

Using Phylogenetically Based Comparative Methods in Anthropology: More Questions Than Answers

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The study of adaptation is designed to answer questions about the evolution of organic diversity and entails, as one of its standard tools, analysis of the distribution of traits across individuals, species. This comparative method, used to identify cases of convergent evolution, provides some of the strongest evidence for adaptation, and is central not only to modern biology but also to the social sciences, including anthropology.¹ Thus many key ideas in our discipline, among them that states evolve under conditions of geographical circumscription² or that matrilocality is associated with warfare³ are based on correlations, sometimes impressionistic and sometimes calculated, among various institutional and environmental features. As evolutionary studies of behavior flourish in anthropology,⁴ a proper comparative approach to the study of adaptation becomes increasingly important.

Over recent years biologists have emphasized the significance of evolutionary history to the study of adaptation (Box 1). This has led to many methodological innovations, including a radical revision of the comparative method within biology. These developments grew from the recognition that a correlation between two traits arising from shared ancestry does not necessarily say anything about whether or not these traits are related functionally. Thus, the hypothesis

that animals living in patchily lit forests achieve low visibility by evolving broken coloration patterns such as spots or stripes cannot be tested by looking at cross-tabulations between coloration and environment because crypticity may have evolved only in a single ancestor. In short, for testing hypotheses about the evolutionary origins of traits, species that share characters due to a common history cannot be considered independent sources of data, a point that Darwin himself appreciated.

In recent years biologists have begun to use a variety of methods to address the statistical problem arising from shared ancestry. Most of these approaches use Felsenstein's⁵ method of independent contrasts in which phylogenetic reconstructions of species are compared in order to determine independent instances of evolutionary change on which statistical tests can be based.^{6–8} Quite simply, these phylogenetically based comparative methods permit determination of whether pairs of traits hypothesized to be functionally related (for example, spots and forest living) change together in repeated independent occasions more than would be expected to occur by chance.⁹ In ap-

plying these ideas to human cultural traits, it is important to clarify one troubling issue at the outset. Similarity among related species does not necessarily rule out an adaptive explanation for the maintenance of a trait by stabilizing selection. Thus, in guarding tests from the problem of pseudoreplication, phylogenetically based comparative methods are conservative with respect to uncovering the adaptive significance of character traits in so far as they address origins questions only.

Anthropologists have taken seriously the challenge of statistical interdependence among societies. Moreover, some practitioners have begun to adopt phylogenetically based comparative methods. In this paper I explore some of the key questions that are raised in an application of such methods to a study of cultural variability in East Africa.¹⁰

THE CHALLENGE TO ANTHROPOLOGY

Lack of statistical independence among human cultures, in both worldwide and continuous-area comparative research, arises from shared ancestry, borrowing between neighboring groups, conquest, and other mechanisms. The problem was first pointed out by Sir Francis Galton in his 1889 evaluation of E. B. Tyler's comparative work and, as "Galton's problem," has engaged discerning comparativists ever since.^{1,11,12} Two methods have been used to correct for this problem. First, there is the Standard Cross-Cultural Sample,¹³ which samples societies from the *Ethnographic Atlas* following a two-millennia and two-hundred-mile separation rule,¹⁴ which is somewhat analogous

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Box 1. Phylogeny, Adaptation, and History

As in anthropology, there has been much debate within biology over both the concept and definition of adaptation, as seen in some recent overviews.^{101,108} In general, however, there is broad agreement that an adaptation is a phenotype that exhibits higher evolutionary fitness than does other phenotypes in the same environment. For many biologists, a historical approach is implied. Thus, an adaptation must have been shaped by natural selection over evolutionary time to serve its current role, as originally argued by Williams.¹⁰⁹

There are two principal approaches to the study of adaptation.¹⁰⁰ The first

is to focus on specific phenotypic traits and determine how these contribute to individual fitness and how they are maintained in a population, as well as to identify their mechanistic underpinnings; these studies often entail optimality modeling and experimental manipulation. Phylogenies are then used to determine when and why these phenotypes may have arisen in the species' history. The second approach, the comparative method, is to look for associations between specific phenotypes and environments, taking phylogenetic information into account^{5,110} in order to determine the conditions in which a

particular phenotype might arise across distinct evolutionary lineages.

As Martins¹⁰⁰ pointed out in a recent review, the first approach relies on an in-depth understanding of the history of single traits, whereas the latter, by contrast, is purely statistical, requiring a large number of taxa and evolutionary changes in both the phenotype and the environment to achieve statistical power. Inevitable problems associated with such data sets lie at the heart of controversies over the comparative method and point to the importance of using both approaches where possible.

to the supraspecific taxonomic approaches initially used by biologists.¹⁵

Second, there is an autocorrelational approach, originally developed for spatial patterns but subsequently generalized to analyze autocorrelation in any form of network.^{11,16} In this approach, the variation among different societies is partitioned statistically among history or proximity and the specific cultural evolution of that society, a method also used by biologists.^{17,18} While both methods correct for shared ancestry to some degree, they each have problems. The Standard Cross-Sectional Sample disregards both the variation within clusters of societies and the possibility that between-cluster similarities are due to shared ancestry, whereas the statistical approach fails to make explicit a particular evolutionary model whereby traits might evolve over time.¹⁹

Recognizing these inadequacies, Mace and Pagel¹² drew anthropologists' attention to phylogenetically based comparative methods, arguing that they are superior to current methods because they identify independent instances of cultural change. Various applications to empirical questions followed.^{20–22} With this work a venerable (if unfashionable) tradition within anthropology was revived. That tradition views anthropology as an historical science that deals with traceable continuities and

change over time.²³ But despite Aberle's²⁴ spirited presidential address to the American Anthropology Association promoting historical reconstruction as the appropriate juncture for parallel theory development within ethnology, archeology, linguistics, and biological anthropology, most anthropologists, unlike biologists, have shown little enthusiasm for the phylogenetic method. Some, such as advocates of ethnogenetic theory, object to the application of cladistic models to human society,²⁵ primarily because social groups have multiple ancestors. Others suspect that the revised method will have little impact on the outcomes of comparative studies in anthropology because the signature of history is weak compared to the strength of current selection pressures.^{26–28} Yet others propose alternative methods that directly trace the specific phylogenies or patterning of different cultural traits and institutions.^{29–32} It remains an open question whether phylogenetically controlled comparison is necessary.³³

