PHYLOGENETIC APPROACHES IN ANTHROPOLOGY AND PREHISTORY

MAPPING Our Ancestors

EDITORS

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FOREWORD BY NILES ELDREDGE



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Cultural Phylogenies and Explanation: Why Historical Methods Matter

Carl P. Lipo, Michael J. O'Brien, Mark Collard, and Stephen J. Shennan

Imagine finding a collection of things and having to figure out how each one got to be the way it is. In addition to learning about, say, the chemical and physical characteristics of the objects, resolving this issue would lead you to ask about their history. Are they related to one another? If so, are they equally related, or are some items related more closely and some more distantly? These are not easy questions to answer, but they are ones with which natural and social scientists wrestle on a regular basis. They also are central to the chapters in this book.

Interest in genealogical, or "phylogenetic," relationships has a long tradition in the natural sciences. Although efforts at explaining the natural world in phylogenetic terms can be traced to at least 350 B.C. and Aristotle's Historia Animalium, most of the major steps in developing a means of describing biological organisms in a way that reflects their affinities have occurred in the last 300 years. One of these was the publication in 1735 of Carolus Linnaeus's Systema Naturae. Linnaeus popularized what has become one of the core ideas of biological phylogenetics, namely that species can be grouped into a hierarchy of progressively more inclusive taxa. Further progress in building a robust set of methods for delineating phylogenetic relationships among organisms came in 1859 with the publication of Charles Darwin's On the Origin of Species. Although it was not immediately recognized, Darwin's theory directed biologists interested in relatedness to limit their descriptions to one form of similarity-the kind that results from heredity. Traits that two or more taxa share because they inherited them from a common ancestor are termed "homologies."

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A robust numerical method that made use of this portion of Darwin's theory emerged in the twentieth century at the hands of Walter Zimmerman (1931) and especially Willi Hennig (1950, 1966). The key component of this method, termed "phylogenetic systematics," or more commonly "cladistics," is its focus on a subset of homologous traits, namely those that are considered to be "derived" rather than "ancestral." Derived traits are character states exhibited

Figure 1.1



In (a) feathers appear during the evolution of Taxon 2 out of its ancestral taxon. The state "feathered" is termed an "apomorphy." In (b) Taxon 2 has produced two taxa, 3 and 4, both of which contain feathered specimens. The appearance of feathers in those sister taxa and in their common ancestor (B) makes it a "shared derived" character state, technically termed a "synapomorphy." In (c) one of the taxa that appeared in the previous generation (Taxon 4) gives rise to two new taxa, 5 and 6, both of which contain feathered specimens. If we focus attention only on these two new taxa, "feathered" is now an "ancestral" character state, technically termed a "symplesiomorphy". Note that it is shared by more taxa than just sister taxa 5 and 6 and their immediate common ancestor. But if we include Taxon 3 in our focus, having feathers is a synapomorphy because, following the definition, it occurs only in sister taxa and in their immediate common ancestor.

by a set of sister taxa and their immediate ancestor but no other taxon (figure 1.1). The final products of cladistic analyses are treelike structures called "phylogenetic trees," or "cladograms,"¹ that depict relationships among taxa.

In Figure 1.1(a) feathers appear during the evolution of Taxon 2 out of its ancestral taxon. The state "feathered" is termed an "apomorphy." In (b) Taxon 2 has produced two taxa, 3 and 4, both of which contain feathered specimens. The appearance of feathers in those sister taxa and in their common ancestor (B) makes it a "shared derived" character state, technically termed a "synapomorphy." In (c) one of the taxa that appeared in the previous generation (Taxon 4) gives rise to two new taxa, 5 and 6, both of which contain feathered specimens. If we focus attention only on these two new taxa, "feathered" is now an "ancestral" character state, technically termed a "plesiomorphy" (shared ancestral character states are termed "symplesiomorphies"). Note that it is shared by more taxa than just sister taxa 5 and 6 and their immediate common ancestor. But if we include Taxon 3 in our focus, having feathers is a synapomorphy because, following the definition, it occurs only in sister taxa and in their immediate common ancestor.

The principles that drive phylogenetic methods are not restricted to the study of biological entities. Indeed, phylogenetic methods are simply algorithms for building phylogenies once descriptions of taxa are made. The important point is that phylogenetic methods can be used to relate any set of features that change in nonrandom fashion over time, regardless of the mechanism or process.

