Transmission, Phylogenetics, and the Evolution of Cultural Diversity


Anthropology and by extension archaeology have always had as a primary goal documenting the enormous cultural diversity that serves as the hallmark of humanity and explaining how and why this diversity took the form that it did (Boas 1895, 1904; Leaf 1979; Lowie 1937). Often this diversity is said to be the product of evolution, but even a casual perusal of the literature suggests that those who use the term with respect to cultural phenomena separate it both conceptually and analytically from biological evolution. Whereas biologists since the time of Darwin have generally viewed organic evolution as an undirected process, anthropologists have viewed cultural evolution more in Lamarckian, or directed, terms. Most early models of cultural evolution (e.g., Morgan 1877; Tylor 1871) viewed it as both progressive, in that it raised humans up from primitive to advanced stages, and orthogenetic, in that it was fueled by an internal driving force. Some early models (e.g., Kidder 1932; Lowie 1918; Wissler 1923) contained scattered elements of Darwin’s theory of descent with modification, but they lacked explicit mechanisms of change. For example, cultural transmission was acknowledged both as diffusion— the movement of a culture trait from one culture to another—and as enculturation—the process of learning one’s culture, but largely ignored was the question of why and how those mechanisms effected change at particular times and in particular places (see ch. 2).

Irrespective of the kind of evolutionary model preferred, anthropologists found it difficult to trace the complex evolutionary histories of cultural lineages and to differentiate between instances of independent invention and instances of diffusion and cultural borrowing (Goldenweiser 1916; Steward 1929). The latter two processes obviously involve transmission, whereas independent invention does not.

Darwin’s cousin, Francis Galton, identified the problems that arise from ignoring the distinction when he commented on E. B. Tylor’s (1889) call for a comparative anthropology. Galton pointed out that comparative studies of adaptation are irrelevant if we cannot rule out the possibility of a common origin of the adaptive feature under examination. Escaping this problem requires a working knowledge of the phylogeny of taxa included in the analysis (Mace 2005). This rule applies equally to both cultural taxa and biological taxa. Both kinds of classes contain individuals that were created through transmission, which means that they have phylogenetic histories.

The importance of understanding these histories was not lost on our intellectual forebears, who developed a variety of methods for tracing the development of cultural traits. Some methods focused on ethnological traits—belief systems, descent systems, political institutions, and the like (e.g., Eggan 1954)—and others focused on both ethnological and archaeological traits (Sapir 1916; Strong 1953). All the methods implicitly assumed that cultural evolution involves descent with modification, but any suggestion that there was more than a metaphorical link between biological and cultural evolution invariably triggered intense criticism (e.g., Brew 1946; Steward 1941). Further, culture was viewed as being highly reticulate, running like a braided stream in channels that are constantly diverging and converging. Without clear, unequivocal, and irreversible divergence, how could one hope to trace ancestry except in the most superficial way? Perhaps a trait could be traced back in time, but how did it relate phylogenetically to other traits? This question was usually left unanswered.

The period circa 1950–1980 witnessed little anthropological emphasis on phylogeny, as historical pursuits were eclipsed by other interests, both
in the United States and abroad (Jones 2003; Kirch and Green 2001). The situation began to change dramatically in the 1980s, leading to the point now where phylogenetic methods have become as much the "gold standard" in anthropology as they have in biology (Huelsenbeck et al. 2000:2349). Our impression is that this modern interest in phylogeny can be attributed to three factors: (1) an exponential increase in genetic data compared with what was available previously (Cann et al. 1987; Cavalli-Sforza et al. 1988; Cavalli-Sforza et al. 1994; Stoneking 1993); (2) advances in analytical and computing methods, which allow the integration of large data sets (e.g., Farris 1989; Goloboff 1991; Maddison and Maddison 2000; Swoford 1998); and most important, (3) a heightened awareness among social scientists of issues in evolutionary biology and a willingness to see (i) human culture as a phenotypic phenomenon and (ii) cultural transmission as both an inheritance system and a significant source of cultural variation arising from imperfect copying (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Cloak 1973, 1975; Durham 1991, 1992; Henrich and Boyd 1998; Henrich and McElreath 2003; Mesoudi et al. 2004).

We hope both anthropologists and archaeologists find this chapter of interest. Our task is twofold: first, to illustrate by way of examples from Africa and Oceania some of the approaches used by cultural phylogeneticists and, second, to explore several epistemological issues that underlie their work. Our overarching goal is to demonstrate that phylogeny depends on transmission, irrespective of mode (O'Brien and Lyman 2003a). This means that cultural transmission is as legitimate a mechanism for creating phylogenetic relationships as genetic transmission is. Using language that Cavalli-Sforza and Feldman (1981) have borrowed from epidemiology, cultural transmission can be vertical in the sense of parent to offspring, analogous to genetic transmission, but it can also occur in the opposite direction—from offspring to parent. It can also be horizontal—between people of the same generation. As we will see, this might be problematic for phylogenetic analysis if analytical emphasis were strictly on individuals (Grandcolas and Pellens 2005; O'Brien and Lyman 2003a), but, as in biology, it is on collections of individuals—populations and other large-scale units. The question is this: Are phylogenetic signals swamped at the level of these more inclusive units, or, despite the fact that populations transmit cultural elements between themselves, are phylogenetic signals still strong enough to be detected? In some, but certainly not all, cases, the answer to the latter question is yes. Unraveling cultural phylogeny might be more difficult than if transmission were strictly vertical between individuals, and then only in one direction, but as we will show, this is a methodological problem, not a theoretical one (Bellwood 1996).