Here I explore this question, and specifically the strengths and weaknesses of phylogenetically based comparative methods for anthropological work. My ideas spring from a study that compared the use of both conventional statistical analyses and phylogenetically based comparative methods to test

some of the principal hypotheses for sociocultural variation in East African family organization (Box 2).¹⁰ In this collaborative work, we started with the general assumption that cultural traits subject to natural and, most likely, cultural selection will show few historical continuities as descendant populations adapt to their various environments, thereby generating a new level of independence among daughter populations. More particularly we proposed that this erasure of history would be more pronounced in studies of local rather than global variation. Broad differences between social institutions such as dowry versus bridewealth or matriliney versus patriliney might indeed be attributable to ancestral conditions that persist through poorly understood processes of cultural inertia and change, as in a recent reanalysis of the worldwide association of dowry and monogamy.³⁴ However, finer scale local or regional variations are more likely to be sensitive to current selective conditions. Thus, we hypothesized that fine-scale characters such as the size of a marriage payment or the degree of cooperation among cowives are likely to be acutely tuned to specific socioecological conditions, and hence, in phylogenists' parlance, more derived. If this were indeed the case, the application of phylogenetically based comparative methods would be unlikely to alter observed as-

sociations within the phylogenetically uncorrected data, and both corrected and raw analyses should produce the same results. More generally, we follow the lead of biologists^{35,36} in contrasting the results of phylogenetically corrected and conventional analyses in order to unravel the implications of the new methodology for empirical tests.

Most existing comparative anthropological work employing phylogenetic techniques has been based on worldwide or continental comparisons of various precoded data sets taken from Murdock's *Ethnographic Atlas*,³⁷ using either genes or language families to construct phylogenies. There are, however, strong methodological grounds for following Eggan's³⁸ recommendation that comparison be restricted to relatively homogenous areas. Regionally controlled comparisons of this type are less likely to foster comparison of inappropriate elements and more likely to reveal true correlates of variation. For these reasons, they are much preferred by some social anthropologists.³⁹ Because population changes over time are more feasibly reconstructed in shallower regional histories, regional studies are also arguably more suitable for phylogenetic reconstruction. This is particularly the case when language is used as an indicator of history. While the pattern of deep linguistic branching is notoriously controversial,⁴⁰ detailed regional histories can be successfully reconstructed using linguistic evidence, often together with oral traditions and archeological material, as in Eastern and Central Africa.^{41–47}

AN INDETERMINATE OUTCOME

The results of both the conventional and the phylogenetically controlled tests of hypotheses for family variation in East Africa are shown in Table 1. Of thirty-six tests associated with twenty-two distinct hypotheses, seven of the thirteen supported by conventional statistics are also supported by phylogenetically based comparative methods. Of those twenty-three that are not significant in the conventional analysis, four are significant in the analysis using phylogenetically based comparative methods. A comparison of the two methods does not tell us which cultural traits are phylogenetically independent and which are not

(indeed, there are now methods to determine this directly.⁴⁸) However, an examination of each cell is helpful in determining what it means to apply phylogenetically based comparative methods to human cultural traits.

Looking first at the upper left cell (A) of Table 1, we see that just about half of the conventionally significant results retain significance in phylogenetic comparative analysis. Correlated traits that appear in this cell, such as gerontocratic organization in societies where the resources critical to subsistence are inherited (#6.1), appear near the tips of

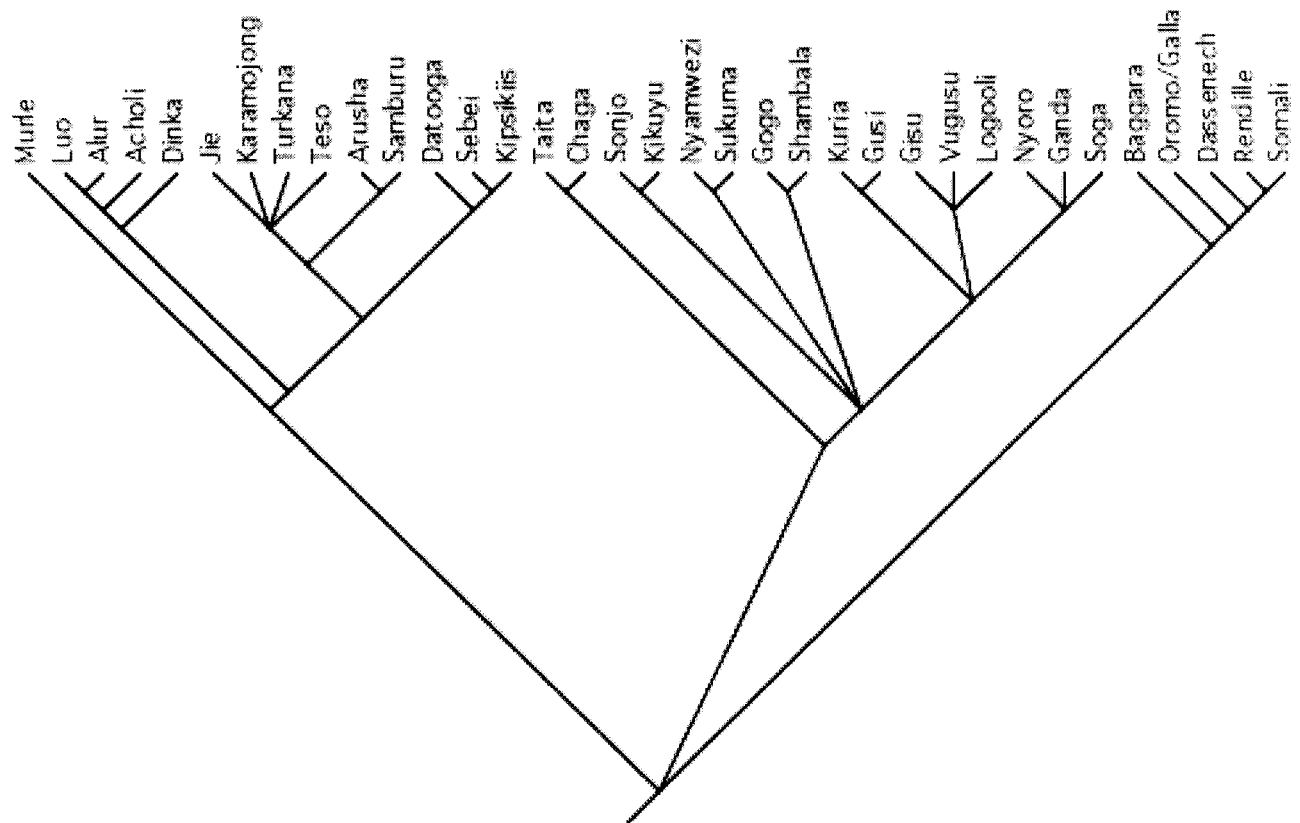
Broad differences between social institutions such as dowry versus bridewealth or matriliney versus patriliney might indeed be attributable to ancestral conditions that persist through poorly understood processes of cultural inertia and change, as in a recent reanalysis of the worldwide association of dowry and monogamy. However, finer scale local or regional variations are more likely to be sensitive to current selective conditions.