In recent years, a growing number of social scientists have begun to use phylogenetic methods, especially cladistics, to address questions of cultural evolution. The datasets used in these studies come from a wide range of locations, including the Pacific (e.g., Gray and Jordan 2000; Hurles et al. 2003; Jordan 1999; Kirch and Green 1992, 2001), Africa (e.g., Foley 1987; Holden 2002; Holden and Mace 1997. 1999; Mace and Pagel 1994), Europe (e.g., Collard and Shennan, 2000; Gray and Atkinson 2003; Renfrew and Boyle 2000), Asia (e.g., Tehrani and Collard 2002), and North America (e.g., Lipo 2001; Lipo et al. 1997; O'Brien and Lyman 2003a; O'Brien et al. 2001, 2002).

The subject matter is similarly diverse. The growing literature on the use of phylogenetic methods in studies of material culture includes applications to stone tools (Foley 1987; Foley and Lahr 1997, 2003; O'Brien and Lyman 2003a, 2003b; O'Brien et al. 2001, 2002; Robson Brown 1995, 1996), baskets (e.g., Jordan and Shennan 2003), pottery (e.g., Collard and Shennan 2000), carpets (e.g., Tehrani and Collard 2002), written texts (e.g., Spencer et al. 2004) and even entire industries (e.g., Anderson 2003). The use of phylogenetic methods is also seeing a growing usage in sociocultural anthropology (e.g., Borgerhoff Mulder 2001; Borgerhoff Mulder et al. 2001: Holden and Mace 1997, 1999; Jones 2003; Mace and Pagel 1994; Sellen and Mace 1997), in historical linguistics (e.g., Gray and Atkinson 2003; Gray and Jordan 2000;

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Molden 2002; Jordan 1999; Platnick and Cameron 1977; Rexová et al. 2003), and in multi-disciplinary studies (e.g., Hurles et al. 2003).

Adopting phylogenetic methods that have been developed primarily in biology and paleontology creates a set of theoretical, methodological, and empirical challenges as we attempt to apply the methods anthropologically. From a practical standpoint, do the methods accomplish what we want them to? From an epistemological standpoint, are they appropriate methods to use? And at the most fundamental level, are the products something that we as anthropologists need? Put simply, should we even care about phylogeny?

Phylogeny and Cultural Evolutionary Research

Let us return to the example we used in the opening paragraph: we have a collection of things and are interested in figuring out how each got to be the way it is. This is a phylogenetic problem. For the sake of argument, let us say that the things in the collection are artifacts recovered from an archaeological site. One means of creating a sequence is to examine artifact form. Analysis of form has long been used as a means of studying cultural continuity, the assumption being that artifact similarity often is a function of common ancestry (O'Brien and Lyman 1999). As Albert Spaulding (1955: 14) argued, variation in material culture "can be related to the proposition that cultural change is systematic rather than capricious and to the auxiliary proposition that an important basis for the systematic behavior of culture is its continuous transmission through the agency of person to person contact." Artifact variation, when described appropriately, can be explained as a function of descent with modification. Archaeologists such as A.V. Kidder (1932) and James Ford (1936) knew this, and it formed the basis of the approach that came to be known as culture history (Lyman et al. 1997).

The culture history approach to anthropology is broadly compatible with the biological model that views heritable change as descent with modification. Archaeologists have been modeling change in artifact form in this way since the birth of the discipline (e.g., Evans 1850; Petrie 1899). One example is E. B. Sayles's (1937) diagram (figure 1.2) showing the evolution of manos and metates from Snaketown, Arizona. In this figure, Sayles makes the claim that mano and metate forms have a single ancestor and diversify over time. This is descent with modification.

Another example is James Bennyhoff's (1994) map of the relations of Central Valley, California, projectile points, beads, and amulets (figures 1.3 and 1.4). Bennyhoff detailed change in these artifact classes through time and linked cases where he believed divergence occurred among artifacts (as with the amulets and beads) as well as convergence (as with the projectile points). These time-space charts are an embedded feature of archaeology and provide a framework for studying culture change. And for good reason: whenever our goals include explaining change through time, it is necessary to build models

Figure 1.2 Wevelopment of Manos and Metates at Snaketown, Arizona (after Sayles 1937)



of relatedness. These models isolate characters suspected to be the result of inheritance as they vary through time and across space.

