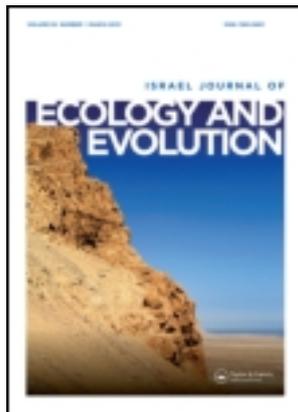


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Trees, thickets, or something in between? Recent theoretical and empirical work in cultural phylogeny

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Trees, thickets, or something in between? Recent theoretical and empirical work in cultural phylogeny

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Anthropology has always had as one of its goals the explanation of human cultural diversity across space and through time. Over the past several decades, there has been a growing appreciation among anthropologists and other social scientists that the phylogenetic approaches that biologists have developed to reconstruct the evolutionary relationships of species are useful tools for building and explaining patterns of human diversity. Phylogenetic methods offer a means of creating testable propositions of heritable continuity – how one thing is related to another in terms of descent. Such methods have now been applied to a wide range of cultural phenomena, including languages, projectile points, textiles, marital customs, and political organization. Here we discuss several cultural phylogenies and demonstrate how they were used to address long-standing anthropological issues. Even keeping in mind that phylogenetic trees are nothing more than hypotheses about evolutionary relationships, some researchers have argued that when it comes to cultural behaviors and their products, tree building is theoretically unwarranted. We examine the issues that critics raise and find that they in no way sound the death knell for cultural phylogenetic work.

Keywords: cultural phylogeny; language evolution; phylogenetic analysis; phylogenetic inference; reticulation

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Introduction

Anthropology has always had the dual goals of documenting the enormous cultural diversity characteristic of humanity and explaining how and why that diversity takes the form it does. Increasingly over the past quarter century or so, anthropologists have begun to rely on phylogenetic methods developed in biology to investigate cultural diversity (e.g. Foley 1987; Mace & Pagel 1994; O'Brien et al. 2001; Collard & Shennan 2008). There are several reasons for this (Mace & Holden 2005; Collard et al.

2006a; Gray et al. 2007, 2010; O'Brien et al. 2008), the most important being a heightened awareness among social and behavioral scientists of parallel issues in evolutionary biology (e.g. Mace & Pagel 1994; Pagel 1999; O'Brien & Lyman 2003; Mesoudi et al. 2004, 2006) and a willingness to see human culture as an inheritance system in which variation arises from both deliberate invention and imperfect copying (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Henrich & Boyd 1998; Henrich & McElreath 2003; Mesoudi et al. 2004; Mesoudi 2011). The latter point means that cultural transmission is as legitimate a mechanism for creating phylogenetic relationships as genetic transmission is (O'Brien & Lyman 2000, 2002a; Grandcolas & Pellens 2005; Mace & Jordan 2011). As with DNA and morphology, the history of cultural changes is recorded in the similarities and differences of character states, or traits, as they are modified over time by subsequent additions, losses, and transformations (Brown & Lomolino 1998).

Phylogenetic reconstruction is based on a model of descent with modification in which new taxa arise from the bifurcation of existing ones. It defines ancestor–descendant relationships in terms of relative recency of common ancestry: Two taxa are deemed to be more closely related to one another than either is to a third taxon if they share a common ancestor that is not also shared by the third taxon. The evidence for exclusive common ancestry is evolutionarily novel, or *derived*, character states. Two taxa are inferred to share a common ancestor to the exclusion of a third taxon

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if they exhibit derived character states that are not also exhibited by the third taxon.

Various methods have been used for phylogenetic inference, each based on different models and each having its own strengths and weaknesses (Pol & Siddall 2001; Archibald et al. 2003; Sober 2004; Goloboff & Pol 2005). One, *maximum parsimony*, is based on a model that seeks to identify the least number of evolutionary steps required to arrange the taxonomic units under study. Parsimony trees are evaluated on the basis of the minimum number of character-state changes required to create them, without assuming a priori a specific distribution of trait changes. Two other commonly used methods, *maximum likelihood* and *Bayesian inference*, are probabilistically based, where the criterion for constructing trees is calculated with reference to an explicit evolutionary model from which the data are assumed to be distributed identically (Kolaczowski & Thornton 2004). As we discuss below, cultural phylogenies that are based on language evolution have relied largely on probabilistic methods (e.g. Gray et al. 2009; Greenhill & Gray 2009; Currie et al. 2010; Currie & Mace 2011). Those not based on language evolution – archaeological phylogenies, for example, which are more prospective – tend to rely on parsimony (e.g. Tehrani & Collard 2002; Jordan & Mace 2006; Buchanan & Collard 2007, 2008a; O'Brien et al. 2001, 2012).

It is difficult to overemphasize that trees, whether they comprise organisms or cultural products, by-products, and behaviors, are hypothetical statements of relatedness, “given the model and parameters used” (Archibald et al. 2003, p. 189), not irrefutable statements of precise phylogenetic relationships. Unfortunately, critics of cultural phylogenetics have consistently overlooked this point, perhaps because cultural phylogenists have failed to make clear the distinction between methods of phylogenetic inference – “tree-building” methods – and phylogenetic comparative methods, which rely on the trees to understand patterns of descent in order to examine the distribution of adaptive (functional) features. Together, the methods are based on the

logical proposition that given data about the present distribution of traits across taxa and knowledge about the historical relationships between these taxa, it is possible to infer what the traits were like in the past and how they have changed to give rise to their present distribution (Currie & Mace 2011, p. 1110; also see Pagel 1999).

The modern comparative method is designed to escape what Francis Galton pointed out in 1889: Comparative studies of adaptation, irrespective of whether the adaptation is a product of convergence or parallelism, are irrelevant if we cannot rule out the possibility of a common origin of the adaptive features under examination (Naroll 1970). To escape Galton's problem requires a working knowledge of the phylogeny of taxa included in an analysis. As Felsenstein (1985, p. 14) put it, “Phylogenies are fundamental to comparative biology; there is no doing it without taking them into account”. The same applies to comparative studies of cultural phenomena.

The distinction between phylogenetic inference and phylogenetic comparison is shown in Figure 1, which

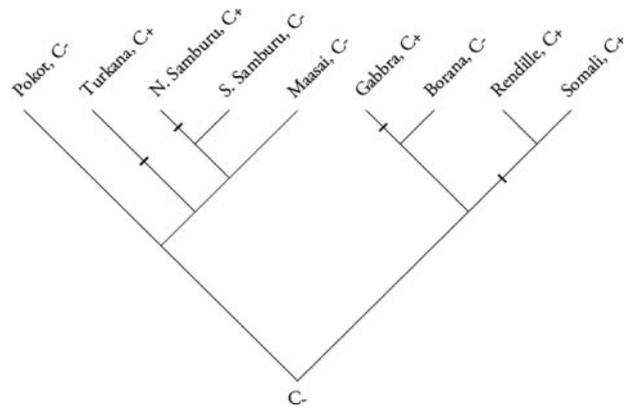


Figure 1. Phylogeny of nine Kenyan pastoralist cultures based on linguistic similarity, showing camel-keeping cultures (C+) and cultures without camels (C-) (after Mace & Pagel 1994). Bars represent the point of camel introduction.

shows a tree constructed by Mace and Pagel (1994) in their analysis of camel herding by East African pastoralists. They were interested in testing the proposition that camel herding is adopted in dry climates (camel herding is indicated by the symbol C+; lack of camel herding is indicated by the symbol C-). To determine whether camel herding was analogous or homologous – Galton's problem – Mace and Pagel used linguistic data to construct a phylogenetic tree. They then placed camel herding (presence or absence) on the branch tips, which represented ethno-linguistic groups. Based on the tree, camel herding apparently arose independently in three branch-tip groups (Turkana, northern Samburu, and Gabbra), as well as in the ancestor that produced the Rendille and the Somali. As Mace and Pagel point out, their tree is only one of several most parsimonious trees. An alternative pattern – one that is equally parsimonious – is that the common ancestor of the four Eastern Cushitic cultures (Gabbra, Borana, Rendille, and Somali) herded camels and the Borana then lost the trait. Regardless of which tree is more correct, Mace and Pagel found a positive correlation between camel herding and a dry environment, including one case – the northern Samburu – in which the practice was adopted in the 1980s as a result of drought.