the tree rather than deep at internal nodes. In other words, the traits in this cell seem to respond facultatively either to other institutional features of the social system or to environmental conditions (or both), such that phylogenetic control has little effect on statistical significance. This is the pattern we had

expected, the apparent erasing of history in a study of fine-scale regional variation. The pattern in this cell is consistent with Ehret's⁴² depiction of East Africa as a region in which cultural features have mixed and merged extensively over the last three millennia⁴⁶ so that the vertical transmission of cultural traits within populations cannot account for all of the current variation. It suggests, too, that the adaptive processes implicated in the hypotheses are ongoing, in line with most evolutionary ecological approaches to cultural variation⁴ and, ultimately, that phylogenetically based comparative methods are not necessary for this kind of comparative anthropological research.

The pattern, however, is far from uniform. These conclusions cannot be generalized beyond the hypotheses that fall in the upper left cell of Table 1. Indeed almost 50% of the significant conventional tests are lost with phylogenetically based comparative methods (cell C). There are several reasons why traits might be correlated with phylogeny, only some of which contraindicate an adaptive explanation. First, under a Brownian motion model of trait evolution (random genetic drift), in which trait changes are uncorrelated with one another and are equally likely to be positive or negative, traits will show phylogenetic correlations, as simulated by Harvey and Pagel.⁶ Second, traits may be truly constrained by evolutionary history as a result of either to some genetic or developmental limitation or selective maintenance for some other biological role (in other words, because of one or more confounding variables³⁶). In the case of cultural traits, we can think of this problem in terms of individuals being reluctant to change a cultural trait that is deeply embedded in other patterns of behavior or institutions.³³ Third, and probably most commonly, phylogenetic correlations may reflect the tendency for related species to experience largely similar ecological factors due to habitat selection⁴⁹; as such, their similarities are maintained through stabilizing selection. Biologists refer to this as phylogenetic niche conservatism,⁶ or adaptive radiation.⁵⁰ Insofar as this is a true cause of similarity among related species, it implies that

Box 2. A Study of Variation in East African Kinship and Marriage



Phylogeny of 35 East African societies based on language affiliation

Uncommonly systematic ethnographic work conducted in British East Africa between the 1920s and late 1950s¹¹¹ focused on a tight range of issues: traditional systems of lineal descent, kinship, marriage, jural rights, social control, and economy. I and my colleagues capitalized on the shared theoretical paradigm, comparable methods, overlapping time frames, and common focus of this ethnography in order to test many hypotheses for sociocultural diversity.¹⁰ In this respect we followed on the innovative work of Schneider,¹¹² Goldschmidt,¹¹³ Häkansson,⁹³ Nugent and Sanchez,¹¹⁴ and others.

We focused on hypotheses pertaining to six key aspects of family and kinship organization: the size of the bride-wealth payment, the timing of the bride-wealth payment, the frequency of divorce, the structure of the house-property system, the nature of cowife relations, and the extent of gerontocracy. Our sample was based on ethnographic descriptions conducted between 1920 and 1960 of 35 patrilineal segmentary societies with systems of authority that vary from being highly informal (Samburu), through embryonic forms of a segmentary state (Alur), segmentary states with divine kingship (Shambala), to centralized

states (Soga). Even though some of the sampled societies are in the *Ethnographic Atlas*,³⁷ new codes were developed that were designed for testing the hypotheses and sensitive to the specifics of this world region.

Hypotheses were tested with both conventional statistics (the likelihood-ratio chi-square) and a common phylogenetic comparative method suited to discrete data values. Working primarily from Ruhlen,¹¹⁵ all sampled populations were placed on a linguistic phylogeny based on phonological analysis and the patterning of lexical and other morphemic innovations (see Figure). Analyses based on this phylogeny were performed with MacClade,¹¹⁶ following specific methods described by Ortolani.¹¹⁷ With character states assigned to terminal taxa, MacClade reconstructs ancestral states along all branches of the phylogeny using a principle of parsimony that minimizes the number of changes in character states within the tree. The statistical test used in MacClade evaluates the probability of a number of gains and losses in a dichotomous dependent variable occurring in the presence of the hypothesized independent variable.¹¹⁸

TABLE 1. Cross-Tabulation of Conventional and Phylogenetically Controlled Tests in a Study of East African Kinship and Marriage¹