Accurately determining the degree to which the sharing of traits is a function of historical relatedness is vital in building evolutionary explanations. In order to explain the distribution of cultural traits across populations we must be able to identify those traits that are present as a result of historical contingency ("homologies") versus those that are a product of processes other than descent ("homoplasies"). Consider a case of explaining why projectile points found distributed in densely wooded upland environments are different from those found along oak-savannah valley bottoms.² We might find, for example, that some of the points in the uplands are slightly smaller than contemporaneous ones in the lowlands. A chi-square test might demonstrate statistical significance in the pattern, and we might therefore be tempted to explain the differences as a function of the different environments. Such an explanation is plausible but potentially wrong. It is possible that the lowland and highland groups may have inherited their preferences regarding projectile-point length from different common ancestors. If this were the case, it would be inappropriate to treat the groups as independent data points in a statistical analysis (Harvey and Pagel 1991). Reconstructing phylogeny is therefore a vital pre-

Figure 1.3 Historical Evolution of Beads and Amulets in the Central Valley, California (after Bennyhoff 1994)



Figure 1.4 Historical Evolution of Projectile Points in the Central Valley, California (after Bennyhoff 1994)

	Cosumnes District: Augustine Pattern			
Calhoun (Middle/Late Transition)	Eichenberger (Early Phase 1)	Hollister (Middle Phase 1)	Johnson (Late Phase 1)	Mosher (Phase 2)
0 2220				
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requisite when testing hypotheses about the role of environments in structuring variability in cultural behavior. As the zoologist Paul Harvey (1996: 257) has noted, "if we want to understand why different traits are more commonly represented in one community than another we shall frequently find phylogenetic information useful. It can only help, and it will produce statistically appropriate degrees of freedom."

Culture-historical time-space charts are definitely the sort of product we need. However, the means of generating them must be vastly improved. We must be able to build maps of relatedness in ways that are theoretically justified, reproducible, and quantitatively defensible. The majority of culturehistorical depictions of patterns of descent are little more than intuitive claims about relationships based on experience and authority. Although these maps do a reasonable job of determining large-scale differences (for example, distinguishing between early and late manifestations), they are incapable of resolving small-scale differences. At best, they are nominal-level representations of relatedness. Here is a significant reason for us to care about phylogenetics; phylogenetic methods such as cladistics offer us a means of systematically deriving theoretically justifiable maps of relatedness using explicit algorithms in a way that is repeatable. These methods are integral to all forms of evolutionary explanations, whether biological or cultural, since the central tenet of evolution, descent with modification, requires us to track related entities as they change through time and across space. Without showing relatedness, explanations of change are simply chronological, not evolutionary, statements. Thus, phylogenetic methods are central to our quest for explaining the natural world.

Issues in Cultural Phylogenetics

Given the requirements of evolutionary studies, regardless of whether the subject matter is language, artifacts, or social institutions, we see phylogenetics as an important component. Critics, however, have not only raised a number of issues with respect to the appropriateness of various methods for unraveling cultural phylogenies but have also questioned whether cultural phylogenies can even be understood, regardless of the method used. If the criticisms are valid, they not only limit the applicability and effectiveness of various phylogenetic methods, they call into question the entire phylogenetic enterprise. We summarize some of these issues below, leaving it to various chapter authors to address them in more detail.

Culture versus Genes

Some researchers argue that phylogenetic methods are inappropriate for studying cultural evolution because they rest on a false analogy. This argument is not new (e.g., Brew 1946). It holds that cultural transmission is not analogous to genetic transmission—that unlike with genes, culture is not a transmission system in which physically identifiable entities are passed from person to person structurally intact (Atran 2001; Aunger 2000; Sperber 1996). As such, we cannot directly apply biological methods to cultural data. In an intuitive sense this argument appears defensible. Obviously the "things" that pass between people in a cultural-transmission system are not sharply defined objects. However, simply because we cannot see the transmitted "things" does not mean that we cannot see their effects.