Some examples of cultural phylogeny

Cultural phylogenetic studies can be divided into three general categories, the boundaries of which are anything but hard and fast: (1) studies that trace lines of transmission, and hence of descent, back to a common ancestor and then examine the processes that underlie the geographic distribution and cultural evolution of descendants and oftentimes the rate of evolution (e.g. Ross 1989; Moore & Romney 1994; Shennan 2000, 2001; Shennan & Collard 2005; Buchanan & Collard 2007, 2008a, 2008b; Pagel et al. 2007; Atkinson et al. 2008; Kitchen et al. 2009; García Rivero 2010; Tehrani et al. 2010; Dediu 2011; Matthews et al. 2011; Bown 2012; Buckley 2012); (2) studies that first create nested taxa (clades) and then map them geographically (e.g. Collard & Shennan

Table 1. Examples of cultural traits examined using phylogenetic methods.

<i>Basketry</i> – Jordan and Shennan, 2003
<i>Hominids and stone tools</i> – Foley, 1987; Foley and Lahr, 1997
<i>Hunter-gatherer technology</i> – Jordan and Shennan, 2009
<i>Lactose digestion</i> – Holden and Mace, 1997
<i>Languages</i> – Gray and Jordan, 2000; Forster and Toth, 2003; Gray and Atkinson, 2003; Holden and Mace, 2003, 2005; Holden et al., 2003, 2005; Rexová et al., 2003; Holden, 2006; Gray et al., 2009; Greenhill and Gray, 2009
<i>Marriage patterns</i> – Pagel and Meade, 2005; Fortunato et al., 2006; Jordan et al., 2009; Fortunato and Jordan, 2010
<i>Native American architecture</i> – Jordan and O’Neill, 2010
<i>Neolithic pottery</i> – Collard and Shennan, 2000
<i>Neolithic stone plaques</i> – García Rivero, 2010
<i>North American projectile points</i> – O’Brien et al., 2001, 2002, 2012; O’Brien and Darwent, 2006
<i>Peopling of North America</i> – Buchanan and Collard, 2007, 2008a,b
<i>Political complexity</i> – Currie, Greenhill, Gray, et al., 2010; Currie and Mace, 2011
<i>Sexual dimorphism</i> – Holden and Mace, 1999
<i>South Pacific pottery</i> – Cochrane and Lipo, 2010
<i>Spread of farming</i> – Gray and Atkinson, 2003; Holden and Mace, 2003; Holden, 2002, 2006
<i>Turkmen textiles</i> – Tehrani and Collard, 2002, 2009a,b; Tehrani et al., 2010; Matthews et al., 2011

2000; Gray & Jordan 2000; Holden 2002, 2006; Gray & Atkinson 2003; Jordan & Shennan 2003, 2009; Holden et al. 2005; Atkinson & Gray 2006; Tehrani & Collard 2009a, 2009b; Currie et al. 2010; Currie & Mace 2011; Bouckaert et al. 2012); and (3) comparative studies that rely on understanding patterns of descent in order to determine whether certain cultural traits are instances of convergence or shared ancestry (e.g. Mace & Pagel 1994; Holden & Mace 1997, 1999, 2003, 2005; Sellen & Mace 1997; Borgerhoff Mulder et al. 2001; O’Brien et al. 2001, 2002, 2012; Holden et al. 2003; Mace & Holden 2005; Mace & Jordan 2005; Pagel & Meade 2005; Fortunato et al. 2006; Jordan et al. 2009; Rogers et al. 2009; Fortunato & Jordan 2010; Jordan & O’Neill 2010; Calude & Pagel 2011; Larsen 2011). Table 1 lists some of the products of culture that have been investigated phylogenetically. The list is not meant to be exhaustive, but rather to show the wide range of work that has been done across the cultural phylogenetic landscape.

Studies in all three categories can involve numerous lines of evidence, including archaeological and ethnological. For example, O’Brien and colleagues’ (2001, 2002; O’Brien & Lyman 2003) archaeological application of phylogenetic methods focused on the long-standing problem of the evolution of projectile-point form in the southeastern United States during the Paleoindian period (ca. 13,300–11,900 years ago). O’Brien and colleagues began by recording three qualitative and five quantitative characters on a sample of 621 specimens representing a range of projectile-point types. They then subjected the specimens to paradigmatic classification (Dunnell 1971; O’Brien & Lyman 2002b) in order to cluster them into classes (taxa) with unique combinations of character states. They then carried out a phylogenetic analysis of the 17 classes that contained at least four specimens. To

root the tree, one of the 17 taxa was selected as the outgroup on the basis of least-step occurrence seriations and chronological considerations. The phylogenetic analysis yielded a single most parsimonious tree, which was evaluated in terms of its fit with the data set by a goodness-of-fit statistic, the consistency index (CI). This index ranges between 1.0 and 0.0, with values close to 1 indicating a good fit between the tree and the data set and values close to 0 indicating a poor fit. The tree had a CI of 0.59, which suggested that it was a reasonable depiction of the relationships among the classes. In the final part of their study, O’Brien and colleagues used the tree to investigate the character-state changes that occurred in the course of the evolution of Paleoindian-period projectile-point form.

One feature that many cultural studies share, especially those in categories 2 and 3 above, is a reliance on linguistic data to create the basic cultural phylogeny (Pagel 2000, 2009). Once language trees are constructed, other cultural features – objects as well as behaviors – can be mapped onto the branch tips (e.g. Holden & Mace 1997, 1999, 2003, 2005; Holden & Gray 2006; Currie et al. 2010; Currie & Mace 2011). Of all cultural traits, why single out language as a basis for phylogeny? Most studies adopting this approach employ reasoning similar to that of Borgerhoff Mulder (2001): (1) linguistic phylogenies offer better resolution of sister groups than do molecular phylogenies; (2) linguistic data are available for more groups than are molecular data; (3) language, whether written or spoken, evolves through a process similar to how prokaryotes and eukaryotes evolve (Platnick & Cameron 1977; Cameron 1987; Rexová et al. 2003; Atkinson & Gray 2005; Howe & Windram 2011); and, most important, (4) language, at least its core elements, is less prone to horizontal movement (e.g. borrowing) than are genes, which can “leak” over the boundaries of cultural groups with minimal cultural exchange (Harpending & Eller 2004; Mace & Holden 2005). To that list we would add that, on average, language and culture evolve on a more similar timescale than do culture and genes. In sum, we agree with Pagel (2009, p. 414) with respect to language trees: “there is no doing comparative linguistics or comparative anthropology without them, and new linguistic or anthropological research programmes should routinely make their construction a priority”.