Phylogenetically Controlled Analyses	Conventional Analyses	
	Significant	Nonsignificant
Sig	7 A #1.2 HIGH BRIDEWEALTH in centralized house-property systems #1.4 HIGH BRIDEWEALTH where wife obtains full jural memberships of husband's lineage #2.1a PROTRACTED MARRIAGE PAYMENTS where resources are difficult to assemble #2.1d PROTRACTED MARRIAGE PAYMENTS where resources are difficult to assemble #3.2 DIVORCE COMMON where wife retains membership of natal lineage #4.1b CENTRALIZED HOUSE-PROPERTY COMPLEX where environment is risky #6.1 GERONTOCRATIC SYSTEMS where critical subsistence resources are inherited	4 B #2.2 PROTRACTED MARRIAGE PAYMENTS where there is no cultivation #3.1 DIVORCE COMMON where bridewealth is low #5.1a POOR RELATIONS AMONG COWIVES when living at close proximity #6.2b GERONTOCRATIC SYSTEMS where resources are scarce
Non Sig	6 C #1.1b HIGH BRIDEWEALTH where transferable wealth is available #1.3b HIGH BRIDEWEALTH where cattle are not critical to subsistence #1.3c HIGH BRIDEWEALTH where cattle are not critical to subsistence #3.3 DIVORCE COMMON where a bride can filiate children into her natal lineage at divorce #4.1a CENTRALIZED HOUSE-PROPERTY COMPLEX where environment is risky #5.1b POOR RELATIONSHIPS AMONG COWIVES when living at close proximity	19 D #1.1a #2.4 #1.3a #3.4 #1.5a #4.2 #1.5b #5.2 #1.5c #5.3 #1.5d #5.4 #1.5e #6.2a #1.6 #6.2c #2.1b #2.1c #2.3

¹ Table includes a thumbnail description of hypotheses that were supported ($P < 0.05$) by phylogenetically based comparative methods (Cell B, concentrated changes test), conventional analyses (Cell C, Chi-square test), or both (Cell A). Hypotheses not supported by either kind of test (Cell D) are not given thumbnail descriptions. Hypotheses with alphabetized notations are operationalized in more than one way; for example, for the hypothesis (#4.1) that centralized house-property systems are an adaptation to risky environmental conditions, house-property type is tested against low rainfall (#4.1a) and livestock keeping (#4.1b), both measures of environmental risk.

the phylogenetic component removed by phylogenetically based comparative methods is itself partially adaptive.^{51,52}

This third process is highly relevant to the study of cultural traits. In humans, linguistically related groups often live in similar environments, reflecting a tendency to migrate to habitats similar to the ones from which they came. For example, Nilotic and Cushitic societies generally live in drier zones than do the Bantu, a pattern well preserved in our sample. To the extent that habitat selection occurs, a great deal of ecological variation is statistically hidden once linguistic phylogenies are incorporated into the analysis. This problem, which plagues studies that attempt to tease out ecological from historical

causes of variation,⁵³ can perhaps best be tackled by partialing out the effects of geography on history, and vice versa.³⁰ I favor this third process as an explanation for the cases that fall in cell C insofar as five of the six measures of the independent variables are linked to either environment (#1.3c, #4.1a) or subsistence (#1.1b, #1.3b, #5.1b). In other words, I suggest that where phylogenetically based comparative methods fail to support conventional chi-square analyses that is because linguistically related groups tend to live in similar environments, not because traits like bridewealth size, divorce, house-property systems, and cowife relations are culturally constrained (slow to change) in any true sense nor because they are adaptively neutral. Note, however, that this

is an interpretation of the pattern and cannot be derived directly from the data.

The upper right quadrant (B), where four associations not supported conventionally are significant in phylogenetic comparative analyses, is hard to understand. Similar findings in other studies have been attributed to specific effects within particular lineages.³⁵ For example, the finding that an association between common divorce and low bridewealth (#3.1) is only significant when phylogeny is controlled suggests that some one of the variables differs substantially between linguistic groups. Subsequent analysis did show that divorce is much commoner among Bantu than Nilotic and Afro-Asiatic peoples and further, that a statistically significant

association between low bridewealth and divorce is found only in the latter groups.

THE NEED FOR HISTORICALLY CONTROLLED COMPARISONS

I started with the expectation that phylogenetically based comparative methods are unnecessary for highly labile human cultural traits epitomized by the relatively muted regional variations in such traits as bride-wealth amount, cowife relationships, and divorce frequency. How nice it would be to have reached the undoubtedly welcome conclusion that anthropologists looking at patterns of social organization need not worry about constructing phylogenies. Unfortunately, this conclusion is not warranted if the standard claim of advocates of phylogenetically based comparative methods is accepted: that tests of the adaptive origins of character traits must be based on phylogenetically independent data contrasts irrespective of the cause of phylogenetic independence. In fact, it was already clear at the worldwide level that attempts to replicate conventional studies with phylogenetically based methods can fail.³⁴ Gaulin and Boster's⁵⁴ association among monogamy, social stratification, and dowry (based on 1066 *Ethnographic Atlas* societies) does not stand up to phylogenetic control, although Hartung's⁵⁵ association among polygyny, son inheritance, and bridewealth (based on 850 *Ethnographic Atlas* societies) does. Despite these ambiguities with worldwide data, I had expected to draw a cautious "welcome" conclusion for regional studies, namely that finer-grain studies of the presumably more labile traits that vary within cultural regions do not require historical control. Unfortunately, even this more guarded conclusion is not warranted because almost half of the significant associations between socioecological variables and cultural variables pertaining to family organization are lost when phylogeny is controlled.

Despite all of this, I characterize the outcome of these tests as indeterminate for the principal hypothesis. This is because however we scrutinized the data we could find no consistent sub-

stantive or statistical reasons for why some hypotheses fell into one box and some into others. Also, I am not comfortable with entirely rejecting the hypotheses that fell into Cell C because of the interpretive issues with phylogenetically based comparative methods discussed earlier. The exercise nevertheless brings into sharp relief a series of questions concerning the application of phylogenetically based comparative methods to cultural traits, leading me to the second part of my title.

While some see traits as tightly linked to biological populations or language groups, others view traits as relatively free-floating entities in mere temporal association with a population. Yet others, such as proponents of ethnogenetic theory, question the whole notion of populations descending from a single parent inherent in any evolutionary "free". . .

WHAT IS THE APPROPRIATE METHOD OF HISTORICAL CONTROL IN ANTHROPOLOGY?