Sometimes cultural transmission is said to take place via gene-like units called "memes" (Dawkins 1976). Although the concept of meme enables us to conceptualize a unit for measuring cultural transmission, we agree with Lake (1996) that much of the memetics literature creates confusion by conflating the physical expression with the content being transmitted (e.g., Blackmore 1999; Gabora 1996). The example of an image or string of words, copied and passed around while retaining its essential identity, is commonly used as a memetic example of cultural transmission. This image is inappropriate.

If physical expression is not part of the process of cultural transmission, then what does transmission consist of? What is passed on? In a word, information is passed on. Clearly, we are not the first to say this (e.g., Cloak 1973, 1975; Dawkins 1976). But in order to address the criticism that cultural evolution is at best analogous to genetic evolution (and then only vaguely so), we have to be clear that transmission is about the passage of information between individuals at whatever scale and using whatever physical means is available (chemical, molecular, sound, or light). Thus, there cannot be a single, physical entity in any system of information transmission. There are no "strings of words."

It is important to recognize that the lack of a single physical entity is true even in the case of genetic transmission, where there are numerous physical entities—DNA, transfer RNA, and many proteins—that carry and pass on information. As we have delved deeper into the mechanisms of genetic transmission, we have learned that DNA does not play an exclusive role in transmitting information between individuals. Similarly, in cultural transmission there are also a number of physical mechanisms that result in the transmission of information.

Even though we might not all agree on the mechanism or even on what is transmitted between individuals, we should be in general agreement that some information is passed on. Thus, the distinction between genetic transmission and cultural transmission is artificial. Both genes and culture are transmission systems. They differ mechanistically and also in terms of their dynamics, but this is irrelevant to their information-theoretic structure. They differ as well in the degree of average fidelity of transmission, but this is a quantitative, not a qualitative, difference.

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This has important implications for the "analogy" argument and for the potential use of phylogenetic methods in the study of cultural inheritance. Using this model of transmission, we can see that the goal of phylogenetics is simply to build maps that allow us to track information across space and through time, regardless of the physical means by which this information is transmitted. All the methods require is that information be transmitted, by whatever means (O'Brien and Lyman 2003a). Thus the "analogy" argument that seeks to divide cultural from biological forms of evolution is spurious.

Homology and Homoplasy

Anthropologists have long been aware that care must be exercised in studying relatedness so as not to confuse similarity that results from shared ancestry from similarity that is a product of technological constraints, development, or from a common solution to an environmental condition (Cronk 1999). This means that as we try to explain the distribution of cultural material we must be able to distinguish homologous similarity from all other kinds of similarity (homoplasies). Biologists currently recognize several forms of homoplasy (Collard and Wood 2001; Lieberman et al. 1996; Lockwood and Fleagle 1999; Sanderson and Hufford 1996). Analogous and convergent homoplasies are caused by adaptation to similar environments (Simpson 1953). Analogies and convergences differ in that natural selection operates on different developmental processes in the former, but on the same developmental processes in the latter (Lieberman et al. 1996). Parallel homoplasies result from aspects of ontogeny (i.e., development) that limit phenotypic diversity, but which have no necessary connection with the demands of the environment (Wake 1991). A fourth type of homoplasy is reversal, in which, for example, a trait increases and then decreases (Simpson 1953). Most cases of reversal are probably due to natural selection, but the authors of a recent assessment of silenced-gene reactivation have suggested that reversal may also be neutral with regard to adaptation (Marshall et al. 1994). The last form of homoplasy that biologists recognize is homoiology. Homoiologies result from phenotypic similarities in the way that different genotypes interact with the environment (Lieberman et al. 1996).

Some of these forms of homoplasy probably do not need to be considered when dealing with artifacts and cultural practices, but others clearly do. Potential examples of the cultural equivalent of parallelism can be readily identified. For instance, painted designs will rarely be found on the interior of narrow-necked jars because of the mechanical constraint caused by neck restriction and physical inability to apply designs (Krause 1978). Evidence for convergence in cultural behavior is even more plentiful. For example, once considered to be strong indications of relatedness, things like pyramid construction and paramount chiefdoms have proven to be the result of convergence. Likewise, populations have repeatedly found baked clay to be a highly efficient solution to the creation of watertight and fire-resistant vessels. The common triangular shape of projectile points found worldwide represents an other excellent case of convergence. The physics of flight and impact strongly favor a common solution to prey disablement. Thus projectile points used to tip arrows from prehistoric Afghanistan look remarkably like those from lateprehistoric eastern North American contexts. This similarity is once again no a product of common descent but of evolution "finding" the best configuration for stone projectile points launched from bows (see chapter 7 for additional discussion). Even forms of decoration can be highly convergent, a. Meggers, Evans, and Estrada found in their comparison of Jomon and Ecua dorian ceramics (Meggers et al. 1965).