Ignoring word borrowing, linguistic similarity is the result of cultural transmission and heritable continuity. By “heritable continuity” we mean a genetic-like connection between two things that is produced by transmission and results in an unbroken sequential ordering of things along a temporal continuum (O’Brien & Lyman 2000). Continuity, however, does not imply complete fidelity. Linguistic change, such as that seen in the gain or loss of words or shifts in sound and meaning, can occur either as a result of cognitive processes or through transmission, the latter a case of drift. These are not mere metaphorical analogues of biological features; rather, they are products of the same kinds of mechanisms that create and maintain genetically based variation in organisms (Wiener 1987).

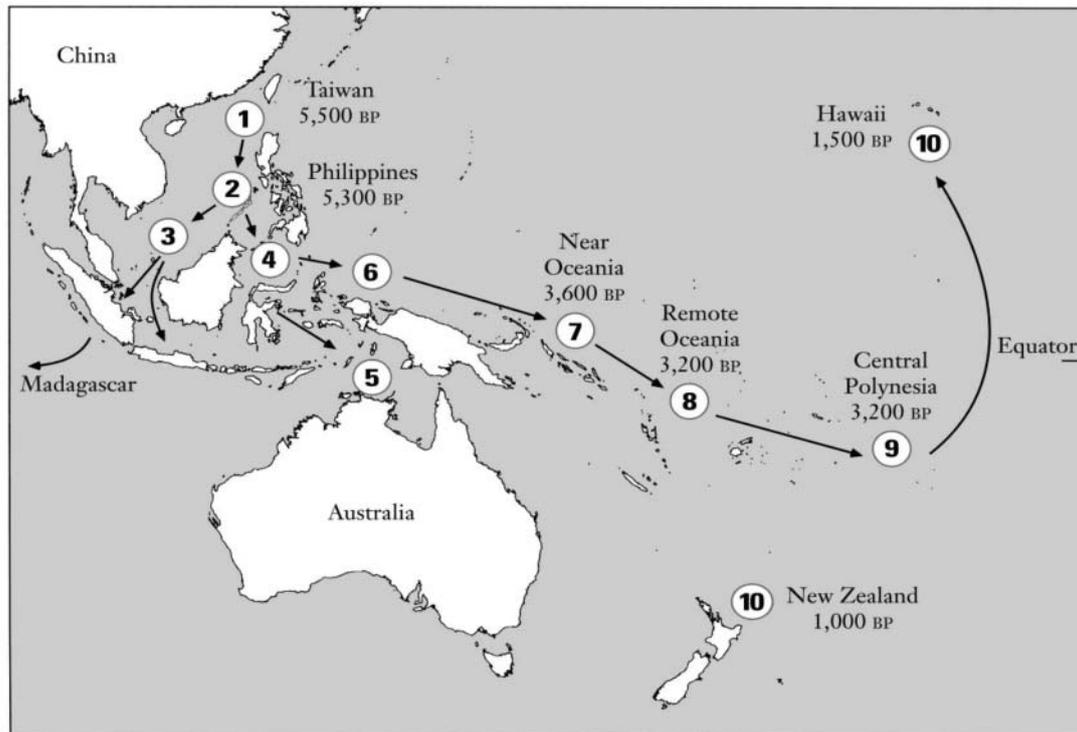


Figure 2. Express-train model of Austronesian colonization of the Pacific (after Gray & Jordan 2000; adapted from Diamond 1988, 1997). Approximate archaeological dates of settlement are indicated for each station: 1, Taiwan; 2, Philippines, Chamorro, Palau; 3, Borneo, Indonesia, Malay; 4, Sulawesi; 5, central Malayo-Polynesian; 6, southern Halmahera/western New Guinea; 7, Near Oceania; 8, Remote Oceania; 9, central Polynesia; 10, eastern Polynesia.

Language trees have been used to answer at least six kinds of questions about cultural evolution (Gray et al. 2007):

- (1) Homelands – Where did linguistic groups originate?
- (2) Population expansions and sequences of cultural change – In what order did cultural lineages diverge and spread?
- (3) Dating divergence events – When did cultural lineages diverge?
- (4) Rates of cultural change – What factors affect rates of cultural change?
- (5) Adaptation – Are particular cultural traits adaptations, or are they the result of common origin (Galton's problem)?
- (6) Ancestral states – Are the cultural traits ancestral or derived?

These questions are by no means mutually exclusive, and some or all play roles in the studies we briefly discuss below, which come from the South Pacific and southern Africa.

Figure 2 shows a proposed model for the colonization of the Pacific by Austronesian-speaking people within the past 6000 years. The model begins with the assumption, based on archaeological data from excavated sites and molecular data from nonrecombining loci (mitochondrial DNA and Y chromosome), that around 6000 B.P. there was an expansion of Austronesian-speaking Neolithic

farming people out of south China and Taiwan (Melton et al. 1995; Bellwood 1997; Lum 1998; Lum & Cann 1998; Green 1999; Hurles et al. 2003).¹ The expansion was rapid throughout the Pacific, taking roughly 2100 years to reach the western edges of Polynesia, a distance of 10,000 km (Bellwood 1991, 1997; Blust 1995). Diamond (1988) referred to the rapid colonization metaphorically as an express train to Polynesia; hence the model has become known as the “express-train” model. Although its proponents do not necessarily agree on all details of the colonization process, they emphasize the sequence, root, and age of the Austronesian family, as well as a degree of admixture with non-Austronesian populations.

Gray and Jordan (2000) analyzed 77 Austronesian languages with 5185 lexical items to test one key aspect of the express-train model – the colonization sequence shown in Figure 2 – in a manner similar to how biologists test propositions about the sequence of events in genetic evolution. If the model is correct, the languages should do two things: (1) share more in common with neighboring languages than with those farther away, and (2) line up in a west-to-east gradient in terms of relative age, with Polynesian languages being the youngest and Southeast Asian languages being the oldest. Gray and Jordan converted the linguistic data into a set of taxa (languages) and binary characters (cognate words) and used the tree-building program PAUP* 4.0 (Swofford 1998) to find the set of trees that required the fewest evolutionary events to explain the ordering of taxa.² A single most parsimonious tree was produced