Most models of cultural evolution assume that cultural groups evolve through descent with modification occurring through a hierarchical branching process whereby daughter populations are more similar to their parent population than they are to other populations.^{56–58} Laying aside

possible ethical dimensions to this debate,⁵⁹ the view that human history can be captured through the construction of phylogenies is controversial for several reasons. First, unlike species phylogenies, where each has a pretty clear hierarchical relationship to the others on account of most of its DNA having been channeled through the same history, within-species phylogenies exhibit no unique branching among units, be these individuals or populations. Second, humans have extraordinary capacities for the horizontal transmission of cultural traits, between as well as within groups, with elaborate systems of communication allowing for borrowing, learning, exchange, imitation, stealing, and even imposition of traits between societies. Third, cultural transmission fosters high rates of innovation, permitting rapid evolutionary change. Fourth, cultural transmission does not preclude recombination, whereby merging groups combine elements of each, a classic example being the Ariaal, a fusion of northern Kenyan Samburu and Rendille pastoralists.⁶⁰ It is therefore not only very difficult to reconstruct accurate phylogenies of human cultural traits, but questionable that a single phylogeny captures much of a group's history.⁶¹

The first position, that cultural groups evolve through descent with modification, was most strikingly described by Vansina,⁴⁷ who traced the importance of tradition and internal innovation as opposed to the impact of external innovations in the history of the western Bantu expansion in the Congo basin, a theme emphasized also by Kirch⁶² and Durham.⁵⁸ But, as noted, there are problems with this view. It is often unclear with what consistency the elements within a so-called cultural group or society stick together, to what hierarchical units they adhere, and how, indeed, these hierarchical units should be defined. In addition, what is the impact of the horizontal transmission of traits through trade, diffusion, and conquest on the integrity of such units, and how seriously does this weaken the assumption of descent with modification? There is a wide continuum of viewpoints^{61,63} with respect to the disentangling of descent and diffu-

sion. While some see traits as tightly linked to biological populations or language groups, others view traits as relatively free-floating entities in mere temporal association with a population. Yet others, such as proponents of ethnogenetic theory, question the whole notion of populations descending from a single parent inherent in any evolutionary "tree," preferring to think of the history of cultural groups as "a braided river bed."²⁵ Intriguingly, this debate has echoes, albeit with different terminology, across many fields, with, for example, Bellwood⁶⁴ examining the respective roles of reticulate and phylogenetic models in analysis of the archeological record and Blute⁶⁵ teasing out the roles of history and necessity in the way sociologists think about the world. Boyd and Richerson⁶⁶ offer a particularly clear discussion of the broader relationships between history and evolution.

These different viewpoints have major implications of with respect to the question of how controls for phylogenetic similarities should be implemented and, indeed, whether or not current methods are appropriate. For those of the first opinion, that cultural traits are tightly linked to populations, a single phylogeny captures quite nicely the history of a population's full array of traits^{12,20–22}; the question then becomes which phylogeny best captures this history. For those of the second and third opinions, each trait or cluster of traits potentially has its own separate history,^{29,30,53,67–69} with different anthropologists emphasizing different forces that might guide this history. For this latter group, a simple tree may not adequately represent the history of the entirety of a society's character traits (Figure, Box 2), and is likely to obscure further and perhaps more critical historical associations. This group's caution regarding trees mirrors the concern of biologists who find tree construction particularly problematic when only discrete data points are available.⁷⁰

At one level, the rampant borrowing of traits across cultural boundaries constitutes no problem for testing hypotheses about human behavioral adaptation by means of cross-cultural comparisons. Indeed, most evolution-

ary anthropologists consider it irrelevant whether a trait is invented or borrowed, a distinction that in any case is often difficult to determine empirically post facto. Whereas for Galton "independence" meant "independently invented, not copied,"⁷¹ most contemporary anthropologists interested in the adaptive origins of traits count the acquisition of a borrowed trait from another group as an independent case of adaptation.¹² Thus, the fact that among the Pahari, an Indo-Aryan-speaking group of north-

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western India, women marry more than one man⁷² supports a hypothesis for polyandry as an adaptation to resource limitation and tripartite economy,⁷³ even though this Hindu group is likely to have borrowed polyandry from its Tibetan neighbors rather than invented it independently.⁷⁴ Indeed, a case for adaptation can be made so long as the trait of interest was not imposed through conquest,⁶⁹ borrowed as part of an indissoluble

package such as a highly integrated religion or technology,⁷⁵ or result from one group borrowing wholesale the culture of another as, for instance, when the Kenyan Mukogodo began to live as Maasai in an attempt to intermarry with them.⁷⁶ In other words, the borrowing group must have some "choice," adopting each trait because of its function, real or perceived,⁷⁷ not simply as a badge of identity or as an unanticipated outcome of conquest. A nice example is the Kenyan Gusi's borrowing of Luo sorcery customs to cope with the deterioration in co-wife relationships, contingent on rapid population growth.⁷⁸ In short, for the purposes of testing adaptive hypotheses, many comparative anthropologists do not distinguish innovation from borrowing, in rather the same way that comparative biologists do not differentiate the *de novo* appearance of a trait from the emergence of functionally similar traits in unrelated lineages.

Others, however, find the prevalence of lateral transmission far more troubling and reckon it deserves serious theoretical attention. In an innovative thesis, Pocklington³⁰ focuses on the critical nature of the assumed evolutionary process underlying the phylogeny, an issue constantly raised in the literature on phylogenetically based comparative methods. Only when we understand the mechanisms whereby traits are transmitted between generations can we develop plausible models against which to test functional hypotheses. Furthermore, because of all the borrowing that goes on in cultural evolution (its reticulate nature), it may be wiser to model the statistical relationship among societies as a matrix rather than as a phylogenetic tree. On this argument there are grounds for tackling the statistical problems inherent in comparative data with the phylogenetic autocorrelation methods mentioned earlier,^{17,18,52,79} methods that are well suited to both branching and reticulate processes.

The next step in this area of research is, then, to compare the results of methods such as those used in the East African study summarized here to results based on both other

phylogenetic comparative approaches and network autocorrelational techniques, thus following the lead of comparative biologists, who systematically evaluate the utility of different approaches.^{7,19} More fundamentally, there is a need to focus more directly on the transmission properties of cultural traits (Box 3) to see which tree, if any, best characterizes the evolution of the cultural trait of interest and therefore qualifies for use in determining independent character changes.

IS IT LEGITIMATE TO BASE A CULTURAL PHYLOGENY ON LANGUAGE?