In culture as in biology, it appears that there may be a surprisingly small se of solutions to many problems that would initially appear to have many de grees of freedom. This means that as we try to explain the distribution o cultural material, we may find that much of what we think is homologou similarity may turn out to be cases of analogous or convergent similarity Culture historians were sensitive to this issue and sought to minimize the chance of using homoplastic similarity by evaluating the complexity of trait, the presence of a probable ancestral trait in the same geographic area, the quantity of other shared traits, and the geographic proximity of the localitie (Steward 1929; see O'Brien and Lyman 2000a). Each criterion was thought help minimize the likelihood that a trait independently appeared multiplication times and in multiple places. Concern over confusing homologous and ho moplastic variability is one reason why the use of adaptively neutral variant may produce more robust measures of inheritance than studies that make up of functional traits (Dunnell 1978; Lipo and Madsen 2000). Because they d not affect inclusive fitness, such variants are likely to reflect patterns of inhe. itance rather than adaptation to similar environmental conditions. Howeve even these procedures provide no guarantees. Each case must be evaluated in the possibility of homoplasy.

Cultural Phylogeny and Horizontal Transmission

Efforts to identify homologies in cultural materials are further complicate by the need to take into account a form of homoplasy not mentioned in (preceding section, namely homoplasy that results from "horizontal transmusion," the transmission of information between contemporaneous entitie Critics argue that information about relatedness will be drowned out by noias a result of borrowing and recent interaction, thus limiting the application certain phylogenetic methods to cultural phenomena. Certainly, given the common perception that cultural transmission is reticulate as opposed to eve branching, it is reasonable to argue that any method needs to be examined are

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justified before we uncritically assume that it will work as well for artifacts and languages as it does for biological data. In addition, we also have to recognize that despite the range of applications we can dream up for cladistics and other phylogenetic methods, the methods were originally designed to distinguish among patterns of inheritance over large amounts of time and space and within a transmission system that was assumed at the time to be strongly vertical.

Issues raised by horizontal transmission relative to cultural phenomena are essentially the same as those it raises in biology (O'Brien and Lyman 2003a). One must wonder whether a different set of methods would have emerged in biology had phylogeneticists had to deal from the start with the problem of tracing information flow in a system without a sharp distinction between vertical and horizontal transmission-that is, if "branching" were not a fairly reasonable assumption. In fact, phylogeneticists exploring the origins of life have encountered precisely this situation. Many biologists have been frustrated that during the earliest phases of evolution it appears that horizontal transmission "erased" all of the records of the oldest branches on the tree of life. But we need to remember that horizontal transmission is relatively common even today (Skala and Zrazýy 1994; Woese 2000).

In general, vertical transmission appears only in complex organisms with DNA transmission, where the system has evolved to conduct periodic, not continuous, transmission in an all-in-one exchange of information. This turns out to be fairly rare in biological systems. On a taxonomic basis, the vast majority of life over the last three billion years has not been organized along lines where mechanisms exist to constrain information flow to strict "vertical" lines. Constraining information during transmission is a derived trait. Terminal sequestration of the germ line is relatively recent and also taxonomically restricted (Buss 1987).

Managing cases in which information is not constrained in synchronous bundles is not an insurmountable task. It simply means that there is not necessarily going to be one "best" phylogeny for any specific transmission group, genetic or cultural. Rather, we are often going to end up with different phylogenies for different sets of traits, which may imply different sources and patterns of transmission. Some traits may coincide in terms of a phylogeny, which implies that they moved as a package, whereas other traits are likely to have followed unique pathways of descent. In addition, we have to allow for the possibility that the phylogenies of some traits will be best represented by treelike diagrams, whereas those of other traits will be more appropriately depicted by what John Terrell (2001) calls "maximally connected networks," or reticulated graphs (see chapters 5 and 6 for further discussion and examples).

