Chapter 8
The Uses of Cultural Phylogenetics in Archaeology

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Introduction

Studies on the processes of cultural transmission and cultural evolution have been at the center of archaeological research and debate for the first two decades of the twenty-first century (García Rivero 2016; Lipo et al. 2006; Mace and Jordan 2011; Richerson and Christiansen 2013; Shennan 2009; Whithen et al. 2011). During this time, the methods of cultural phylogenetics have gradually become established as the standard method for describing and analyzing these processes (Mace et al. 2005) and have consequently found numerous applications in historical linguistics, social science, anthropology, and archaeology (Levinson and Gray 2012; Mace and Jordan 2011; Mesoudi 2011).

Despite the success of these methods' applications and the increasing presence of phylogenetic analyses in archaeological research, many of the key concepts of phylogenetics and their purpose in studies of material culture may seem somewhat intricate to many archaeologists, especially those unacquainted with the jargon of evolutionary science. This chapter will first introduce some basic concepts of phylogenetics, focusing on those which are relevant for understating its uses in cultural studies. The second section will review some of the most fruitful applications of phylogenetics in archaeology and discuss the types of research questions that can be addressed with these methods. In the final section, I lay out some of the most recurrent challenges of using cultural phylogenetics in archaeological research and look into how researchers are rising up to them.

Basic Concepts in Phylogenetics

In biology and paleontology, phylogenies are family trees generated by real or hypothesized ancestor-descendant relations between species or groups of species, based on shared morphological traits, genes, or proteins. In these fields, phylogenetic methods aim at reconstructing evolutionary histories by tracing lineages back to a most recent common ancestor (Sterelny and Griffiths 2012). Phylogenies are usually represented as branching tree diagrams, called cladograms, where a single branch is constituted by a last common ancestor (the node or branching point) and all its descendant lineages, which in conjunction are called a *clade*. The working assumption is that the more traits two or more

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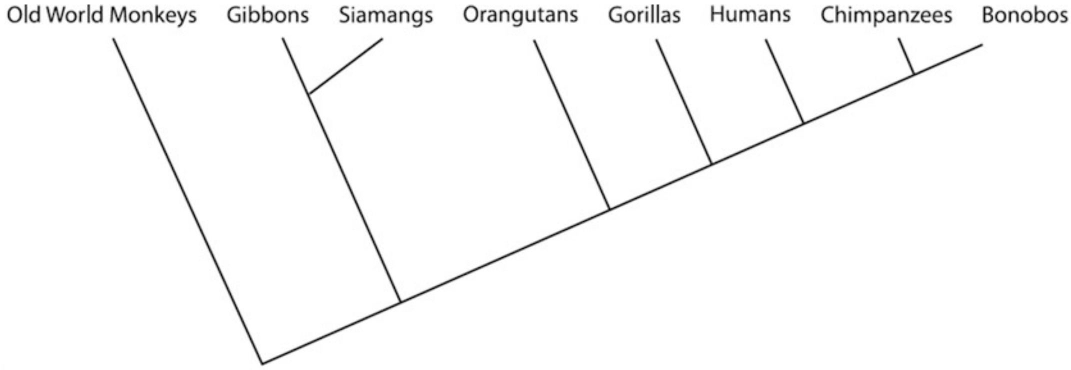

Fig. 8.1 Fragment of the phylogenetic tree of primates (After Shoshani et al. 1996)

species share, the more closely related they are to each other through a recent ancestor than to any species outside their clade. The members of a clade are therefore united by shared traits inherited from the same ancestral species; such traits are called synapomorphies or, more commonly, homologies, whereas those that evolve independently are known as homoplasies (Meisel 2010; Tëmkin 2016). Among extant primates, for instance, chimpanzees, bonobos (*Pan*), and humans (*Homo*) form a clade, having shared a common ancestor with each other more recently than with any other great ape (Fig. 8.1). Two examples of the many homologies of the *Pan-Homo* clade are high encephalization and delayed puberty (Shoshani et al. 1996).[1]