If the use of phylogenies is valid (and this will depend on the outcome of more work in the vein of that reported in Box 3), what phylogeny best captures “the cultural path that most of the ancestors of the majority of members of that culture followed”?¹² On one hand, following Ehret,⁴² a strong case can be made for claiming that linguistic evidence forms the most comprehensive and dense documentation of a group’s social history, with archeological and ethnographic evidence providing critical supplementation where available. This view is directly supported by Cavalli-Sforza, Menozzi, and Piazza’s⁸⁰ extensive evidence that linguistic variation generally parallels genetic variation at least at the worldwide scale. It is also supported by other studies,^{79,81} including an early anthropological tradition reviewed by Zegura,⁸² and those works mentioned in Box 3, though there have been critiques.⁸³ On the other hand, Ehret’s⁴¹ extensive lexical data shows that African age-set organization has been repeatedly borrowed between protolinguistic units over the last 5,000 years, producing a thorough intertwining of language and culture.

There emerge from these debates several reasons why linguistic trees can be more informative about the path of cultural evolution than genetic trees. First, linguistic phylogenies provide better resolution than do genetic phylogenies at the branch tips, the units at which anthropologists typically record trait values. Because lan-

guage differences typically evolve at rates rather similar to those of cultural differences, and certainly much more quickly than that of genetic difference, language can separate groups that are difficult, if not impossible, to distinguish using genetic data. Second, language data are available for all groups, whereas genetic data are certainly not. Third, language may be a better key to cultural history than are genes, insofar as genes can leak over the boundaries of cultural groups with minimal cultural exchange.⁸⁴ In contrast, language change (deeper than lexical borrowings) commonly entails the adoption of a series of other cultural traits. Language phylogenies therefore are more sensitive to the kinds of horizontal borrowing that we know are so prevalent at certain junctures in human history as, for example, the spread of Quechua from Chile to Columbia under the Inca conquest. Finally, linguistic differences, like genetic differences, are easy to handle because they can be thought of as evolving in a phylogenetic way. Once obviously borrowed terms are excluded, common cognate lexical items usually denote a common origin, such that the resulting pattern can be easily plotted on a branching tree structure.⁴²

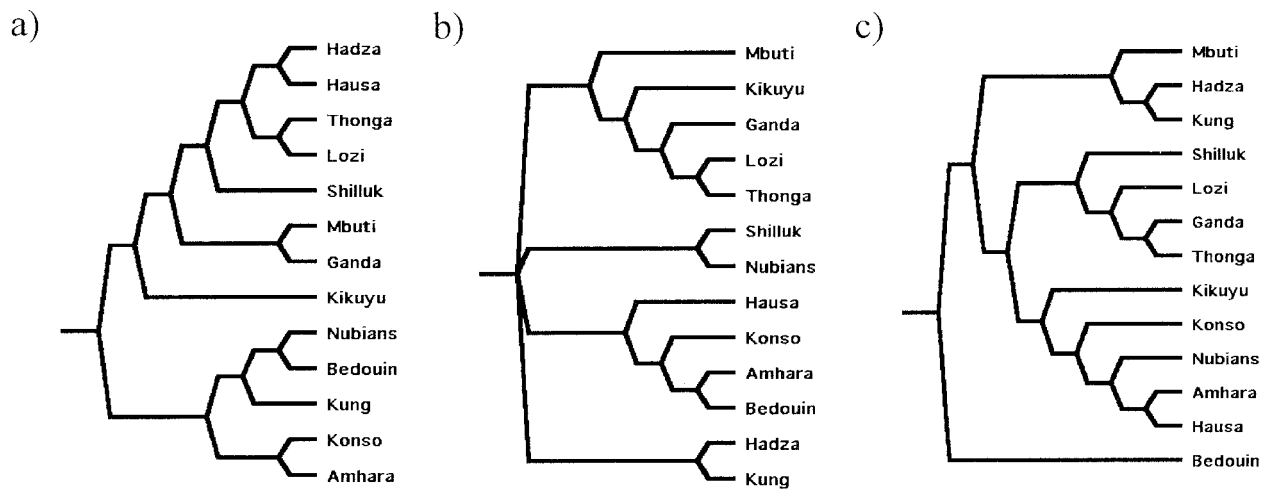
In short, it seems that, subject to further refinements to the studies reported in Box 3, it is currently legitimate to base cultural phylogenies on linguistic data. It may be particularly valid to do so in contexts where intermarriage between groups renders demic patterns of distinctiveness difficult to uncover or where demic spread has been a significant force in cultural change, as in the “express train” model for colonization in the Pacific by Austronesian speakers⁸¹ or the population expansion that accounted for the spread of agriculture in prehistoric Europe.⁸⁵ However, it is important to remember that language is only a cultural trait and therefore subject to all the associated whimsies of transmission. As Boas⁸⁶ so forcefully argued, there is no inherent causality among genes, language, and culture. Using language to reconstruct history is merely a tool, one that will be more useful in some cases than others.

WHAT TO DO ABOUT UNCERTAIN ANCESTRAL STATES?

When using phylogenetically based comparative methods, ancestral character states need to be inferred from traits estimated for other more recent populations, a procedure that can become very tricky at deep internal nodes of a tree, far back in the past. What methods have been used to make such estimates? The most common applications of phylogenetically based methods, such as MacClade, have relied on the principle of parsimony. Effectively this entails constructing a tree that minimizes the number of evolutionary events required to explain the observed distribution of traits. The problem with parsimony is that it does not take into account the variable lengths of different branches of the tree. This may not be a problem where the rate of evolutionary change is very slow or where tree branches are roughly equal in length. However, where traits evolve rapidly and repeatedly, and where trees have some very long branches, parsimony can underestimate expected rates of change and give unreliable answers.⁸⁷

There are two kinds of solutions to this difficulty. The first is to avoid making any estimates at all, but rather to use pairwise tests to conduct comparisons among extant species having evolutionary histories that can be traced from a common ancestor but are not shared with other taxa being compared.⁸⁸ The advantage of this method is that ancestral characters need not be inferred; the disadvantage is that a lot of variation is ignored, leading to low statistical power.⁸⁹ The second way of avoiding the problems associated with inferring absolute values at internal nodes is the maximum likelihood method.⁹⁰ This method takes into account branch lengths, incorporates explicit models of trait evolution, and then uses probability distributions to determine the likelihood with which a given tree accounts for a particular distribution of traits. This method is well suited to human studies.⁹¹ As noted, anthropologists will need to keep a close eye on a growing number of simulation studies

Box 3. How Traits Spread



Trees are based on (a) genetic,⁸⁰ (b) linguistic,⁴⁰ and (c) cultural similarity for 13 African populations, using data assembled by Pocklington.³⁰ To determine which tree should be used to infer independent events we need to know which tree best characterizes the evolution of the cultural traits we are interested in.