Some of the concern that anthropologists have with the use of phylogenetic methods in the cultural case involves the origins of method as a means for measuring variability structured by vertical transmission. Cladistics is thus treated as applicable only in systems of biological reproduction. However, A set vertical transmission is not the general case, even in biology. An assumption that biological reproduction is a process of vertical transmission works well only in situations where there is terminal sequestration of the germ line of the tack of openness to horizontal transfer can be assumed. However, and dy speaking, nothing about tree analysis requires these assumptions. Cladistics works on any inherited information and can be used to determine the plattice degree of horizontal and vertical transmission, as the chapters in this volume ably demonstrate.

What we do have to question is the nature of cultural transmission (e.g., veriodic versus continuous transmission) and whether we should expect to be able derive a single tree that maps to a single phylogeny. This is an empirical finance that must be determined case by case. However, cultural phenomena are probably best represented by a general case in which transmission occurs unultaneously in vertical and horizontal dimensions and is not packaged into bundles bounded in time and space. The general case has important implications for our efforts to study historical relatedness among cultural phenomena. Most importantly, this means that when we study phylogenies in culture and language, our analyses will necessarily produce numerous trees. We should expect many trees for any population, each tracing the history of particular traits or sets of traits across sets of biological individuals. Richard Pocklington discusses this issue in chapter 2 of this volume.

Trees have to be evaluated first on formal and sampling criteria, then on correspondence. Trees are "correct" when the sampling strategy is good and the trees are built properly without violating the mathematical assumptions of the models used to build them. Differences among trees are data about different patterning of information flow, not an indication that one has not found the "one true phylogeny" among a series of taxa.

Foundation for the Volume

This volume brings together a number of scholars who have been working on the theoretical, methodological, and empirical issues involved in mapping patterns of cultural descent through the use of cladistics and other phylogenetic methods. Taken as a whole, the chapters provide a solid demonstration of the potential of phylogenetic methods for studying the evolutionary history of human populations using a variety of data sources. We hope the chapters provide a foundation for future work and offer inspiration to continue the application and development of methods for determining descent relation ships and constructing evolutionary histories.

A few final points are worth noting. First, this is not a "how-to" manual on building phylogenetic trees, although methods play a major role in many of the chapters. There are a number of good books that cover the procedures and algorithms needed for building trees, including Felsenstein's (2004) *Inferring Phylogenetic Trees Made Easy.* For a basic

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introduction to cladistics, we suggest Brooks and McLennan's (1991) *Phylog*env. Ecology, and Behavior and Kitching et al.'s (1998) *Cladistics: The Theory* and Practice of Parsimony Analysis. Wiley et al.'s (1991) primer *The Compleat Cladist: A Primer of Phylogenetic Procedures* provides a good review of the basic principles and terms necessary for understanding cladistic methods. In addition, O'Brien and Lyman's (2003) *Cladistics in Archaeology* provides an introduction to the construction of phylogenies in the context of archaeological materials. We also need to make it clear that phylogenetic methods include more than cladistics. Several authors discuss related methods include material compositional analyses and seriation.

Second, although cladistics makes use of assumptions about branching to build maps of relatedness, and the final product of cladistics is a tree, the production of trees is not the central goal of this research. Instead, the research shares a simple commitment to determining evolutionary relationships. Trees are nothing more than hypotheses about relatedness that, once created, must subsequently be evaluated with external information. Hypotheses other than branching can potentially explain the generation of patterns of similarity, regardless of how it is measured. As Terrell (1988, 2001) and others have pointed out, geographical proximity and temporal differences are alternative hypotheses that can account for descriptions of material culture, linguistics, and genetics, Determining the "best" hypothesis is an empirical issue.

Third, there are numerous technical terms involved with phylogenetic methods. These terms are unavoidable, given that we must carefully specify the kinds of things being described and the manner in which they are described. Although technical terms such as "homoplasy," "synapomorphy," "phylogenesis," and "clade" are necessary for reasons of clarity and precision, the chapters have been written to make their presentations as clear and as jargon free as possible.

Notes

- Technically, a cladogram is an unrooted tree, although cladists tend to use the terms interchangeably. A cladogram becomes a tree when a starting point, or root, is identified. Most authors in this volume use the term "phylogenetic tree," indicating that the cladistic arrangement of their taxa has been rooted.
- 2. This example is adapted from Harvey (1996).

Part 2

Fundamentals and Methods