The criterion of similarity between species or taxa is determined by the comparison of their characters, which are the attributes of form, structure, or composition that distinguish each of them. For example, comparable characters for primate species may be genetic, such as the location of a particular gene on a chromosome (Chen and Li 2001), morphological, such as the shape and size of the skull and teeth (Shoshani et al. 1996), or even behavioral, like diet or group size (MacLean et al. 2012). The variants of those characters' expressions among species, called character states (e.g., absent/present, long/short, large/small), help determine relatedness. The result of the character states analysis results in a diagram. The most common is the phylogenetic tree or cladogram, represented by branching lines that group taxa by shared descent, i.e., the phylogeny of a group. Phylogenetic trees, then, trace vertical evolutionary processes like divergence, branching episodes, convergence, continuity, or extinction, but other diagrams, such as networks, help visualize reticulate or horizontal processes as well, like hybridization, recombination, fusion, and horizontal gene transfer (Morrison 2016; Tëmkin 2016). Thus, the most common representations of phylogenetic trees are branching cladograms and reticulate networks, which can be portrayed in many different styles (Fig. 8.2).

In broad lines, phylogenetic analysis proceeds by selecting the study group, determining the evolutionary relevant characters, and comparing these across the entities in the study group (Marwick 2012). The character states are first integrated in a data matrix, and then an out-group is distinguished for comparison (Maddison et al. 1984; Buchanan and Collard 2007). The latter may be a close relative of the study group, generally a species that diverged earlier (Holden and Shennan 2005). Looking at the character states of the out-group helps the researcher infer the ancestral states of the last common ancestor. Then, if any character states are found in the study group but not in the out-group, parsimony

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[1] Note that clades are hierarchically nested, i.e., each clade is included within a larger cluster. For example, chimpanzees and bonobos constitute a clade because they shared a common ancestor most recently. At the same time, these two cluster with humans in another clade, since all three show greater similarity with each other than with gorillas, and again gorillas form a clade with humans, chimpanzees, and bonobos because these four are more similar to one another than to orangutans and so on (Nickels and Nelson 2005).

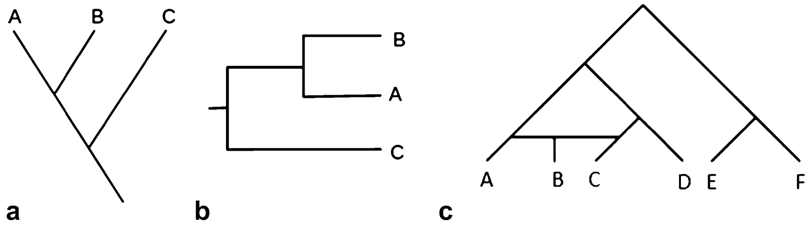
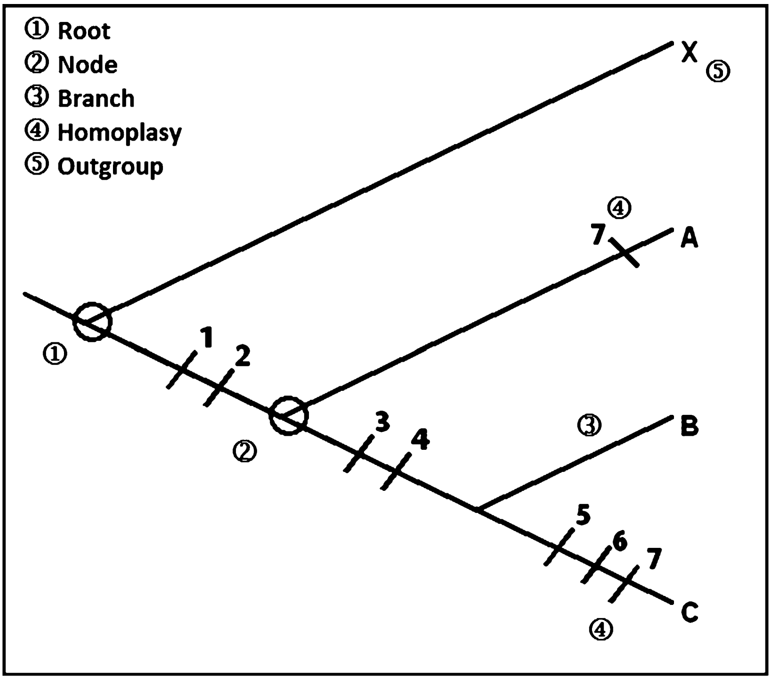