ANTHROPOLOGICAL STUDIES

Phylogenetic studies undertaken in anthropology during the last 20 years tend to fall into three categories: (1) studies that trace lines of transmission, and hence of descent, back to a common ancestor (a prototype) and then examine the processes that underlie the geographic distribution and cultural development of descendants (e.g., Flannery and Marcus 1983; Foley 1987; Gamkrelidze and Ivanov 1990; Green 1991a; Hage 1999; Kirch and Green 1987, 2001; Kopytoff 1987; Moore and Romney 1994; Renfrew 1987, 1992, 1998, 1999, 2000; Ross 1989; Rushforth and Chisolm 1991; Shennan 2000, 2001; Shennan and Collard 2005; Vansina 1990); (2) studies that first create nested groups of related taxa (called clades) and then map the taxa geographically (e.g., Atkinson and Gray 2006; Bryant et al. 2005; Collard and Shennan 2000; Collard and Tehrani 2005; Gray and Atkinson 2003; Gray and Jordan 2000; Harmon et al. 2006; Holden 2002, 2006; Holden et al. 2005; Jordan and Shennan 2003, 2005; Renfrew and Boyle 2000; Renfrew et al. 2000; Tehrani and Collard 2002); and (3) comparative studies that rely on understanding patterns of descent in order to examine the distribution of adaptive (functional) features (e.g., Borgerhoff Mulder et al. 2001; Darwent and O'Brien 2006; Foley and Lahr 1997; Guglielmino et al. 1995; Hewlett et al. 2002; Holden and Mace 1997, 1999, 2003, 2005; Holden et al. 2003; Mace and Holden 2005; Mace and Jordan 2005; Mace and Pagel 1994; Mace et al. 2003; O'Brien and Lyman 2003a, 2003b; O'Brien et al. 2001; O'Brien et al. 2002; Pagel and Meade 2005; Sellen and Mace 1997). The boundaries between approaches, especially between categories 2 and 3, are not hard and fast. All three can involve numerous lines of evidence, including archaeological, ethnological, and
molecular information (e.g., Diamond and Bellwood 2003), but a feature many of them share is a reliance on linguistic data to create the basic cultural phylogeny. 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 evolves in a cladogenetic (branching) manner (Cameron 1987; Platnick and Cameron 1977; Rexová et al. 2003); 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 and Eller 2004; Mace and Holden 2005). Thus when anthropologists speak of “cultures,” what they most often are referring to are ethnolinguistic groups—groups of people who speak the same language.

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 and Lyman 2000a). Continuity, however, does not imply complete fidelity. It is during transmission that linguistic change occurs, such as in the gain or loss of words or shifts in sound and meaning. 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). Similarities between the goals of systematic biology and historical linguistics have long been noted, dating back at least to the nineteenth century (Wells 1987). Darwin notes the similarity in the Origin: “If we possessed a perfect pedigree of mankind, a genealogical arrangement of the races of man would afford the best classification of the various languages now spoken throughout the world; and if all extinct languages, and all intermediate and slowly changing dialects, had to be included, such an arrangement would, I think, be the only possible one” (1859:422). Darwin is speaking of a language taxonomy that resembles the Linnaean taxonomy, but a truer representation is a phylogenetic tree, which shows ancestors and descendants as opposed to increasingly generalized groups of hierarchically ordered taxa.

In terms of the kinds of characters (traits) used to create a tree, linguistic characters are as amenable to division along ancestral/derived lines as biological characters are. We can think in terms of ancestral characters as being retentions and derived characters as being innovations. Both kinds of characters are homologous, the product of common ancestry, but the retentions are of less use in understanding phylogeny because they do not allow us to order the taxa that have the characters. All we know is that the taxa are somehow related to each other. For example, the presence of a highly complex structure such as a vertebral column is evidence that humans, birds, and literally thousands of other taxa are somehow related—a relatedness that led taxonomists to create the subphylum Vertebrata. But the vertebral column is a character that extends so far back in time as to be essentially useless in terms of helping us understand how the myriad backboned organisms of the last 400 million years are related phylogenetically. Thus we focus on innovations, which are shared only by two or more related taxa and their immediate ancestor.

Figure 4.1 illustrates one use of linguistic trees to investigate human behavioral adaptation, here a study of camel herding by East African pastoralists. Mace and Pagel (1994) propose that camel herding is an adaptation adopted in dry areas of East Africa—a proposition that can be tested only after distinguishing between camel herding as an analogous or a homologous character. Modern phylogenetic methods avoid the problem of non-independence among populations (recall our earlier mention of Galton’s comments on Tylor’s 1889 essay) because two branches descending from a node are by definition independent (Felsenstein 1985a; Harvey and Pagel 1991).

Mace and Pagel use linguistic data (Ruhlen 1987) to create a phylogenetic ordering of nine Kenyan pastoral groups and then identify those that herded camels and those that herded cattle but not camels. Archaeological evidence indicates that the appearance of camels in the region postdated the linguistic split between Nilotic and Kushitic peoples; thus the common linguistic ancestor shown at the base of the tree did not herd camels. Camel herding apparently arose independently in three groups (Turkana, northern Samburu, and Gabbra)
as well as in the ancestor that produced the Rendille and the Somali. Thus camel herding is an analogous character as far as those three groups are concerned. An alternative and equally parsimonious explanation 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 explanation is correct, there is 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.