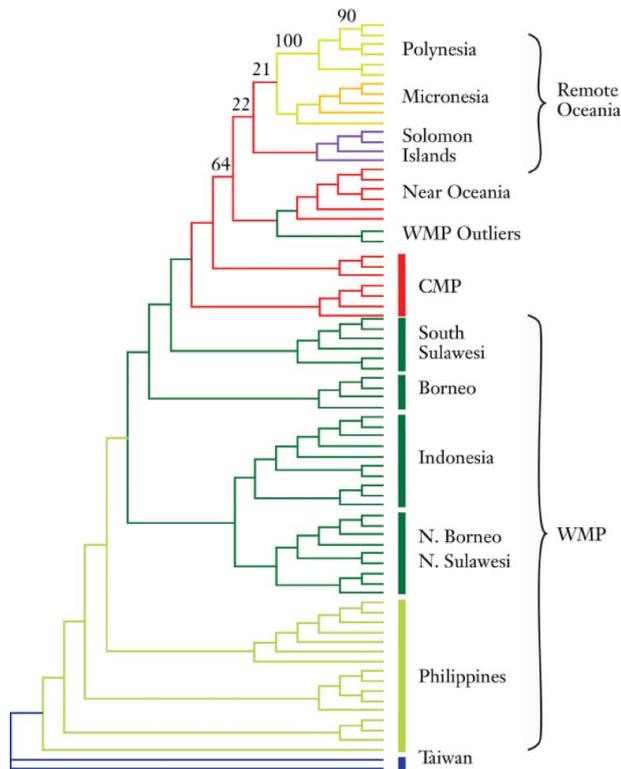


Figure 3. Phylogenetic tree of 77 Austronesian languages created by maximum parsimony (after Gray & Jordan 2000; Hurler et al. 2003). The tree shows considerable agreement with traditional linguistic groupings, which themselves reflect historical relationships, not just geographical proximity. CMP and WMP represent Central Malayo-Polynesian and Western Malayo-Polynesian, respectively. The tree is rooted with two Formosan (indigenous Taiwanese) languages. Taxa used to root a tree are known as outgroups. Outgroup taxa supposedly diverged from the set of taxa under study (ingroup taxa) prior to the point at which those taxa diverged from each other. Outgroup taxa thus should contain more retentions (ancestral traits) than the ingroup taxa, thereby giving us a solid entry point from which to begin ordering the ingroup taxa. Bootstrap values, which can be thought of as indicators of the strength of taxonomic arrangement, are shown above some of the branches in the Oceanic clade. Consistent with the pause in settlement, the eastern Polynesian subgroup has strong bootstrap support.

(Figure 3). In accordance with the express-train model, the west-to-east gradient shows up clearly, with the Western Malayo-Polynesian groups being ancestral, followed by Central Malayo-Polynesian languages, Western Malayo-Polynesian outliers, Near Oceanic languages, and finally Remote Oceanic languages, which are the most derived. To examine quantitatively the fit between the model and the tree, Gray and Jordan used the geographic

stations shown in Figure 2 as ordered character states and mapped them onto the tree. They found that the topology (shape) of the tree was highly compatible with the model, meaning that the character-state tree fit the language tree with significantly fewer steps than would occur by chance (13 steps versus 48.9 steps).

Hurler et al. (2003) examined the fit more closely, noting that bootstrap values, as predicted from archaeological data (Green 1991, 1999; Spriggs & Anderson 1993; Kirch 1997, 2000; Kirch & Green 2001), are high for the separation of the Polynesian clade (the six grouped taxa and their common ancestors shown in gold in Figure 3) but lower for the early Oceanic branches. The consistency index for the lexical tree is only 0.25, which indicates a considerable amount of borrowing among languages. This is not surprising given that Austronesians were adept navigators. Archaeological (Weisler & Kirch 1996; Weisler 1998) and molecular (Matisoo-Smith et al. 1998) evidence indicates that population interaction and exchange occurred even between distant archipelagoes.

As we noted above, once language trees have been constructed, they can be used to examine other aspects of culture. For example, Currie et al. (2010) and Currie and Mace (2011) used Bayesian and maximum likelihood methods to analyze a dataset of 84 Austronesian-speaking societies – a slightly larger sample than Gray and Jordan (2000) used – to examine the kind of sociopolitical organization that characterized each society. Once the language phylogeny had been reconstructed, they coded the branch tips, representing ethnolinguistic groups, in terms of the type of organization each group exhibited. Figure 4 illustrates this principle in simplified form. The results showed that the cultural evolutionary sequence of band → tribe → chiefdom → state that has long been a standard cultural model of cultural evolution (e.g. Service 1962; Haviland 2001), though never tested empirically, held up remarkably well when the organization types were placed on branch tips. Currie et al. (2011) found that in the best fitting model, sociopolitical complexity rose and fell over time in a sequence of small steps; the second-best fitting model showed that increases were sequential but decreases could be either sequential or more dramatic. The conclusion was that large, non-sequential jumps in sociopolitical complexity did not occur during the evolutionary history of the societies. Further, despite all the myriad contingent pathways of human history, regularities in cultural evolution existed and could be detected using computational phylogenetic methods.

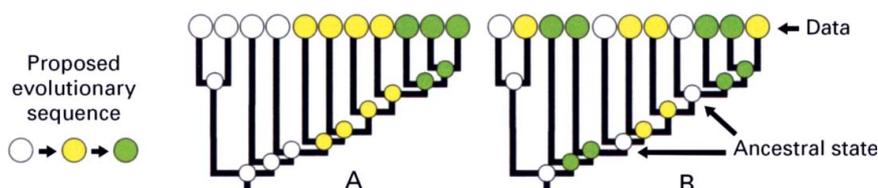


Figure 4. Inferring sequences of trait evolution using phylogenies (after Currie et al. 2010). By mapping trait data onto the tips of a phylogenetic tree, it is possible to make inferences about the evolutionary process(es) that gave rise to the data. In this example, the proposed evolutionary sequence, white → yellow → green, appears to fit the data in Tree A much better than in Tree B.

Currie and Mace (2011) extended the analysis and found that sociopolitical organization co-evolved with the wider presence of hereditary social stratification.

Another example of using language trees to examine cultural evolution comes from Bantu-speaking parts of sub-Saharan Africa. Holden and Mace (2003; also Holden et al. 2003) were interested in why matrilineal societies, in which relatedness through females is culturally more significant than relatedness through males, almost never keep large livestock (Aberle 1961; Schneider 1964). They proposed that when matrilineal societies acquire cattle, they either become patrilineal or adopt a form of mixed descent. They used as a sample 68 Bantu- and Bantoid-speaking populations from sub-Saharan Africa pared from a slightly larger sample (Holden 2002). Phylogenetic analysis showed that Bantu languages conform well to a tree model, probably because Bantu radiation reflects a population expansion associated with the spread of farming (Ehret 1998; Bellwood 2001, 2005). Later work by Holden and Gray (2006) showed that rapid radiation in the Bantu languages meant that while tree models fit well, multiple trees were equally robust. The Bantu-language tree coded for type of descent system and presence or absence of cattle is shown in Figure 5. It supports the hypothesis that acquiring cattle led formerly matrilineal Bantu-speaking cultures to change to patrilineal (tracing descent through one's father) or other forms of descent. Cattle also have greater fitness benefits than females among Kenyan pastoralists, making it adaptive for parents to transmit livestock to their sons (Mace 1996).

Challenges to cultural phylogeny

Even keeping in mind that phylogenetic trees are nothing more than hypotheses about evolutionary relationships (Platnick 1977), is such a procedure – tree building – theoretically warranted? Some researchers have said “no”; others have said “maybe”, pointing out that although phylogenies might in some cases be fairly accurate representations of cultural descent, there is no way of knowing (see below for references). We can frame the various issues in terms of four questions (O'Brien et al. 2008): (1) Do cultural features, because they are inorganic, carry phylogenetic information in the first place? (2) Even if they do, because cultural evolution can involve reticulation as a result of nonvertical transmission, are potential phylogenetic signals muted to the point of being undetectable? (3) Is there a concordance among language, culture, and biology, so that if one of them is reconstructed, the others can be assumed to tag along in lock-step fashion? (4) Related to number 3, at what scale(s) can cultural phylogeny be examined?

Do cultural features carry phylogenetic information?

As long as the issue is skeletal biology, comparative anatomy, or genetics, anthropologists have no problem viewing humans in more or less the same light as other organisms, but when the topic turns to cultural features – stone tools, ceramic vessels, kinship systems, and the like – some

researchers view things differently (see below for references). Because humans are culture-bearing animals, so the argument goes, evolutionary processes that work on other organisms – selection, drift, and the like – have little or no effect on humans. Thus we might speak of human features such as language as “evolving”, but it is evolution only in the sense of change over time, not in the Darwinian sense.

