraging theory and diet-breadth models are simply starting points for behavioral analysis. Although on occasion the charge has been leveled,<sup>54</sup> no behavioral ecologist we know would argue that humans always act rationally and in strict accordance with a list of resources ranked in terms of net rate of energy gain. Rather, the theory and models generated from it provide a yardstick of objective economic rationality that is used as a basis for the comparative study of behavior.<sup>51</sup> This is not problematic as long as the distinction between microevolutionary (ecological, ethnographic) and macroevolutionary (archeological) time is maintained. With respect to this distinction, our collective interest is in trying to figure out whether what we see archeologically represents a short-term or long-term behavioral strategy and what its effects, if any, were on human fitness.

Bettinger<sup>51</sup> was correct when he stated that optimal-foraging theory, the centerpiece of the behavioral ecology approach, is middle-range theory,<sup>55</sup> a bridge between meaning and the phenomena under investigation. We might argue over the role of inference in archeology,<sup>56</sup> but we can hardly deny that inference plays a part in both evolutionary archeology and human behavioral ecology. We have often made the distinction between immanent and configurational properties,<sup>21</sup> the former invariant regard-

less of time or space, the latter subject to time and space. However, we have left unexplored a potentially large middle ground between the two. It is here that behavioral ecologists have a leg up on evolutionary archeologists. If we had enough snapshots of the archeological record of, say, a specific geographic locale, each measured by the yardstick of objective economic rationality, and if we could determine that there was heritable continuity between each pair of snapshots, then we would be in a position to monitor not only macroevolutionary processes but perhaps microevolutionary change as well.

Some behavioral ecologists would still argue that much of the change we see archeologically is attributable to phenotypic plasticity,<sup>15</sup> whereas most evolutionary archeologists would argue that much of it is attributable to selection, but at this point we do not see this as particularly problematic. The issue is an empirical one: given that evolution involves the differential persistence of heritable characters, either there is a change in relative frequencies of replicators, whether they be genes or culturally transmitted replicators, or there is not. Empirical research should clarify whether selection, drift, or other evolutionary processes are at work or, conversely, whether visible change is simply the adjustment of a labile phenotype. Regardless of the answer, we agree that various decision-making forces such as individual learning and social transmission filtered by rules have had profound effects on the evolutionary trajectory of humans. Previous rejection of mentalistic processes by evolutionary archeologists was based on simplistic cause-and-effect, intention-explanation studies. Better studies now exist,<sup>57,58</sup> and they have led to workable models of cultural evolution under the influence of various combinations of decision-making forces, selection, and drift. Perhaps the best statement on the interplay of these variables in the evolutionary process is by Richerson, Bettinger, and Boyd.<sup>59</sup> It bears reading by human behavioral ecologists and evolutionary archeologists alike.

## CONCLUSION

What have become known as evolutionary archeology and human behavioral ecology are not unified bodies of principles and methods but, to be taken seriously, they must become just that. Is there room for theoretical and methodological challenges? Most decidedly so, just as there are in evolutionary biology and paleobiology almost six decades after the Modern Synthesis of the early 1940s. What is important in Darwinian evolution is that variation, however it is generated, exists, and that transmission, however it is realized, takes place. Reproductive success among variant forms of organisms will result in large part, although not exclusively, from selection, drift, and, in the case of humans, evolved mentalist processes. Similarly, replicative success among variant artifact forms will result from the same processes. Thus we cannot agree that cultural evolution carries too many biological connotations and therefore should be labeled cultural "development" instead.<sup>60</sup> The Darwinian mechanisms of selection and transmission, when incorporated into an explanatory theory, provide precisely what culture historians were looking for: the tools to begin explaining cultural lineages—that is, to answer why-type questions. As Dennett<sup>61</sup> put it, the power of Darwin's "theory of natural selection is not the power to prove exactly how (pre)history was, but only the power to prove how it could have been, given what we know about how things are" (p. 319).

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DOI 10.1002/evan.20004

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