Similarly, Holden and Mace (2003; also Holden et al. 2003) are 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 propose that when matrilineal societies acquire cattle, they either become patrilineal or adopt a form of mixed descent. They use as a sample 68 Bantu- and Bantoid-speaking populations from sub-Saharan Africa (Figure 4.2) pared from a slightly larger sample (Holden 2002). Phylogenetic analysis shows that Bantu languages conform well to a tree model, probably because Bantu radiation reflects a population expansion associated with the spread of farming (Bellwood 2001, 2005; Ehret 1998). The Bantu-language tree coded for type of descent system and the presence or absence of cattle is shown in Figure 4.2. It supports the hypothesis that acquiring cattle led formerly matrilineal Bantu-speaking cultures to change to patriline (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).

Language trees have also been used with archaeological and molecular data to examine the spread of human populations (Cann 2001; Renfrew 1992, 1998; Renfrew and Boyle 2000)—what has to be one of the most fascinating topics on the anthropological agenda of the early twenty-first century (Bellwood 2005). Figure 4.3 shows one proposed model for the colonization of the Pacific by Austronesian-speaking people within the past 6,000 years. The model begins with the assumption, based on archaeological data from excavated sites and molecular data from nonrecombining loci (maternally inherited mitochondrial DNA and the paternally inherited Y chromosome), that around 6000 B.P. there was an expansion of Austronesian-speaking Neolithic farming people out of south China and Taiwan (Bellwood 1997; Green 1999; Hurles et al. 2003; Lum 1998; Lum and Cann 1998; Melton et al. 1995). The expansion was rapid throughout the Pacific, taking roughly 2,100 years to reach the western edges of Polynesia, a distance of 10,000 km (Bellwood 1991, 1997; Blust 1995). Diamond (1988) has 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 colo-
Figure 4.2. Bantu-language tree representing past relationships among 68 African cultures (after Holden 2002, 2006; Holden and 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 a method known as maximum parsimony, which makes as few ad hoc phylogenetic hypotheses as possible. This means that the tree requires the fewest evolutionary events to explain the ordering of taxa.
nization process, they emphasize a minimum of admixture between the Austronesian speakers and the already established Melanesian speakers who occupied Near Oceania.

Opponents of the express train model (e.g., Terrell et al. 1997; Terrell et al. 2001) argue that ancestral Polynesians were derived from the established Melanesian populations and that intensive, continued prehistoric contact among Polynesian people obscured their phylogenetic histories. This model has become known as the "entangled bank" model (Terrell 1988). Note that it has two parts, the first of which is not necessarily in contradiction with the express train model. Neither the spread of Polynesian speakers into Remote Oceania nor the tempo of that spread depends on Taiwan or China as a source of the speakers. There are, in fact, studies that suggest that the Austronesian languages originated within island Southeast Asia during the Pleistocene (>11,000 years B.P.) and spread through Melanesia and into the remote Pacific within the past 6,000 years (Oppenheimer and Richards 2001; Richards et al. 1998). Proponents of this "slow boat" model detect a genetic signal of recent dispersal (<10,000 B.P.) that can be traced back from Polynesia only as far as the islands of Southeast Asia, although there is no doubt that the ultimate origin of these lineages is continental Asia (Harles et al. 2003). The critical feature of the entangled bank model, then, is not what it says about origin or tempo but, rather, what it says about any attempt to phylogenetically model the spread of humans throughout the Pacific. It says that it cannot be done. A series of recent studies, however, suggests that there is indeed a detectable phylogenetic signal being transmitted from Oceania.

Gray and Jordan (2000) analyzed 77 Austronesian languages with 5,185 lexical items to test one key aspect of the express train model—the colonization sequence shown in Figure 4.3—in a manner similar to how biologists test propositions about the sequence of events in biological evolution. If the model is correct, the languages should do two things: (1) share more in common with neighboring languages than with those further away and (2) line up in a west-to-east gradient in terms of age, with Polynesian languages being the youngest and Southeast Asian languages, the oldest. Gray and Jordan converted the linguistic data into a set of taxa (languages) and binary characters (cognate words) and used PAUP* (Swofford 1998)—a set of tree-building programs—to find the set of trees that requires the fewest evolutionary events to explain the ordering of taxa. A single most-parsimonious tree was produced (Figure 4.4). Note that in accord with the model, the west-to-east gradient shows up clearly, with the Remote Oceanic languages being the most derived, followed by Western Malayo-Polynesian outliers, Central Malayo-Polynesian languages,
and finally the more ancestral Western Malayo-Polynesian groups. To examine quantitatively the fit between the model and the tree, Gray and Jordan have used the geographic stations shown in Figure 4.3 as ordered character states (meaning, for example, that the expanding population landed sequentially in station 7, then 8, then 9, and finally 10) and mapped them onto the tree. They found that the topology (shape) of the tree is highly compatible with the model, meaning that the character-state tree fits the language tree with significantly fewer steps than would occur by chance.