Some evolutionary biologists (e.g. Mayr 1982; Gould 1987a, 1987b, 1991, 1996; see also Angier, 1997) also have problems incorporating human culture under the Darwinian umbrella. Gould (1987a, p. 70), for example, opined that

Human cultural evolution proceeds along paths outstandingly different from the ways of genetic change. . . . Biological evolution is constantly diverging; once lineages become separate, they cannot amalgamate (except in producing new species by hybridization – a process that occurs very rarely in animals). Trees are correct topologies of biological evolution. . . . In human cultural evolution, on the other hand, transmission and anastomosis are rampant. Five minutes with a wheel, a snowshoe, a bobbin, or a bow and arrow may allow an artisan of one culture to capture a major achievement of another.

In our view, this “cultural exceptionalism” is flawed (O'Brien et al. 2006). The *individuals* who made and used stone tools, who recognized specific people as kin, and who developed certain political institutions were subject to Darwinian evolutionary processes the same as any organism (O'Brien & Lyman 2000, 2002a). Social institutions and products of technology are active components of the adaptive process. Regardless of how individuals obtained them – for example, learning them from parents or copying them from peers – cultural variants represent alternative solutions to adaptive problems and can have different reproductive consequences for their makers and users (Leonard & Jones 1987; O'Brien & Holland 1992). Cultural phenomena are parts of human phenotypes in the same way that skin and bones are, and as such they are capable of yielding data relevant to understanding both the process of evolution and the specific evolutionary histories of their possessors (O'Brien & Lyman 2000). This view should not be unduly troubling. Biologists (e.g. Bonner 1980, 1988; Dawkins 1982; Hansell 1984; Turner 2000; Odling-Smee & Turner 2011) routinely view such things as a bird's nest as part of its phenotype in the same way that they view its beak and feathers. Why should cultural behaviors or their products be thought of any differently (O'Brien & Holland 1995; Laland & O'Brien 2010)?

Does reticulation destroy phylogenetic signal?

Some anthropologists have argued that cultural phylogeny is nearly impossible to reconstruct because of the nature of cultural evolution (Terrell 1988, 2001, 2004; Bateman et al. 1990; Welsch et al. 1992; Moore 1994a, 1994b, 2001; Welsch & Terrell 1994; Dewar 1995; Terrell & Stewart 1996; Terrell et al. 1997, 2001; Hornborg 2005). They view cultural evolution as a different kind of process

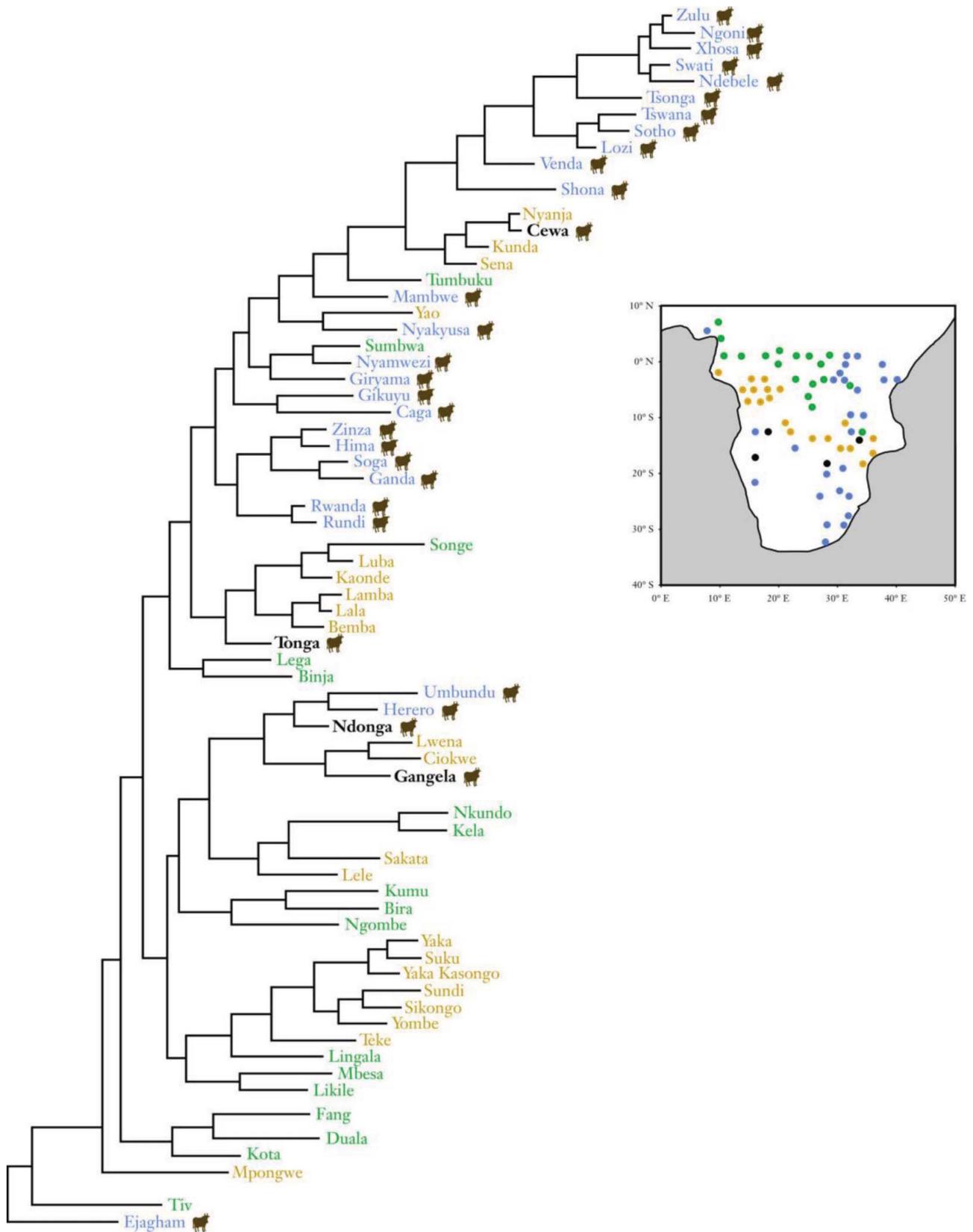


Figure 5. Bantu-language tree representing past relationships among 68 African cultures (after Holden 2002, 2006; Holden & Mace 2003). Descent rules and the presence or absence of cattle are indicated in both the language tree and inset map by colors: green, patriliney or mixed descent, no cattle; blue, patriliney or mixed descent, with cattle; yellow, matriliney, no cattle; black, matriliney, with cattle. The tree was created by maximum parsimony.

from biological evolution, with a faster tempo and a different mode – horizontal transmission – that creates reticulation, thus eradicating most or all traces of phylogenetic history and reducing the cultural landscape to little more than a blur of interrelated forms. This process is often referred to as *ethnogenesis* (e.g. Moore 1994a, 1994b; Collard & Shennan 2000; Hornborg 2005; Towner et al. 2012), defined broadly as cultural evolution that occurs “through the borrowing and blending of ideas and practices, and the trade and exchange of objects, among contemporary populations; the source of change is external” (Borgerhoff Mulder et al. 2006, p. 54).