Many theoretical frameworks explore how cultural traits are transmitted between both individuals and groups.^{67–69,119} Unsurprisingly, these models show that traits that are not strictly vertically inherited (transmission asymmetry⁶⁸) can have an evolutionary fate decoupled from that of their hosts³⁰ in a manner somewhat analogous to how, in the evolution of parasites, horizontally transmitted strains are normally more virulent than vertically transmitted strains.¹²⁰ Pocklington³⁰ has given a nice graphical demonstration (Figure in box) of how cultural phylogenies may represent neither the population of people bearing these traits (demic history) nor the history of the languages used by these populations (linguistic history). While there are similarities among pairs of trees, a reduction of the three to a single tree would produce a completely unresolved star-shaped polytomy, offering no historical resolution at all.⁵ Determining empirically how much of cultural trait transmission is not vertical, how this varies over relevant evolutionary time scales, and how generalizable is Pocklington's example, is critical to the proper development of phylogenetically based comparative methods and, incidentally, to the unraveling of the nature of gene-culture conflict.

There is, as yet, little empirical understanding of how different kinds of traits spread over time. Whereas Hewlett and Cavalli Sforza¹²¹ showed the importance of parental models (vertical transmission) between individuals over short time scales, Pocklington has found that over longer periods of time similarities in only two of the eight clusters of cultural traits are correlated with genetic similarity; in other words, vertical transmission represents only a small proportion of cultural transmission.³⁰ In a new analysis, very similar in structure to that of Pocklington's, Hewlett, de Silvertri, and Guglielmino³² find a stronger role for vertical transmission. Few other studies have investigated the associations between elements of culture and language. Those that have generally have used shared language as a measure of shared history. Thus Jorgensen¹²² showed that

social, religious, and technological variables cluster in Salish language families in spite of environmental variability and geographic dispersion, leading to the conclusion that shared history accounts for much cultural variation. Burton and White¹²³ observed that a linguistic phylum, Bantu, explains 50% of the variability in "women's contributions to agriculture," even when other significant determinants are controlled. Similarly, sexual dimorphism, hunting, agriculture, and polygyny are quite strongly related to linguistic phylogeny,¹²⁴ as are family and kinship traits both within Africa⁵³ and worldwide.¹²⁵ Some such studies have been highly controversial.^{126–129} Furthermore, patterns of correlation between traits may vary depending on the scale of the analysis; for instance, Weng and Sokal¹³⁰ find a positive correlation of language with incipient agriculture within language families, but a negative association between families.

In general, demic history seems to be a significant force in shaping the distribution of cultural traits, and the use of phylogenetic trees may therefore be justified. Note, however, that these studies are unsystematic with respect to assumptions and method. For example, they use different diagnostic criteria to identify vertical versus horizontal transmission, employ divergent methods for determining trait similarity, and control in different ways, if at all, for geographic proximity. Additionally, some use language as a measure of genetic history whereas others consider language as a cultural trait. Finally, none adequately explore the role of adaptation to shared ecological conditions in contributing to character trait similarity. Without doubt, much more will be understood about the spread of cultural traits with methodological and conceptual advances in this field of study,³⁰ new developments in the quantitative study of intracultural variation,^{131,132} and efforts to use simulation experiments to detect distributional patterns that are diagnostic of different modes of cultural transmission.²⁹

that compare the merits and demerits of different methods and their applications.^{7,19,92}

WHY EMPHASIZE CHANGE OVER STABILITY?

Most phylogenetically based comparative methods examine the origin of traits, not their maintenance; in other words, only character state changes are scored. This method is extremely conservative,²⁸ particularly where discrete data are used. It also may not be appropriate to the hypotheses being tested. For example, take a Nilotic group with a particular marital adaptation, high bridewealth, to its environmental adaptation, a centralized house-property system, shown as hypothesis #4.2 in Table 1. Now imagine that this group produces a daughter population that moves into a similar environment (habitat selection)⁴⁹ and retains its high bridewealth payment. The persistent co-occurrence of these two traits in some sense supports the hypothesis that high bridewealth is an adaptation to a centralized house-property system,⁹³ even though the daughter population would not be scored as an independent contrast. In fact, most predictions within evolutionary ecology, as well as within sociocultural anthropology, address the maintenance rather than origin of traits. Consequently, an independent contrast test focusing only on correlated gains and losses exposes the hypothesis to an excessively stringent test. Furthermore, and probably even more importantly, it is quite possible that the conditions fostering the maintenance of traits might be quite different from those favoring origin.⁷⁷ This is particularly so under the cultural evolutionary processes hypothesized by Boyd and Richerson⁶⁸ and by niche construction theorists.⁹⁴ For example, high marital stability, or low divorce, might persist in a population as a result of a social conformist norm even when the environmental or social conditions of the particular ethnographic context indicate frequent divorce, though how long that might persist is, of course, critical.

The fact that phylogenetically based comparative methods generally address the origins rather than the maintenance

of traits raises a broader epistemological issue. What if the adaptive hypothesis fails, and we reach the conclusion that a co-occurrence of traits is due to “shared history”? Does this really explain anything? Thus, for example, Burton and White’s⁹⁵ finding that Bantu-speaking explains 50% of the variability in how much women contribute to agriculture, even when other significant determinants are controlled, begs the question, not only of why this relationship came about, but why it persists. Here it becomes easy to empathize with the complaint of sociocultural anthropologists and some biologists that phylogenetically based methods “blackbox” critically important and largely un-

... a strong case can be made for claiming that linguistic evidence forms the most comprehensive and dense documentation of a group’s social history, with archeological and ethnographic evidence providing critical supplementation where available.

known cultural processes, even though some other biologists argue otherwise.⁹⁶ Most contemporary applications of phylogenetically based methods skirt the theoretically thorny question of how to define and analyze continuity and change over time, the stuff that absorbs sociocultural anthropology.^{97,98}