Hurles et al. (2003) has examined the fit more closely, noting that bootstrap values, as predicted from archaeological data (Bellwood 1998; Green 1991b, 1999; Kirch 1997, 2000; Kirch and Green 2001; Spriggs and Anderson 1993), are high for
Figure 4.5. Detecting potential borrowing among 11 Polynesian languages (after Hurles et al. 2003). In (a) the languages are arranged on a parsimony tree; in (b) they are arranged in a splits graph to show borrowing that took place within the western (blue) and eastern (red) Polynesian clades.

The separation of the Polynesian clade (the six grouped taxa and their common ancestors shown in gold in Figure 4.4) but lower for the early Oceanic branches. The lexical tree has a relatively low consistency index (.25), which indicates considerable borrowing between languages. This is not surprising given that Austronesians were adept navigators. Archaeological (Weisler 1998; Weisler and Kirch 1996) and molecular (Matisoo-Smith et al. 1998) evidence indicates that population interaction and exchange occurred even between distant archipelagoes. The issue is whether this interaction creates such a reticulated phylogeny that no method can unravel it. Critics (e.g., Terrell 2004) argue that phylogenetic programs always produce molecular, linguistic, and other trees, irrespective of the appropriateness of the data (see below). Cultural phylogeneticists answer that there is a range of techniques for evaluating the robustness of tree models. Hurles et al. (2003), for example, compare a tree for 11 Polynesian languages (Figure 4.5) to a split decomposition graph (Bandelt and Dress 1992). Although evidence of borrowing is present, there is clear separation
between the two clades shown in the phylogenetic tree, one containing western Polynesian languages, and the other, eastern Polynesian languages. Significantly, the borrowing occurred between languages within a clade and not between languages in separate clades. These results indicate that the phylogenetic signal in Polynesian languages is not swamped by borrowing.

INTELLECTUAL CHALLENGES
The issue of signal swamping in Oceania is a segue into a broader examination of epistemological issues that need to be addressed with respect to cultural phylogenetic studies. It is a relatively easy matter to take a cultural data set and produce trees. Is such a procedure warranted? Some anthropologists have replied in the negative. Although we do not agree with this position, the issues critics raise are worth considering in detail. We discuss four of them below, posing them as questions: (1) Do cultural features, because they are inorganic, carry phylogenetic information? (2) Even if they do, because cultural evolution can involve reticulation, 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 lockstep fashion? (4) Related to number (3), at what scale(s) and with what units can cultural phylogeny be examined?

Do Cultural Features Carry Phylogenetic Information?

When it comes to humans as subjects of study, anthropologists and archaeologists have no problem viewing them in more or less the same light in which they view other organisms, as long as the issue is skeletal biology, comparative anatomy, or genetics. However, when the topic turns to cultural features—for example, stone tools, ceramic vessels, and kinship systems—some anthropologists and archaeologists tend to view things differently. They argue that because humans are culture-bearing animals, the evolutionary processes that work on other organisms—selection, drift, and the like—have little or no effect on humans. Thus whereas we might speak of human features such as language as “evolving,” it is evolution only in the metaphorical sense of change over time, not in the Darwinian sense (Bamforth 2002). Early anthropologists often referred to the evolution of culture as development to make it clear that it was entirely separate from organic evolution (e.g., Steward 1955; White 1959). This was a natural extension of the view that culture sets humans beyond the reach even of organic evolution.

One problem with this perspective is that we face considerable difficulties coming to grips with the transition from a predominantly genetic to a predominantly cultural mode of information transmission (Leonard and Jones 1987). Critics might well go along with this argument, but they also would claim that once that transition was made, cultural transmission freed humans from the processes of evolution in the Darwinian sense. Interestingly, some modern evolutionary biologists (Gould 1996; Mayr 1982; see also Angier 1997) also have problems incorporating human culture under the Darwinian umbrella. In our view, this “cultural exceptionalism” is flawed. 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 (O’Brien and Lyman 2000a, 2002b). Social institutions and products of technology are active components of the adaptive process. Regardless of how individuals obtained them (e.g., learned them from parents, copied them from peers), cultural variants represent alternative solutions to adaptive problems and can have different reproductive consequences for their makers and users (Leonard and Jones 1987).

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. This view should not be unduly troubling. Biologists (e.g., Bonner 1980, 1988; Dawkins 1990; Turner 2000) 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 pots, projectile points, descent systems, and political institutions be thought of any differently? Certainly we should have no trouble accepting that the behaviors that lead to the creation of a ceramic vessel are phenotypic.

Accepting the results of behaviors as phenotypic, then, requires only another small step. Once we make that step we can begin to talk about the processes that shaped the variation that is so evi-
dent across the broad scale of humanity—variation that provides the phylogenetic clues that one looks for in order to construct evolutionary history (O’Brien and Lyman 2000a, 2000b).