To put things in perspective, cultural evolution probably is, in most respects, faster than biological evolution, and it can involve reticulation, but are these aspects necessarily problematic? We would say no. For one thing, biological evolution can involve not only reticulation (Arnold 1997; Endler 1998; Doolittle 1999), where between-species hybridization might be as high as 15–25% in plants and as high as 10% in animals (Rhymer & Simberloff 1996; Mallet 2005), but also cospeciation (Page 2003) and endosymbiosis – one organism coming to live inside another and eventually becoming an obligate symbiote (Velasco 2012), and lateral (horizontal) gene transfer – the physical transfer of genetic information from one organism to another, preexisting organism (Rosewich & Kistler 2000; Dagan & Martin 2006, 2007), including between bacteria and eukaryotes (Dunning Hotopp et al. 2007).

Despite these issues, biologists have not abandoned the use of phylogenetic trees. Rather, they admit that the history of life is messy (Bell et al. 2010) and that there may in fact, be no such thing as *the* tree of life (see O'Malley et al. 2010) – or, if there is, we will never find it. Biologists recognize that they deal with subtrees of that “tree” and that those subtrees are nothing more than models (Archibald et al. 2003). Cultural phylogenists (e.g. Collard et al. 2006a, 2006b; Muscio 2010) have recognized the same thing. As Velasco (2012) points out, the significant question is not whether a particular history is a tree but rather how well a tree-like model depicts that history (see also Franklin-Hall 2010). Thus,

the treatment of all taxa should be rooted in the method itself, not in our belief about what the result of an analysis should represent. A [phylogenetic tree] is either *useful or useless* (in terms of reflecting the character patterns), rather than *true or false* (in terms of reflecting the course of phylogeny) (Skála and Zrzavý 1994, pp. 311–312).

A key issue here is conflation of terms and concepts, especially *hybridization*, which has been used in cultural studies to denote *any* instance of horizontal transmission (e.g. Terrell et al. 1997). This equates process (hybridization) with mode (reticulation; Figure 6), which is specious. Consider units of three different scales: Parental units, offspring units, and units of transmission. The mating of two parental organisms will produce an offspring with 50% of its genes originating with each parent – a 50/50 F1. Thus

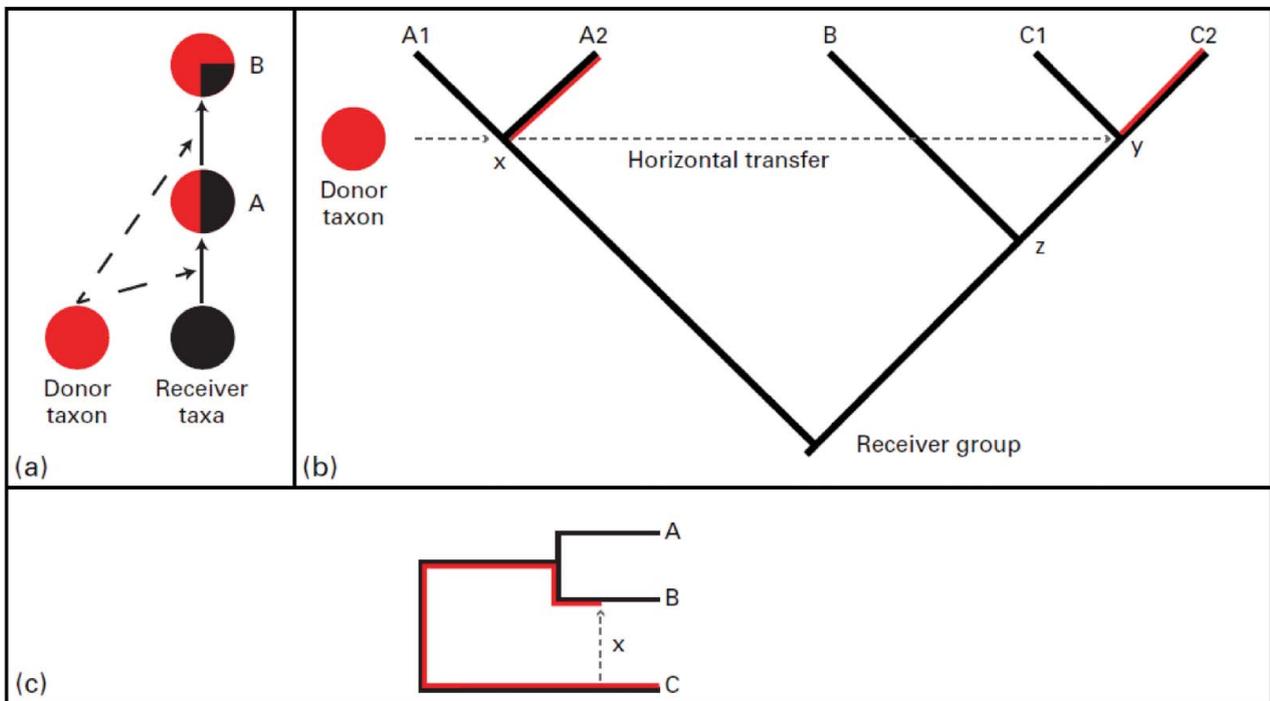


Figure 6. Kinds of horizontal transfer: (a) single horizontal transfer – two single entities, a donor and receiver, of the same taxonomic level exchange traits and produce hybrid taxa (A and B) after replication; (b) nested horizontal transfer (NHT) – a clade changes its composition as the result of the horizontal transfer of traits from an extragroup entity to some of its members (after Muscio 2010). In the graph, two events of NHT to nodes x and y create taxa A2 and C2 and change the shape of tree by the appearance of a new clade – A1 + A2 + x (their common ancestor) – and other, more-inclusive clades – (C1 + C2 + y) and (B + C1 + C2 + z); (c) discrepancies between trait phylogeny and terminal-taxon phylogeny resulting from horizontal transfer. The lateral transfer of trait x from C to B locates those two taxa in the same group, whereas the rest of the traits would separate C from A + B.