Fig. 8.2 Basic cladograms. (**a**) and (**b**) are identical but drawn in different styles and orientations. (**a**) cladogram with diagonal branches. (**b**) cladogram with rectangular branches. (**c**) simplified network cladogram



	1	2	3	4	5	6	7
A	1	1	0	0	0	0	1
B	1	1	1	1	0	0	0
C	1	1	1	1	1	1	1
X	0	0	0	0	0	0	0

Fig. 8.3 Example of a cladogram with the character state matrix from which it was generated. Taxon B and C form a clade to the exclusion of A based on the shared possession of the character states for characters 3 and 4. Taxa A, B, and C form another clade based on the similar character states for characters 1 and 2. Taxon C is the most derived taxon, with derived characters states for characters 5, 6, and 7. Character 7 is a homoplasy, in a derived state in taxa A and C, even though these do not share a most recent common ancestor. In an alternative, equally parsimonious cladogram, taxa A and C form a clade to the exclusion of taxon B (After Buchanan and Collard 2007)

dictates that those evolved only in the former and were not inherited from the latter (Buchanan and Collard 2007). The resulting cladogram will trace how the study group relates and deviates from the out-group, revealing the evolutionary relationships between them (O'Brien and Lyman 2003) (Fig. 8.3). This way, by tracing common descent on the basis of character comparison (identifying shared ancestral characters vs. shared derived characters evolved in a clade), phylogenetic methods allow researchers to carry out quantitative assessments of the degree of relatedness between species, as well as to infer the traits of extinct species, and to identify the timing and location of significant evolutionary changes (MacLean et al. 2012).

Since different character state matrices generate different cladograms, it is frequent to obtain several classificatory proposals of how the entities in the study group relate to one another. To choose among alternatives, cladistics methods generally apply the principle of parsimony (García Rivero 2016). This means that when there are different possible explanations, the simplest one will be adopted as the most probable, and because in evolution stasis is more common than change, when selecting among different phylogenetic trees, the one requiring the least evolutionary steps will be preferred (Eldredge 1989; Gould 2002; Mayr and Ashlock 1991). To carry out the analysis, phylogenetic approaches implement a number of computational tools and packages to generate character state matrices and cladograms; some widely used programs are PAUP* (Swofford 2000), Mesquite (Maddison and Maddison 2007), and TNT (Goloboff et al. 2008)—specifically for phylogenetic analysis, and R (Paradis 2011)—a statistical computing program.[2]

Since phylogenetic classification and analysis trace common descent and variation from an ancestral form, phylogenetics may very well be used to infer the histories of cultural traits, as long as these undergo the evolutionary processes of drift/selection, transmission, and modification (Levinson and Gray 2012; Mesoudi 2011; O'Brien et al. 2001; Tëmkin 2016; Whiten et al. 2011). In this sense, cultural evolution refers to the emergence and change of cultural forms by means of descent with modification, and, just like in biology, cultural phylogenetics aims at understanding cultural evolution through relations of relatedness by reconstructing the "genealogical" relations of artifacts and artifact traditions (Currie 2013).