**Does Reticulation Destroy Phylogenetic Signal?**

Several anthropologists have argued that cultural phylogeny is impossible to reconstruct because of the nature of cultural evolution (Dewar 1995; Moore 1994a, 1994b, 2001; Terrell 1988, 2001, 2004; Terrell and Stewart 1996; Terrell et al. 1997; Terrell et al. 2001; Welsch and Terrell 1994; Welsch et al. 1992). They view cultural evolution as a vastly different kind of process than biological evolution, with a faster tempo and often a different mode, often referred to as *reticulation*. They argue that the faster tempo and different mode act in concert to swamp most or all traces of phylogenetic history and thus reduce the cultural landscape to little more than a blur of interrelated forms. This line of reasoning is not new: Anthropologists from the late nineteenth century on have recognized that horizontal transmission produces reticulation. The key criterion often used to distinguish intralineage change from extralineage change was the order of magnitude evident in the change: The greater the magnitude, the more probable the source of change was external (e.g., through diffusion or conquest). This same criterion is used today. Rarely is "magnitude" quantified, with most investigators relying instead on qualitative assessments such as how strongly one cultural tradition resembles a previously unrelated one. This line of reasoning is circular: How does one know that the two traditions are unrelated?

Cultural evolution probably is, in most respects, faster than biological evolution, and it can involve reticulation, but these aspects are not necessarily problematic. For one thing, biological evolution can involve reticulation (Arnold 1997; Doolittle 1999; Endler 1998; Jablonka and Lamb 2005), especially in the plant kingdom (Rhymer and Simberloff 1996), where between-species hybridization might be as high as 15–20 percent. Yet the presence of populations of hybrids, or *complex taxa* (Skála and Zrzavý 1994), has not precluded phylogenetic analysis (Nelson 1983; Wagner 1983), despite claims to the contrary (Hedberg 1995; Sosef 1997). A key issue here is that critics of cultural phylogenetic analyses have used the term *hybridization* to denote any instance of horizontal transmission and have therefore inappropriately conflated process (hybridization) with mode (reticulation).

The equation of hybridization and horizontal cultural transmission 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 percent of its genes originating with each parent—a 50/50 F1. Thus the offspring unit is an even mixture of its parents in terms of the units of transmission—*replicators*, to use Hull’s (1988a, 1988b) term. Presuming there are units of cultural transmission—memes (Aunger 2002; Blackmore 1999; Dawkins 1976; Pocklington 2001; Sheenan 2002a), semes (Hewlett et al. 2002), culturgens (Lumsden and Wilson 1981), instructions (Cloak 1973, 1975), mnemotypes (Blum 1963), viruses (Cullen 1993, 1994, 2000), or whatever one chooses to call them—horizontal cultural transmission may produce a new unit comprising equal parts of those replicators. But the odds are that it will not. Irrespective of whether transmission always produces a 50/50 F1 offspring, we know the scale of the (genetic) replicators that are transmitted. This is an important issue for understanding cultural lineages, even though the precise scale of the replicators might be unknown. This transmission of cultural replicators will rarely result in a 50/50 F1 offspring is known from a wide range of ethnographic and linguistic data. If, for example, one considers that pottery-making technology can comprise a lineage or a set of closely related lineages, then it should be clear that the transmission from another lineage of a replicator concerning how to shape a vessel does not result in a 50/50 F1. This is because the replicators for preparation of paste, preparation and addition of temper, firing temperature, and the like in the recipient lineage may be unaffected.

To be an instance of hybridization, 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 extralineage genes, and they must spread throughout the population in order to effect *mongrelization* (Levin 2002). If these extralineage genes spread in such a manner, then reticulation is the mode. If those extralineage genes do not spread in such a manner, then no hybrid mongrel species
Figure 4.6. Simplified model of hybridization, introgression, and mongrelization (after O’Brien and Lyman 2003a). Each circle represents an individual organism, each row of circles represents a separate generation, and time passes from bottom to top. Open circles represent individuals in species A, shaded circles represent individuals in species B, and circles that are half open and half shaded represent hybrid individuals. Vertical and diagonal lines represent genetic transmission.

will be produced, and reticulate evolution will not have occurred.

Figure 4.6 illustrates these processes and outcomes. An individual from species A mates with an individual from species B to produce a 50/50 F1 hybrid offspring. That offspring then mates with cohorts (individuals of its own generation) to produce hybrid F2 offspring in each species. Those offspring then produce F3 offspring. In species A the F3 hybrid fails to reproduce, so hybridization in this lineage ceases, introgression does not take place, and reticulate evolution has no effect on the lineage. In species B the F2 hybrid interacts with members of its cohort, as does each succeeding generation of hybrids, resulting in introgression and eventually mongrelization of the entire species lineage such that no “purebred” individuals of the original species exist. Species B is effectively extinct by generation F7 (Levin 2002; Rhymer and Simberloff 1996).

The model in Figure 4.6 illustrates basic concepts and processes of hybridization, but it is simplistic with respect to the units of transmission, whether biological (genes) or cultural (memes or the like). To illustrate this point, we begin with a cultural phenomenon, say basketry, that has eight “memes” in its “memotype” (Figure 4.7), which is equivalent to a “cultural recipe” (Neff 1992) for producing a basket. Each meme is expressed as a cultural character, each of which has four possible character states that occur within the basketry lin-
Figure 4.7. Four models of character state evolution (from O'Brien and Lyman 2003a). Each character (letters) has four possible states (numbers) internal to the lineage, each denoted by 1–4. Character state 5 originates from an extralineage source. Time passes from bottom to top in all. Seminal character state changes are circled. In (a) there is no extralineage influence; in (b) one character (F) changes as a result of extralineage influence; in (c) three characters (F, G, H) change as a result of extralineage influence; and in (d) six characters (B, D, E, F, G, H) change as a result of extralineage influence.