Luckily, biologists are also beginning to recognize that it is not necessarily reasonable to consider a phylogenetic explanation as a null hypothesis.⁵¹ Two particularly exciting modeling initiatives are underway that may prove useful to comparative anthropologists. First, there is now a way of determining whether specified

independent variables are associated not just with the origin, but also the persistence of traits⁹⁹; this method directly acknowledges that traits remaining stable for long periods might also be the product of natural selection in the form of stabilizing selection.^{100,101} A second methodological innovation is the previously mentioned maximum likelihood approach.⁹⁰ Likelihood tests can be used to evaluate different models of evolution. Thus, trees predicated on distinct sets of assumptions about the evolutionary process (fast or slow, gradual or punctuational, regular or irregular across branches) can be tested against one another in order to determine what precise evolutionary processes best account for current distributions of traits. In a recently proposed development, both the selective origin and the maintenance of traits can be examined in this framework.¹⁰² The maximum likelihood approach takes us farther than the standard independent contrasts approach, which simply assumes a neutral-drift model of trait evolution in order to reconstruct ancestral states. It has the further advantage of allowing the temporal order of changes (whether character *x* changes before or after character *y*) to be determined. For example, Holden and Mace⁹¹ have shown that dairying arose in human populations before lactose tolerance rather than vice versa.

Intriguingly, despite the technical focus of phylogenetically based comparative methods on changes over time, the independent contrasts approach that has come to dominate the field actually removes comparative analysis from its historical or particular context, specifically when third variables are not controlled. This lack of concern with specific diachronic processes is probably one reason why sociocultural anthropologists view phylogenetically based methods as “black boxing” social change, as mentioned earlier. A biological anthropologist has noted this same problem. Talking about bipedality, Ross¹⁰³ asks, “What use are comparisons of *A. ramidus* and *A. afarensis* for hypotheses regarding the adaptive value of bipedality if these taxa never lived at the same time, let alone in the same pop-

ulation?" Ross certainly does not intend to undercut the whole idea of the comparative method with this question, but rather to emphasize the importance of history, context, and diachronic particularism, as well as the need to supplement the comparative approach with more focused, ideally experimental, studies of optimality (see Box 1). If this is true in studies of hominid morphology, how much more important must such considerations be when dealing with questions of sociocultural diversity?

FUTURE DIRECTIONS

Phylogenetically controlled comparison is a contentious issue in contemporary anthropology^{27,28,61,104} and constitutes deeply contested turf in modern biology.^{36,89,100} I have already mentioned new directions with respect to matrix analyses, techniques that focus on retention of rather than change in character states, and maximum likelihood methods. I close with some further ideas having both a qualitative and a quantitative thrust.

One new direction lies in incorporating a qualitative natural history of human societies, the bread and butter of sociocultural anthropology and related disciplines. Clearly, phylogenetically based comparative methods in all their guises offer an imperfect statistical approach to the testing of hypotheses, being based on assumptions that may be inappropriate and data points founded on estimation or probability. A more accurate test of any of these hypotheses would obviously entail the use of diachronic data on cultural change at the regional level,^{43,46} using methods of historical processual analysis that explicitly examine continuities in change.^{98,105,106} Unfortunately, the quality of ethnohistorical data is highly uneven. Moreover, such data are available for only a small number of cases, enormously reducing the statistical power with which hypotheses can be tested. However, just as biologists can enhance their use of the comparative method with in-depth experimental research on particular populations, so evolutionary anthropologists can find ways of incorporating phylogenetically based methods into a more standard socio-

cultural perspective. There are several ways this might be done. First, quite simply, ethnohistorical and archeological information can reduce dependence on estimated ancestral states at internal nodes of trees. Second, particular focus can be given to why some supported hypotheses retain statistical significance when phylogeny is controlled and others lose significance; such observations raise a host of questions about the origin and de-

. . . linguistic phylogenies provide better resolution than do genetic phylogenies at the branch tips, the units at which anthropologists typically record trait values. Because language differences typically evolve at rates rather similar to those of cultural differences, and certainly much more quickly than that of genetic difference, language can separate groups that are difficult, if not impossible, to distinguish using genetic data.

ried nature of behavioral patterns and social institutions that beg for empirical investigation rather than simply more delving into parsimony and probability. Third, specific histories will allow us to tackle a key question raised by the East African comparative study and other studies⁵³ of whether apparent phylogenetic signals can be explained away through the process of habitat selection.

Another critical area of future re-

search lies in quantitatively determining the transmission properties of different traits. In so far as phylogenetically based comparative methods depend critically on the accuracy of the assumed evolutionary processes used to generate phylogenetic trees, we clearly need more work in this area before venturing to test hypotheses with trees based on suspect assumptions. Ideally, before we apply comparative tests to any set of characters, we need to identify their transmission properties. Do the traits of interest correlate most closely with proximity in language, genes, or geography? With this information, we could follow the methodological rule that for traits best fitting an historical model we should use a gene-based or language-based phylogeny for adaptive hypothesis testing, whereas traits best fitting a geographic diffusion model should be analyzed differently. However, even this rule needs qualification. The transmission properties of particular traits will have to be estimated for each world region and time period separately, because traits may be transmitted differently in different contexts; for example, religion can spread laterally by conquest or conversion in some circumstances, but vertically by population replacement in others. As such, the transmission properties of any given trait are not inherent in the trait itself but historically defined. The relative importance of vertical transmission in the settlement of Polynesia⁸¹ and horizontal transmission in the emergence of Plains Indian cultures in North America as horse riding spread from Mexico¹⁰⁷ are classic examples.

I offer three general conclusions. First, on the basis of the East African comparative study and other work reviewed here, it is premature, even in regionally localized studies, to assume that the signature of history is weak compared to the strength of current selection pressures, at least without further focused empirical study. Second, only with an independently derived understanding of how traits are transmitted can plausible models be developed against which functional

hypotheses should be tested, with, at this stage, methodological plurality needed regarding the use of tree-based phylogenies or matrices. Third, as regards the use of phylogenetically based comparative methods in the study of human behavioral variability, there are still many more questions than answers, but plenty of exciting avenues to explore.

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