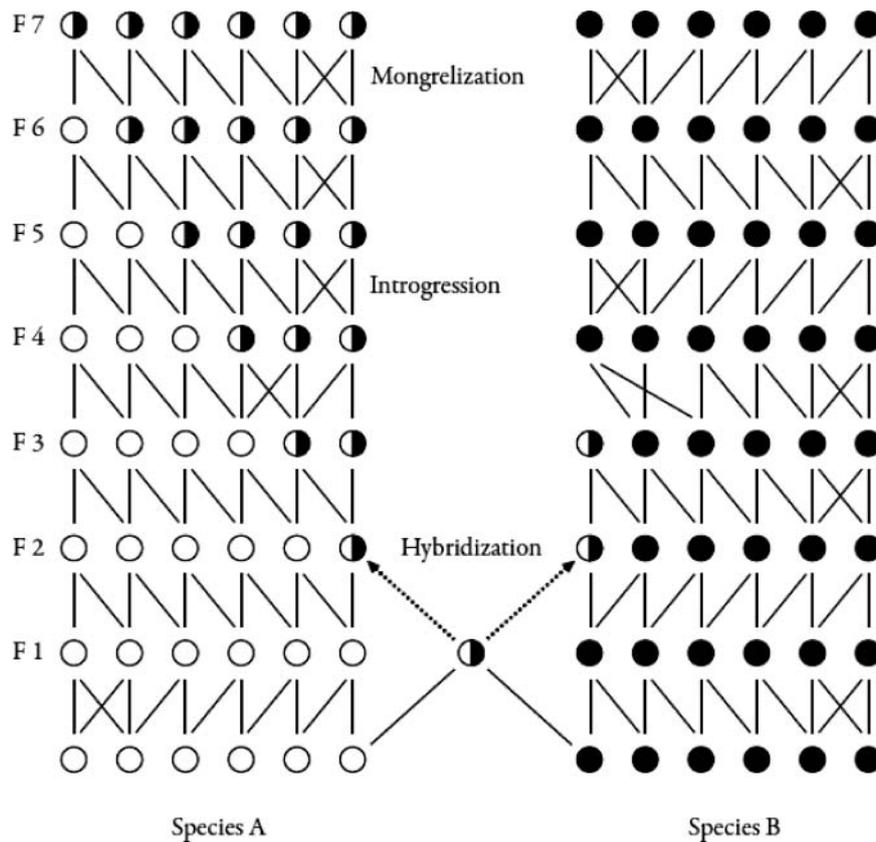


Figure 7. A simplified model of hybridization, introgression, and mongrelization (from O'Brien and Lyman 2003). Each circle represents an individual organism; each row of circles represents a separate generation; and time passes from bottom to top. White circles represent individuals in species A; black circles represent individuals in species B; and circles that are half white and half black represent hybrids. Vertical and diagonal lines represent genetic transmission.

the offspring unit is an even mixture of its parents in terms of the units of transmission. Presuming there are units of cultural transmission, regardless of what one calls them (Lumsden & Wilson 1981; Cullen 2000; Aunger 2002; Shennan 2002), horizontal cultural transmission *may* produce an offspring comprising equal parts of those replicators, but the odds are that it will not.

To be an instance of hybridization, however, not only must something akin to a 50/50 F1 offspring be produced, but that hybrid must then transfer its mixture of genes into at least one of the parent species through *introgression* (Anderson 1949). Subsequent generations must next include the extralinear genes, and they must spread throughout the population in order to effect *mongrelization* (Levin 2002). If these extralinear genes spread in such a manner, then reticulation is the mode. If those extralinear genes do not spread in such a manner, then no hybrid mongrel species will be produced.

O'Brien and Lyman (2003) distinguish among hybridization, introgression, and mongrelization using the model shown in Figure 7. An individual from species A mates with one from species B to produce a 50/50 F1 hybrid offspring. That offspring then mates with individuals of its own generation to produce hybrid F2 offspring in each parent species. In species B the second-generation F3 hybrid fails to reproduce, so hybridization in that lineage ceases, there is no introgression, and reticulate evolution has no effect on the lineage. Conversely, in species

A, the F2 hybrid interacts with members of its own cohort, as does each succeeding generation of hybrids. This results in introgression and eventually mongrelization of the entire species lineage such that no "purebred" individuals of the original species exist. Species A is effectively extinct by generation F7.

Goodenough (1997, p. 178) makes many of the same points 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". Borrowing has not created a "hybrid" culture or language. Further, linguists do not flip a coin to determine whether two or more languages share a phylogenetic history. Innumerable case studies have provided the basis for deciding which linguistic characters might be derived characters – bound morphemes and vocabulary, for example – and which might be something else – syntax, for example (see Nichols 1996). None of this, of course, negates the possibility that two languages can blend to create a new language (e.g. Bakker 1997; McWhorter 2001).

Are language, biology, and culture concordant?

Moore (2001, p. 32) claims that cultural phylogenists assume that genes, language, and culture evolve as a

'package,' so that all three aspects of human life tend to experience congruent or parallel changes. A biological taxonomy of human populations showing their overall genetic relatedness should be compatible with a taxonomy of their languages, technology, or other aspects of culture. By knowing a group's genetic structure, we should be able to predict such traits as their linguistic affiliations, their social structure, and their religion.

This mischaracterizes what comparativists have said, perhaps stemming from a liberal reading of what Lansing et al. (2007, p. 16022) refer to as "well-known studies [that] have identified associations between the languages and genes of human populations at continental and global geographic scales". These include the work of Cavalli-Sforza et al. (1988), Sokol (1988), and Barbujani and Sokol (1990). In an early programmatic statement on the method, Romney (1957, p. 36) made it clear, however, that the *genetic model*

takes as its segment of cultural history a group of tribes which are set off from all other groups by sharing a common physical type, possessing common systemic patterns, and speaking genetically related languages. It is assumed that correspondence among these three factors indicates a common historical tradition at some time in the past for these tribes.

Romney designated this segment of cultural history the *genetic unit* and included within it the ancestral group and all descendant groups, including those in the ethnographic present.

Romney was not claiming an isomorphism among language, genes, and culture. Rather, he was pointing out that a cultural-historical "genetic unit" needs to be defined on independent grounds. If a high correspondence exists among the three variables, then perhaps the genetic unit is an analytically useful device. Significantly, "usefulness" is testable (e.g. Lansing et al. 2007). The point is not to prejudge the nature of the relationship but rather to establish the pattern in order to determine what factors might determine whether there is a positive, neutral, or negative relationship (Foley & Lahr 1997).

At what scale(s) can cultural phylogeny be examined?

Irrespective of the line or lines of evidence, what kinds of units are typically used in cultural phylogenetic analysis? In some cases, such as in the examples from Africa and Oceania we mentioned previously, whole cultures are examined. In other cases, individual characters or bundles of characters are examined (e.g. O'Brien et al. 2001, 2002, 2012; Tehrani & Collard 2002; Jordan & Shennan 2003, 2009; Shennan & Collard 2005; Darwent & O'Brien 2006; Jordan & Mace 2006, 2008; Lipo 2006; Cochrane & Lipo 2010; Matthews et al. 2011). Cultural phylogenetic work is based on several claims: (1) human populations, cultures, and languages are real things and not simply convenient analytical fictions; (2) the entities are historically enduring phenomena despite births, deaths, immigration, and the like; and (3) as with individuals, the entities have ancestors, descendants, relatives,

and patterns of hierarchical descent (Terrell 2001). To critics, these are problematic assumptions, and for some scales of analysis they may be. But cultural phylogenists understand the problem of units and scale, accepting that a phylogeny represents in only the broadest of terms the path that most of the ancestors of the majority of members of a culture followed (Mace & Pagel 1994; O'Brien et al. 2008; Mace & Jordan 2011). The key word is "broadly"; no phylogenist would view a cultural phylogeny using "cultures" as taxonomic units as anything but a broad picture of ancestry (Fortunato et al. 2006; Currie et al. 2010).

Boyd et al. (1997) note that tracing cultural phylogeny is possible to the extent that there are genealogical entities of whatever scale that exhibit sufficient coherence, relative to the amount of mixing and independent evolution among entities, to create recognizable history. If culture is defined as information transmitted between individuals through a variety of means (e.g. Lewis & Laland 2012), then it is not unreasonable to posit the existence of a hierarchy of genealogical entities analogous to the genealogical hierarchy of organic evolution. Thus small elements (words, innovations, components of ritual practice) are linked together in larger, potentially transmittable entities (technological systems, myth, religion), which themselves are collected into "cultures" that characterize human groups of different scales (kin groups, villages, ethnic groups, and so on). These units can cross-cut one another, and thus the analyst must be explicit in defining the unit being used (Pocklington & Best 1997; Atran 2001; Pocklington 2006; O'Brien et al. 2008).