In the context of cultural transmission and archaeology, character states are represented by unique capital letters, A–H, and each state of a character, with a unique number, 1–4. One kind of change is shown in Figure 4.7a, where over time the states of various characters change as a result of innovation (mutation). Presuming the characters are independent, they will not all change states simultaneously as a result of being linked in some manner and thus will reflect what is known as mosaic evolution, or the independent change of characters. Over time, a temporal ordering of baskets may look like that shown in Figure 4.7b, where randomly chosen characters change states at random times. Character states that change are circled; time runs from bottom to top. Note that heritable continuity between generations of character states is reflected by the sharing (overlapping) of many character states by adjacent generations.

What happens when a new character state is introduced from an extralineage source? If we designate any such character state with the number 5 and replace one or more character state changes in Figure 4.7a with a 5 instead of a 1, 2, 3, or 4, we can begin to appreciate not only the importance of the scale of units used in phylogenetic analysis but the emptiness of the argument that because cultural evolution can be reticulate, phylogenetic analysis is impossible. In Figure 4.7b a single extralineage character state appears (why it appears and from where are irrelevant at this stage). Note that the phylogenetic signal provided by the overlapping of character states has
not been muted. Even if three characters (37.5 percent) simultaneously change to state 5, as in Figure 4.7c, the phylogenetic signal is still relatively strong. When six characters (75 percent) simultaneously change to state 5, as in Figure 4.7d, then the phylogenetic signal becomes obscured because the degree of overlapping, which signifies heritable continuity, has been significantly reduced.

Although such muting of the phylogenetic signal can and does occur in both biological and cultural lineages, as some of our own work and that of our colleagues has shown (Borgerhoff Mulder et al. 2006; Collard and Tehrani 2005; Jordan and Mace 2006; Jordan and Shennan 2003, 2005; Nunn et al. 2006; Tehrani and Collard 2002), we underscore that the frequency of cultural cases exemplified in Figure 4.7d relative to the frequency of cultural cases exemplified in Figure 4.7b is unknown (Collard et al. 2006a, 2006b; Shennan and Collard 2005). Nor do we know the parameters under which one or the other scale—for that is all that Figure 4.7 shows—of cultural “hybridization” is likely to occur. Given its detection of homoplasy, cladistics is one way in which we might begin to determine these frequencies and parameters. Goodenough makes an excellent point with respect to language: “Contact between Japan and the United States has resulted in considerable borrowing in language and culture by Japan and some reverse borrowing by the United States, but their languages and cultures retain their respectively distinct phylogenetic identities” (1997:178). 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).

The preceding paragraphs concern the ontology of hybridization, but there are as well empirical precedents for not discarding the baby with the bathwater (O’Brien and Lyman 2003a). Paleobiologists who examine the phylogenetic history of fossils must assume that the units of analysis—sets of morphometrically similar fossils (species or more inclusive taxa)—in fact constitute species and thus do not interbreed. Genetic transmission, in other words, is assumed to occur only within a lineage of some taxonomic scale—species, genera, families, and so on. Phylogenetic analysis of cultural lineages requires the same assumption—that transmission is primarily within either a lineage or a series of closely related lineages rather than between distantly related lineages.

The key question with respect to cultural phylogeny is the same as it is in biology: Are the nested series of taxa arising from our phylogenetic analysis monophyletic? That is, does a set of

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**Figure 4.8.** Three different phylogenetic scenarios that produce a single tree (after Sklæa and Zrzavý 1994). The three scenarios in (a) produce a single character matrix (b) and, correspondingly, a single tree (c) (X–Z, taxa; 1–5, characters; 2', character reversal).
taxa include all descendants of a particular ancestor and only those descendants? If either of those criteria is unmet, then the series of taxa is not monophyletic. Monophyly, however, is not necessarily an evolutionary concept—a feature of an evolutionary lineage possessing only a single ancestor. Rather, monophyly is a concept built around a taxon possessing but a single root on a phylogenetic tree (Skála and Zrzavý 1994). This is a key distinction. The branching topology of a phylogenetic tree does not mean that phylogeny is necessarily always a divergent process. This is evident in Figure 4.8, which shows three different phylogenetic scenarios that can produce the same character matrix and, correspondingly, the same phylogenetic tree. Thus, as Skála and Zrzavý point out, “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). Complex taxa are good subjects for examining this important problem” (1994:311–312). And there certainly is nothing more complex than humans and the things that they think of, transmit, and use.

Are Language, Biology, and Culture Concordant?

Some anthropologists claim that cultural phylogeneticists 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. [Moore 2001:32]

This mischaracterizes what comparativists have said. In an early programmatic statement on the method, Romney made it clear 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” (1957:36). 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. The point is not to prejudge the nature of the relationship but, rather, to establish the pattern in order to find out what factors might determine whether there is a positive, neutral, or negative relationship (Foley and Lahr 1997). This reasoning was used by Vogt (1964) for the Maya, Flannery and Marcus (1983) for the Zapotec and Mixtec, and Kirch and Green (1987, 2001) for Pacific islanders. Kirch and Green (2001) refer to the method as “triangulation”—using independent lines of evidence (linguistic, genetic, ethnohistoric, and archaeological) in phylogenetic reconstruction (see also Diamond and Bellwood 2003).

What Are the Scales and Units of Cultural Evolution?