Applications in Archaeology

The emergence, diffusion, and diversification of artifacts over time and in space (traditions) usually leave a distinctive trace in the material record (Whiten et al. 2011). It is the analysis of those traces which makes it possible for archaeologists to find or infer patterns to reconstruct and explain the paths of cultural evolution (Mesoudi and O'Brien 2009). Phylogenetic methods in archaeology are precisely meant to reveal the course and channels of cultural change.

Evidently, the study of cultural evolution is not new to our field. The notion that social phenomena such as the emergence and dispersal of populations and artifacts may be revealed by tracing back links among different cultural practices has a deep history in the human and social sciences (Richerson and Christiansen 2013; Walsh et al. Chap. 2 this volume). In archaeology, plotting artifact genealogies goes back to the early establishment of the discipline in the nineteenth century (Lipo et al. 2006; García Rivero 2016). A standard method of this kind is the creation of archaeological typologies, which are classifications of artifacts divided in types and sub-types "based upon a consideration of qualitative, quantitative, morphological, technological and functional attributes" (Bahn 1992, p. 519). Like phylogenetic methods, typologies also aim at organizing artifacts in discrete groups in order to better understand their histories; however, making typologies and phylogenies are fundamentally different processes. Typologies are descriptive, based on the overall similarity of an artifact or one of its attributes (e.g., decoration, shape), but there is no necessary element of hierarchy or succession. Therefore typologies are often limited to establishing likeness. Artifact phylogenies, on the other hand, hone in on those homologous attributes (characters) that have been potentially transmitted and modified over time. These, in turn, can then be compared and analyzed quantitatively allowing researchers to infer degrees of relatedness between entities, to identify divergence events, and ultimately to reconstruct patterns of cultural evolution (García Rivero 2016; O'Brien and Lyman 2003). In brief, we could say that in a typology, the predetermined category of the *type* determines

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[2] Each of these has an explanatory website and free online tutorials. For a comprehensive list of Phylogeny programs, see: http://evolution.genetics.washington.edu/phylip/software.html.

the attributes that the artifact should present, but in a phylogeny, it is the attributes which determine whether a type belongs or not to a set (see O'Brien et al. 2001).

So, the appeal of phylogenetic methods in archaeology is that it allows researchers to systematically build theoretically sound maps and classifications of relatedness to track culturally transmitted information across space and through time (Lipo et al. 2006). The first momentous examples of the use of archaeological cladistics are found in the seminal work on Paleoindian stone tool technologies by Michael O'Brien and his collaborators, which really set the foundations for the current state of the field (O'Brien and Lyman 2003; O'Brien et al. 2001, 2002). Since then, the methods of cultural phylogenetics have been applied in archaeology to a growing variety of regions and materials, such as Native Californian baskets (Jordan and Shennan 2003); Middle Paleolithic technology (Lycett 2007, 2011); pottery from Fiji (Cochrane 2008), the European Neolithic (Collard and Shennan 2000), and the North American Southwest (Harmon et al. 2006); Turkmen carpets (Tehrani and Collard 2002) and Iranian textiles (Matthews et al. 2011); symbolic items from the Iberian Neolithic (García Rivero and O'Brien 2014); Northern European Mesolithic bone points (Riede 2008); houses from the American Great Plains (Gjesfjeld and Jordan, Chap. 9 this volume); musical instruments like brass cornets (Eldredge 2000) and the Baltic psaltery (Tëmkin and Eldredge 2007; Veloz et al. 2012); and artistic traditions from Thailand (Marwick 2012) and the European Upper Paleolithic (Tripp 2016), just to mention a few.[3]