As alternatives to the hierarchical model of cultures, Boyd et al. (1997) offer three other models: Cultures as species, cultures as collections of ephemeral entities, and cultures as assemblages of many coherent units. Like Boyd and colleagues, we find no support for the culture-as-species model, although the anthropological literature is replete with vague references to this culture or that culture as if they were natural units. Cultures are routinely equated with species (e.g. Willey & Phillips 1958; Gould 1997), despite the lack of a generally accepted definition of "a culture" that even remotely incorporates the notion of transmission or a generally accepted definition of a species. As a result, any equation of a biological species with a culture is fallacious. Likewise we tend to reject the cultures-as-collections-of-ephemeral-entities model, which rests on the premise that aspects of culture could be the result of units that, given current methods, cannot be observed. We are unaware of any units that, from either a theoretical or empirical standpoint, are beneath our ability to detect. The third model proposed by Boyd et al. (1997) – cultures as assemblages of many coherent units – views the components as collections of memes that are transmitted as units with little recombination and slow change. Thus their phylogenies can be reliably reconstructed to some depth. How deep we can go in the reconstruction hinges on the strength of the "glue" that holds the units together and the degree of openness of cultural systems. If we think of the components in terms of memes, how cohesive is a set of memes and how freely

can memes from the outside enter a set, and in what frequency?

The two models that appear to hold the most promise – cultures as hierarchical systems and cultures as assemblages of many coherent units – are not mutually exclusive, and in fact Boyd et al. (1997) view them as points on a continuum. As they point out, it is difficult to put upper and lower bounds on them, and perhaps because of that we should view them as nonexclusive, overlapping modes, especially if the models are applied to cultures in general. Central to their model of cultures as hierarchical systems is the existence of a conservative “core tradition”, which is rarely affected by diffusion of units from other groups. New core traditions arise mainly through the divergence of daughter cultures. Isolation and integration protect the core from the effects of diffusion, although peripheral elements are subject to cross-cultural borrowing. As for constructing phylogenetic hypotheses, deep core-cultural phylogenies can be inferred, although doing so requires two things: (1) disentangling the effects of borrowing by distinguishing core from peripheral elements; and (2) identifying elements that introgressed into the core.

It seems reasonable to conclude that most cultures have a conservative “core tradition” – similar to Swadesh’s (1964) “morphological kernel” of a language (Kopytoff 1987). The question is whether we can identify it (Jordan and Mace 2006). We might start by examining how archaeologists have long viewed traditions, going back to Willey’s (1945) definition: A line or related lines of development through time within the confines of a certain technique or constant. Willey was defining tradition at the scale of an attribute of a discrete object, but he expanded his definition to include the scales of discrete object and aggregates of objects: A tradition includes broad categories of such things as pottery decoration that undoubtedly have value in expressing historical relationships when the relationships are confined to the geographic boundaries of cultures. A few years later, a group of archaeologists took up the notion of tradition, defining it as a socially transmitted form unit or series of systematically related form units that persist in time (Thompson 1956). It is at the scale of traditions that anthropologists can begin to construct testable hypotheses of cultural phylogeny (O’Brien & Lyman 2000; O’Brien et al. 2008).

Conclusions

The growing interest in cultural phylogeny evident over the past two decades marks a return to the questions that motivated the earliest professional anthropologists (Aberle 1987; Lyman et al. 1997). Data for answering phylogenetic questions are now more numerous and more specific and detailed, and the epistemological nuances and pitfalls are much better known than they were five or six decades ago (Borgerhoff Mulder et al. 2006). Ontological matters, especially whether culture is such a “tangled bank” that phylogeny is impossible to trace, are another issue altogether. On one scale we may be dealing with

whole cultures, and on another with language, technology, or sociopolitical institutions (O’Brien et al. 2008). The shape of individual phylogenies will change as we shift scales because individual subsystems of cultures often evolve independently of one another (e.g. Moylan et al. 2006; Jordan & Mace 2008; Matthews et al. 2011). For example, at one level we might speak of pottery traditions, identifying them on the basis of general characteristics, but when we reduce the scale, we likely will find that clay selection, forming the vessel, and firing it might be bundled characters. Similarly, we will probably find that the trajectories those characters take are independent of the phylogenetic histories of the colors and elements of design applied to vessels (O’Brien & Holland 1992). The same is true of myriad other aspects of culture (Borgerhoff Mulder 2001; Moylan et al. 2006; Pocklington 2006).

Certainly Towner et al. (2012, p. 284) are correct in noting that both phylogenesis and ethnogenesis play roles in cultural macroevolution and that

when, where, and to what extent traits are transmitted horizontally or vertically will depend on a variety of features of the trait, including its functional and symbolic relationship with other traits in the population . . . and the extent to which the trait depends on coordination . . . or other transmission-coupling mechanisms.

This dependence is what gives culture its “tangled” appearance. Further, one cannot disagree with Nelson-Sathi et al.’s (2010, p. 12) statement that “borrowing is a non-tree-like evolutionary event that cannot be reconstructed using phylogenetic trees”. But knowing these statements to be true does not really help us move forward. The only thing that matters is: What model best fits the data? We would always begin with a branching model, make the best fits statistically possible given the data, and then seek to resolve inconsistencies using other methods.

This is what Gray et al. (2007) advocate in their two approaches for assessing the accuracy and robustness of phylogenetic inferences in a principled manner: (1) examining the ability of the inferences to reconstruct known cultural histories and (2) directly manipulating horizontal transfer using simulation studies (e.g. Nunn et al. 2006, 2010; Currie, Greenhill & Mace 2010). As they note, instead of arguing whether the shape and fabric of human history is better modeled as a tree (phylogenesis) or as a thicket (ethnogenesis), it would be more productive to ask where particular aspects of culture lie on at least three dimensions: The rate of change in characters transmitted vertically; the rate of change in characters transmitted horizontally; and the extent to which different aspects of culture are coupled. If we know these things – and they are knowable empirically – then we can answer the question, “Are these particular data more like a tree, more like a thicket, or something in between?” That, to us, is the only real question worth answering. As a final note, we emphasize a point that we have made repeatedly (e.g. O’Brien et al. 2006): Phylogenetic methods are but one tool in the anthropologist’s toolbox – an important one, but one that cannot be applied haphazardly to any

dataset (Collard et al. 2006a, 2006b; Gray et al. 2007; Cochrane & Lipo 2010; Mace & Jordan 2011; Matthews et al. 2011). Other methods – tests for serial independence (Abouheif 1999), iterated parsimony (McElreath 1997), network analysis and split decomposition graphs (Bandelt & Dress 1992; Bryant & Moulton 2002; Forster & Toth 2003; Bryant et al. 2005; Huson & Bryant, 2006; Lipo 2006), tests for matrix correspondence (Smouse & Long 1992), assessment of hierarchical cluster structure (Pocklington 2006), and seriation (O'Brien & Lyman 1999; Lyman & O'Brien 2006) – can and should be used in tandem with phylogenetic-inference (tree-building) methods.

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Notes

1. This may not have been the first migration through the region. Jinam et al. (2012) postulate an “early train” migration originating from Indochina or South China around the late Pleistocene to early Holocene period, ca. 30,000–10,000 B.P.
2. PAUP* is a program built on maximum parsimony. Gray and Jordan (2000) used it in their study of the colonization of the Pacific by Austronesian-speaking people, but in an updated and expanded study, Gray et al. (2009) used BayesPhylogenies (Pagel & Meade 2004, 2005) to work around limitations of the earlier data and methods.

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