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, whole cultures are examined. In other cases individual characters or bundles of characters are examined (e.g., Collard and Tehrani 2005; Darwent and O’Brien 2006; Jordan and Mace 2006; O’Brien et al. 2001; O’Brien et al. 2002; Shennan and Collard 2005; Tehrani and Collard 2002), as illustrated in Figure 4.9. 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 probably are. But phylogeneticists
Figure 4.9. Phylogenetic ordering of prehistoric projectile points from the southeastern United States (after O'Brien et al. 2002). The ordering in (a) was created using the eight landmark characters shown in (b); character states not shown. Only a portion of the phylogenetic tree is shown here. The complete tree has a length of 22 and a consistency index of .59 (after O'Brien et al. 2001; O'Brien et al. 2002).
understand the problem of units and scale, accepting that a cultural 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 and Pagel 1994). The key word is broadly; no phylogeneticist would view a cultural phylogeny using “cultures” as taxonomic units as anything but a broad picture of ancestry.

The issue of the reality of units used in phylogeny has entered the debates in anthropology as it has in biology. Human populations, ethnic groups, and cultures, are not “empirical” (real, natural) units, but this hardly qualifies them as “analytical fictions” (Terrell 2001). The key issue is the difference between empirical and ideational units (Lyman and O’Brien 2002; O’Brien and Lyman 2002a), not between empirical units and analytical fictions. If explicitly defined, units such as “cultures” can have considerable import for particular kinds of analysis. As a corollary, cultures can be defined differently for different analyses. Similarly, in biology the “species” can be a useful analytical unit, despite the existence of up to two dozen different species definitions (Mayden 1997; Wheeler and Meier 2000). Is there a “correct” definition of a species? Probably not. Rather, a species can be viewed as a unit constructed for specific analytical or applied biological purposes (Cracraft 2000). As such, our analytical goals dictate which of the several dozen available species concepts, and thus which kind of unit, is the most appropriate. This approach sidesteps the rather trivial issue of whether species are “real.”

This perspective has significance for anthropology. As with species, it is not difficult to think of cultures and the like as empirical entities. We can, after all, see them—at least we can see the people supposedly participating in a culture—and thus we can describe them. Similarly, it is not difficult to view cultural groups as natural units. Individual humans within a group do many of the same things intraspecific organisms do: They coexist, they communicate, and they interbreed. They also assist one another in various ways as well as compete with one another. If we view these interactions as group-maintaining activities, it is a simple matter to take the next step and elevate the natural group to the level of an Individual—capitalized to denote an aggregate of discrete phenomena as opposed to a single discrete phenomenon (lowercased [O’Brien and Lyman 2003a]).

What could be more real than an individual or an Individual, especially given that neither remains static? An individual, whether an organism or a cultural phenomenon such as a ceramic vessel, a woven rug, or a purification ritual, has a developmental history. Similarly, an Individual has a developmental history. It can add and shed pieces continually—individuals can come and go through birth, death, immigration, and so on—but for some period of time the Individual looks very much like it did the last time we saw it. Boyd et al. (1997) refer to the conservative element as the core tradition (see below). After a time, however, the Individual changes enough in terms of phenotypic characters—language, customs, technology, and so on—that it seems reasonable to label it as a different Individual. This is anagenetic (single-line) evolution—the result of a (usually slow) buildup of change that turns Individual A into Individual A’. Alternatively, for whatever reason, part of group A fissions, and the daughter part moves some distance away from the parental part. After a time, the two Individuals develop different tool traditions, customs, and the like, and after more time they have difficulty communicating with each other. This is cladogenetic evolution.

Regardless of the mode of evolution, are the units—the Individuals—real? We would argue that units such as cultures are not real. Rather, they are ideational units created for specific analytical purposes. The same applies to culture traits—methods of making pots, ways of referring to kin, and so on (Lyman and O’Brien 2003; Pocklington 2006). As such, they should be defined on the basis of some explicit criteria. The specimens, whether individuals or Individuals, placed in a particular kind of ideational unit—a class—are empirical. We can refer to the collection of actual specimens as the corresponding group. This is, however, different from placing specimens in a unit because they “seem to go together.” Groups that are extracted from classes are not analytical fictions. As long as theoretically informed definitions are employed, such groups can be used in cultural phylogeny, just as species are used in biological phylogeny. Or, as discussed below, specific parts of cultures can be examined from a phylogenetic standpoint.

Boyd et al. (1997) note that tracing phylogeny is possible to the extent that there are genealogical entities of whatever scale that exhibit suffi-
cient 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, 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 transmissible 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 crosscut one another, and thus the analyst must be explicit in defining the unit being used (Atran 2001; Pocklington 2006; Pocklington and Best 1997). Without considerable care, these units can take on a reality—a naturalness—and when classified create paraphyletic groups. This result is predictable if we confuse pattern with process and attempt to mix phenotypic similarity and descent.

As alternatives to the hierarchical model of cultures, Boyd et al. (1997) offer three other models: cultures as species, cultures as assemblages of many coherent units, and cultures as collections of ephemeral entities. Like Boyd et al., we find no support for the culture-as-species model, although the anthropological literature is replete with vague references to this or that culture as if they were natural units. Cultures are routinely equated with species (Cullen 1993; Gould 1987b, 1997; Steward 1944; Willey and Phillips 1958), 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 beyond 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 the 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; Vansina 1990). 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).