Not only has the scope of regions and artifacts diversified, but also the aims of research have found many more applications. García Rivero (2016) has divided phylogenetic studies in archaeology in three categories: (1) those that examine the geographical distribution and cultural development of artifacts or traditions by tracking transmission and descent back to a common ancestor or prototype, for example, studies which explain the causes and rates of change in material culture traditions (Tehrani and Collard 2002) and help make inferences about the factors that shaped the traits of artifacts (Mace and Pagel 1994; Mesoudi and O'Brien 2005). (2) Those that create nested groups of artifacts, or clades, to track them geographically or temporally. Here we find works that construct artifact lineages (O'Brien et al. 2001) and those that establish the chronological arrangement of cultural traditions by identifying splitting events in a branch (Gray and Atkinson 2003; Holden and Shennan 2005). In archaeology, like in linguistics, phylogenetic methods can also add to the chronological arrangement of cultural traditions (Gray and Atkinson 2003; Holden and Shennan 2005). For example, by temporally situating a splitting event, a branch, or node in a tree or network diagram, researchers can relatively date traits or specimens whose ages remain unknown. (3) Comparative studies that aim at understanding models of descent to explain the distribution of functionally adaptive traits by, for instance, testing the coevolution of characters or testing competing hypotheses. The patterns of relatedness that emerge from artifact cladograms can then be used to test alternative explanations about the distribution and configuration of material culture across regions and periods (O'Brien and Lyman 2005).

In fact, this latter application, as a strategy to test different scenarios of cultural change, may be one of the most important contributions of cultural phylogenetics to archaeological analyses (Houkes 2011). Like in biology, the comparative method based on formal analogy alone cannot inform researchers about the nature of the similarities and differences between cultural traditions, that is, whether these are rooted in kinship, resulted of parallelism or convergence, or were transmitted horizontally through borrowing.[4] However, phylogenetic methods actually address that issue directly and are therefore able to produce sequences of classification based not only on appearance but on historical hypotheses (García Rivero 2016).

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[3] For more thorough and detailed reviews of relevant contributions of cultural phylogenetics in archaeological research, see García Rivero 2016; Mace et al. 2005; Renfrew and Forster, 2006; Lipo et al. 2006; O'Brien 2008; Shennan 2009.

[4] What is known as Galton's problem.

A good example of how cladistic methods can be used to test competing archaeological scenarios is a recent study by Allison Tripp (2016) on one of the most fascinating and challenging group of artifacts from the European Upper Paleolithic, the so-called Venus figurines. Over 50 such figures have been found from France in the West, to Siberia in the East, and Italy in the South. They are made from materials as diverse as sandstone, bone, clay, ivory, and amber, and in their majority dated to the Gravettian period (*c.* 30,000–20,000 BP), although there are specimens known from before and after. In spite of their wide geographic and temporal span, there has been a tendency to lump these figurines together as a single category, based on some general stylistic similarities, for example, the fact that many (although not all) are small portable statuettes depicting nude females with exaggerated breasts and buttocks. Some researchers have supported this classification, arguing that the figurines comprise a cohesive group determined by their shared core features, such as those mentioned before (Leroi-Gourhan 1968). The opposing view is that the Venuses should cluster in groups according to their regional and chronological distribution and, therefore, despite their apparent similarity, might represent independent regional cultural traditions (Gamble 1982; Gvozdover 1989). The first model supports horizontal cultural transmission patterns (blending), whereas the second implies vertical transmission (branching). Higher similarity between figures from clusters of sites/regions would support horizontal transmission and blending, while higher differences between groups would support branching. To test these opposing views, Tripp suggested a cladistics analysis focusing on multiple variables at the individual artifact level, i.e., specific characters across the set (Fig. 8.4). After selecting only complete full-bodied specimens for study and the earlier Aurignacian Hohle Fels Venus as an out-group, Tipp examined the character state matrix of the sample. The result ultimately supported the second hypothesis that the figurines do not form a cohesive group but rather comprise regional groups generated by vertical information flow. The artifact cladogram revealed, for example, that the Russian figurines (Gagarino, Avdeevo, Kostenki) cluster together to the exclusion of other regions, indicating a definite regional tradition (Fig. 8.5). This paper illustrates well how phylogenetic methods can help us test and contrast specific archaeological hypotheses and demonstrates that traditional archaeological models will not always hold up to a phylogenetic analysis.