Neff places the concept of tradition squarely in a phylogenetic framework that emphasizes the transmission of information:

Inter-individual transfer of pottery-making knowledge must produce historical phenomena that can be referred to as “ceramic traditions.” Shared information dictates where to find clay, how to prepare clay, how to form and decorate pots, how to fire pots, and other aspects of behavior related to pottery-making. Just as the techniques employed by an individual to produce his/her distinctive pots are determined by the pottery-making information that individual carries, so the distinctive, collective phenotypic expressions recognizable in particular regions, during particular time intervals, are determined by information shared among individuals working within a tradition. The importance of ceramic traditions to ceramic evolution is that traditions, like individuals, are partitions of information concerning how to produce pottery-making aspects of potters’ phenotypes; because evolution results from any disruption of information flow through time, ceramic evolution will result both from disruptions of inter-individual transmission of pottery-making knowledge and from disruptions that simultaneously affect the ability to transmit pottery-making knowledge of all individuals working within a ceramic tradition. [1992:152–153]

It is at the scale of traditions that anthropologists can begin to construct testable hypotheses of cultural phylogeny. Traditions are sets of lineages, where an instance of the latter is defined as a single line of ancestry and descent. Lineages can exist at several scales in culture, just as they do in biology, where genes make up cells, cells make up organisms, and organismic lineages form populations. Importantly, lineages are not the same as monophyletic groups (Figure 4.10), although they sometimes are referred to as such. A lineage is a single line of descent that can be represented on a phylogenetic tree as a pathway from the root of the tree or an internal node (both of which are ancestors) to a terminal (the last, or at least the

![Monophyletic Groups](image1)

![Lineages](image2)

*Figure 4.10. Diagrams showing the difference between monophyletic groups and lineages (after de Queiroz 1998). All nine diagrams represent the same phylogeny, with monophyletic groups highlighted on the left and lineages on the right. Additional lineages can be counted from various internal nodes (ancestors) to the branch tips (descendants).*
most modern, descendant). In biology, organisms making up the later part of a population lineage may actually share a more recent common ancestor with conspecifics in a recently diverged lineage than with earlier organisms of their own lineage (de Queiroz 1998). Consider that on average we share 25 percent of our genotype with nieces and nephews, who are not in our lineage, and only 12.5 percent with great-grandchildren, who are in our lineage (Figure 4.11). Some biologists (e.g., Mayr 1995) have used this point to underscore a logical flaw in cladistics, but they are confusing two entirely separate things: descent and genetic relatedness. Lineages are patterns of genealogical descent; monophyletic groups are patterns of phylogenetic relationship.

DISCUSSION
The growing interest in cultural phylogenetics evident over the last two decades marks a return to the questions that motivated the earliest professional anthropologists (Aberle 1987; Harris 1968; Lyman et al. 1997; Stocking 1987). We view this return as important to the growth and continued health of anthropology (Borgerhoff Mulder 2001). Data for answering phylogenetic questions are now much 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 entirely. Not surprisingly, things appear different at different scales. At one scale we may be dealing with whole cultures, and at another scale, with language, technology, or political institutions. The shape of phylogeny will change as we shift scales because individual aspects (subsystems) of culture often evolve independently of one another (e.g., Moylan et al. 2006). For example, at one level we might speak of pottery traditions, identifying them on the basis of gross characters. But when we reduce the scale still further, we likely will find that the preparation of the clay paste, along with the forming of a vessel and its ultimate firing, might not be bundled characters. Similarly, there is every reason to believe that the trajectories that they take will be independent of the phylogenetic histories of the colors and elements of design motifs applied to the vessel. The same is true of myriad other aspects of culture (Borgerhoff Mulder 2001; Moylan et al. 2006; Pocklington 2006).

The unifying goal of anthropology is to document and explain the similarities and differences among cultures across space and through time. This is why issues such as the origins of the use of fire, the rise of urbanism, the appearance of complex sociopolitical organization, the develop-
ment of agriculture, the effects of the technological development of pottery, and the like have occupied so much anthropological attention. Modern phylogenetic methods, although developed in the biological sciences, offer a means of creating falsifiable hypotheses that deal with these issues (Plattnick 1977). The methods are not analytical ends in themselves, nor has the claim been made that one method is necessarily superior to another. One of the advantages of formal phylogenetic methods is that they can give the analyst a principled reason for choosing one method over another.

To this point, phylogenetic trees produced through methods such as parsimony and maximum likelihood appear to have considerable promise for phylogenetic ordering, but we view them as only one weapon in the anthropologist’s arsenal. Other methods—simulation (Nunn et al. 2006), split decomposition graphs (Bandelt and Dress 1992), tests for serial independence (Abouheif 1999), iterated parsimony (McElreath 1997), network analysis (Forster and Toth 2003; Morrison 2005), Bayesian methods such as Markov chain Monte Carlo (Huelsenbeck et al. 2000), tests for matrix correspondence (Smouse and Long 1992), assessment of hierarchical cluster structure (Pocklington 2006), and seriation (Lyman and O’Brien 2006; O’Brien and Lyman 1999)—should be used in tandem with phylogenetic methods such as cladistics. No cultural phylogeneticist, to our knowledge, has said that human history is easy to unravel, despite claims to the contrary (Terrell 2004). What has been said is that the results are well worth the effort.

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