Challenges and Prospects

As we have seen, the analogies between biological and cultural evolution seem enough to justify the use of phylogenetic methods in archaeology. But the processes of biological and cultural evolution also differ in many ways. On the one hand, both organisms and artifacts can be distilled into characters that lend themselves to a phylogenetic approach. On the other hand, the concepts that guide the methods of cladistics in biology are relatively well understood and defined, whereas that is not always the case in culture studies. For instance, it is not at all clear what the equivalent of a cultural homology, and therefore the study unit of cultural change, should be (Tëmkin 2016). Furthermore, because cultural evolution draws on design elements, it includes much higher rates of horizontal transfer, novelty, hybridization, and borrowing than its genetic counterpart. For this reason, its effects can occur much faster and are not limited to continuity or extinction but can involve the reintroduction of lost traits and reversibility to previous states (Eldredge 2000; Meisel 2010; Walsh et al. Chap. 3 this volume). Finally, cultural evolution does not only operate by the Darwinian mechanism of descent with modification but also in Lamarckian fashion, through the inheritance of traits acquired through use or disuse during (operational) life (Gould 1996). These differences have spurred debates on whether methods designed to study genetic evolution may be viable to analyze the various and complex modes of cultural evolution and to what extent (Mace and Holden 2005; Lipo et al. 2006; Tëmkin and Eldredge 2007).

Head	
1. Facial features	(0) absent, (1) present
2. Orientation	(0) forward, (1) downward
3. Proportion	(0) miniature, (1) normal, (2) enlarged
4. Head shape (profile)	(0) round, (1) intermediate, (2) club, (3) pointed, (4) flat
5. Head shape (frontal)	(0) round, (1) intermediate, (2) club, (3) pointed, (4) flat
Torso	
6. Proportion	(0) miniature, (1) normal, (2) enlarged
7. Belly button	(0) absent, (1) present
Arms and hands	
8. Completeness	(0) complete, (1) hand absent, (2) hand + forearm absent
9. Proportion	(0) miniature, (1) normal, (2) enlarged
10. Arm position	(0) absent, (1) at sides, (2) above breaste, (3) below breasts, (4) on abdomen, (5) on hips, (6) away form body,
11. Fingers	(0) absent, (1) present
Legs and feet	
12. Completeness	(0) complete, (1) feet absent, (2) feet + lower leg absent
13. Apart	(0) absent, (1)$^{\wedge}$knees, (2)$^{\vee}$kness, (3) at knees
14. Proportion	(0) miniature, (1) normal, (2) enlarged
15. Realism	(0) normol, (1) abstract
16. Knees turn inward	(0) absent, (1) present
17. Puncture in place of feet	(0) absent, (1) present
18. Tocs	(0) absent, (1) present
Sexual features	
19. Breasts	(0) elongated, (1) intermediate, (2) round
20. Belly	(0) absent, (1) pronounced
21. Hips	(0) narrow, (1) broad
22. Pubic triangle	(0) absent, (1) present
23. Vulva	(0) absent, (1) present
24. Buttock shape (profile)	(0) absent, (1) flat, (2) shelf, (3) intermediate, (4) round
25. Buttock shape (rear)	(0) absent, (1) flat, (2) heart, (3) intermediate, (4) round
Decorations	
26. Head (type)	(0) absent, (1) incision, (2) hat, (3) puncture, (4) hair
27. Torso (front) (type)	(0) absent, (1) incision, (2) rope, (3) puncture
28. Torso (back) (type)	(0) absent, (1) incision, (2) rope, (3) puncture
29. Arms	(0) absent, (1) present
30. Legs	(0) absent, (1) present

Fig. 8.4 Character list of Gravettian Venus figurines (After Tripp 2016, reproduced with permission)

One of the main challenges of applying cultural phylogenetics in archaeology is that although artifact phylogenies do reflect transmission histories, they remain somewhat arbitrary because in absence of an hereditary mechanism equivalent to DNA, there is no necessary congruence in similarity across characters, for example, knowing the overall form of an artifact, e.g. a nail, does not allow us to predict confidently the form of its parts, e.g. round or flat head, or the material it will be made of e.g. steel or brass (Nickels and Nelson 2005). So, phylogenies could be built upon any of these characters.

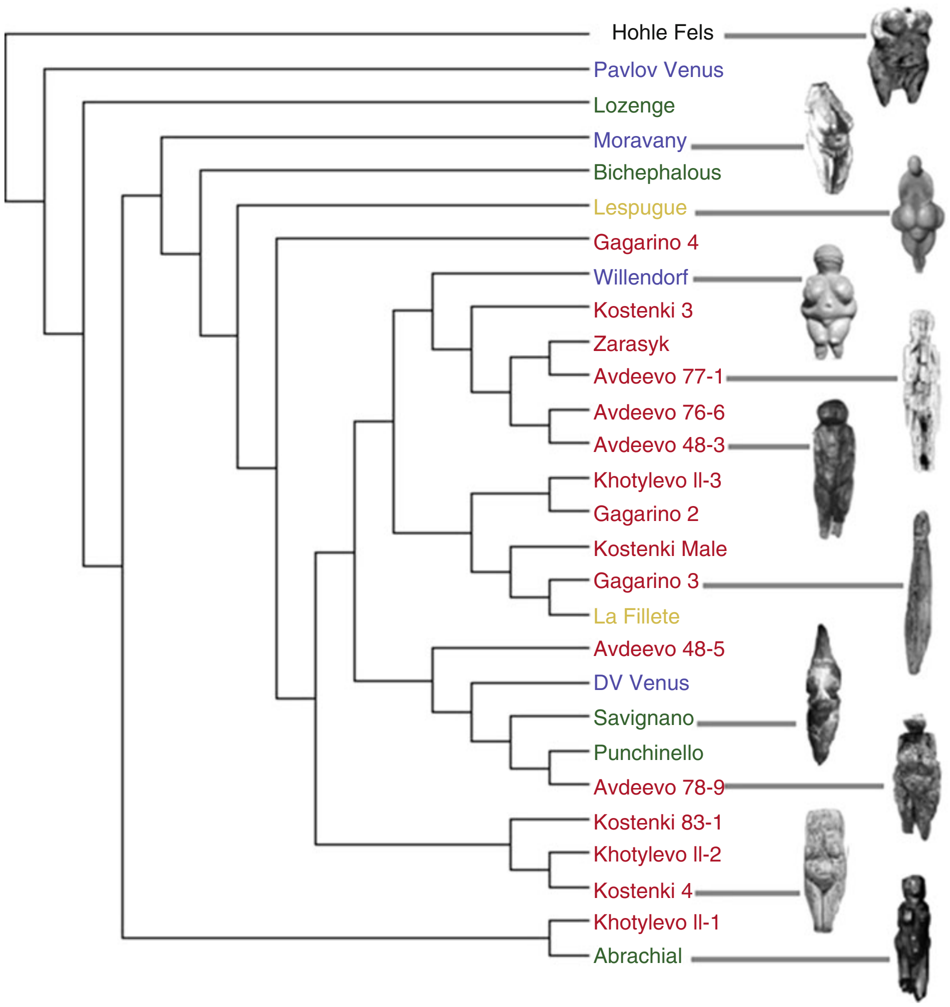

Fig. 8.5 Cladogram of Gravettian Venus figurines suggesting a Russian cluster. (After Tripp 2016, reproduced with permission)

This means that as archaeologists increasingly look to phylogenetics for interpreting the patterns by which cultural traits evolve, their success will partially depend on the accuracy of the cladograms they use in their interpretations (Houkes 2011). For that reason, it is particularly important for cultural evolution researchers to justify their selection criteria, to use all the information available to them to reconstruct the most factual cultural phylogenies and explanations of cultural change.

Again, due to the lack of an equivalent to the genomic component in biological evolution, some of the most common methodological issues in cultural phylogenetics have to do with deciding on the units and scale of analysis, such as the material set (artifact, tradition, culture), the attributes or characters with more information potential, and the interpretation of transmission mechanisms. To identify and select the appropriate units of transmission to be studied, for example, researchers can be aided by using ethnographic data and results of replication experiments (Eren et al. 2016; Mace and Jordan 2011; Mesoudi and O'Brien 2008; Schillinger et al. 2015). Similarly, choosing relevant artifact characters for analysis can be supported by examining different find resolutions (e.g., locale, site, region), which at the same time allows to better identify and test hypotheses of vertical vs. horizontal transmission (Prentiss et al. 2016). Finally, discussions on the nature and form of information transmission and of how to account for the role of the environment in cultural evolution may benefit from incorporating research on social learning and pedagogy, which can throw light on the mechanisms underlying cultural transmission (Knappett 2016; Tehrani and Riede 2008).

Researchers have also been taking important steps toward further formalizing cultural evolution studies in archaeology, for example, by adapting computational and mathematical models to match the specific and unique processes of cultural transmission, such as borrowing and horizontal transfer (Gray et al. 2007; Shennan 2009; Whiten et al. 2011), fine-tuning statistical methods to identify coherent evolution histories, such as Bayesian analyses (Crema et al. 2014; Gjesfjeld and Jordan, this volume; Matthews et al. 2011), using robust statistics measures and performing goodness of fit tests between cladograms and datasets (Marwick 2012), and developing a strong quantitative body of theory to link statistical variation in artifactual traits to account for different sources of transmission and variation (Lycett 2015, 2016; Mace and Holden 2005; Mace and Jordan 2011).

In sum, the biggest challenge to cultural phylogenetics remains that, despite the methodological compatibility with biological phylogenetics, many of the concepts and mechanisms of the latter cannot be applied to cultural evolution. But, by looking at the actual processes and mechanisms of social learning, cultural transmission, and imitation, by comparing attributes and rates of change across different spacial and temporal scales, and by developing methods and theories specific to cultural evolution, archaeologists have been steadily figuring out the different constraints and biases that influence and change cultural traits in different ways, illuminating paths of selection and reproduction that may be particular to material culture. This emerges as the biggest prospect for the immediate future of the field.

Conclusion

As I have reviewed in this chapter, over the past two decades, phylogenetic methods have been successfully employed in archaeology to trace cultural prototypes and their variations, to identify cultural clusters, to examine the distribution of functional traits, and to test ideas about the temporal and geographical spans of cultural forms and transmission mechanisms. So, the use of phylogenetics in archaeology represents a fertile field that allows researchers to generate new historical hypotheses based on the analysis of shared characters, to test them through statistical principles with quantifiable confidence levels, and use them to reconstruct evolutionary relations among material culture sets.

Cultural phylogenetics, then, contributes to archaeological research minimally in four ways: (1) as an aid in the classification of artifacts by measuring the relatedness of particular traits; (2) by testing hypotheses about cultural relatedness; (3) in the absence of a complete record, it can inform about the sequence of changes in cultural forms and the characters of missing types; and (4) it can provide a sound basis for the interpretation and explanation of archaeological phenomena. Through these four aspects, phylogenetics provides archaeology with an important tool to reflect on how the diversity and similarity of cultural traits have evolved throughout human history.

All in all, it is worth exploring the potential that the phylogenetic methods have for formulating new questions about archaeological materials and for testing established hypotheses that explain patterns of cultural origin, development, and loss. Currently, researchers like the ones mentioned in this chapter and many of the contributors of this volume strive to find ways of achieving more accurate artifact phylogenies and a more sophisticated evolutionary framework able to reveal and account for population-level mechanisms of cultural change. Like in biology, the study of cultural evolution does not end with the creation of cultural phylogenies but is a crucial first step toward understanding the processes that underlie it.

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