Chapter 9
Cultural Transmission, Genetic Models and Palaeolithic Variability: Integrative Analytical Approaches

Stephen J. Lycett

Abstract It is increasingly recognised that cultural transmission involves inheritance, variation of practice and the differential representation of particular variants in subsequent generations due to a variety of sorting mechanisms. As such, patterns of cultural variation and change (including those seen in lithic artefacts) can be seen as an emergent property of a process of "descent with modification." Two immediate analytical implications arise from recognition that changes and variation in lithic artefacts are partly brought about by a process of descent with modification, which have particular relevance for Palaeolithic archaeology. The first of these is that understanding the historical process of lineage descent and diversification (i.e. phylogeny) becomes an imperative research goal; the second is that many of the factors known to structure variation in genetic data (e.g. drift, selection, demography and dispersal) will have an influence upon patterns of variation in the attributes of artefacts. Here, using a data set of Acheulean handaxes, it is demonstrated that methodologies designed to address these issues in biology might profitably be used to address analogous questions pertaining to Palaeolithic technologies.

Change and Variation in Lithic Assemblages as a Process of "Descent with Modification"

In recent years, cultural transmission theory has been applied to a wide array of examples in the study of material culture (Eerkens and Lipo 2007). Such a theory is based on the idea that when people engage in artefact manufacture, they employ – at various stages – a set of socially inherited ideas, skills and knowledge that come to influence the final form of that artefact. Hence, the central concept here is that traditions of artefact manufacture seen in the archaeological record reflect the copying or inheritance of ideas from person-to-person. This key concept of inheritance has led

S.J. Lycett (✉)
Department of Anthropology, University of Kent, Canterbury, Kent CT2 7NR, UK
e-mail: S.J.lycett@kent.ac.uk

its proponents to draw comparisons not only between the process of knowledge inheritance and genetic inheritance (e.g. Neiman 1995; Lipo et al. 1997; Shennan 2000), but also between the process of cultural change evident through time in the archaeological record and that of organismal change seen in the fossil record (e.g. Clarke 1968; O'Brien and Lyman 2000; Kuhn 2004; Mesoudi et al. 2006). Central to such a comparison is Darwin's (1859: 459) concept of "descent with modification."

As Darwin outlined, descent with modification is a process that involves inheritance, variation and sorting. Whenever these three phenomena occur together, evolution (i.e. "descent with modification") *must* occur. Note that there is no necessary stipulation regarding how transmission must take place (e.g. via genetic means versus social means)[1] nor a stipulation regarding specific sources of variation (e.g. genetic mutation versus copying a skill imperfectly, or even deliberately choosing to embellish it). Likewise, several means of sorting may influence whether particular variants are passed to subsequent generations in lesser or greater numbers, both in the biological world and in culture. Such mechanisms include – but are not necessarily limited to – artificial selection, natural selection and even stochastic forces (e.g. drift). A further factor to bear in mind is that although genetic inheritance occurs strictly between parents and progeny, the non-kin avenues of inheritance that may occur in the replication of socially transmitted traditions are not excluded when evolution is defined in these terms (a constant source of confusion that arises when talking of cultural evolution that bears emphasising). Indeed, the appropriateness of comparison between biological descent with modification and cultural descent with modification was not lost on Darwin himself, who compared the process of language change to that of change in the natural world when first describing this mechanism (1859: 422).

Lithic artefacts show variety in form within and between assemblages, the source of which has formed a focus of discussion for many decades (e.g. Bordes 1961; Mellars 1970; Binford 1973; Dibble 1987). Yet, the combination of visible repetition in specific knapping routines in the archaeological record over time, combined with ethnographic data concerning the learning of stone artefact manufacture in traditional societies, ensures that social inheritance cannot be ignored as a major vector of influence in forming the available record (Clarke 1968; Mithen 1996, 1999; Shennan and Steele 1999; Stout 2002, 2005; Tostevin 2003; Kuhn 2004). It is perhaps unsurprising, therefore, that in recent years, cultural transmission theory has been applied to lithic artefacts to examine a series of issues (see Shott 2008 for review). Of course, ideas and traditions of artefact manufacture interact with the material world, which may also influence the final form of an artefact (e.g. raw material). Hence, just as the genotype is merely a blueprint for the biological phenotype, the latter of which may be influenced by a variety of environmental factors during growth and development, so the artefact may find itself subject to environmental influences that affect form beyond that of the ideas and skill traditions possessed by its manufacturer. However, as will be shown below, using cultural transmission theory as a basis allows questions concerning these potential forces to be situated in an empirically testable framework.

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[1] It is worth reflecting that Darwin himself knew nothing of genes and the specifics of what later became known as the principles of Mendelian inheritance.

Recent lithic case studies have considered a diversity of issues including the evolution and diversification of specific traditions (e.g. O'Brien et al. 2001; Darwent and O'Brien 2006; Buchanan and Collard 2008; Lyman et al. 2009), colonisation processes in the Americas (e.g. Buchanan and Collard 2007), processes of selection (Lyman et al. 2008), modes of transmission (e.g. Bettinger and Eerkens 1999; Mesoudi and O'Brien 2008a, b; Hamilton and Buchanan 2009) and the effects of natural catastrophes on artefactual variation (Riede 2008). Such a burgeoning literature would appear to attest to the utility of cultural transmission theory as it applies to lithic artefacts. However, despite the recent rise in the application of cultural transmission theory (and associated techniques of analysis) to lithic artefacts, the majority of case studies to date have been conducted on Holocene artefacts made by *Homo sapiens* from the Late Palaeolithic/Mesolithic periods. Only a handful of such studies have applied these same principles to frame formal analyses of artefactual evolution and variation using data from the Lower and Middle Palaeolithic (Vaughan 2001; Lycett 2007b, 2008, 2009a, b; Lycett and von Cramon-Taubadel 2008; Lycett and Gowlett 2008). Such a state of affairs is perhaps even more striking given the growing evidence from both captive and wild chimpanzee populations, which demonstrates that our closest living primate relatives create traditions of behaviour (including technological traditions) via means of social transmission (Whiten 2005; Whiten et al. 1999, 2001, 2005, 2007; McGrew 2004; Biro et al. 2006; Horner et al. 2006; Bonnie et al. 2007; Hopper et al. 2007; Lycett et al. 2007, 2009). Given this evidence, there is no immediate operational reason why the cultural transmission framework of analysis cannot be extended to extinct hominin populations under a unified analytical framework.

Two immediate analytical implications arise from recognition that changes and variation in lithic artefacts are partly brought about by a process of descent with modification, which have particular relevance for Palaeolithic archaeology. Firstly, that phylogenetic methods drawn from biology may be used to understand the evolution and diversification of artefact lineages (Foley 1987; O'Brien and Lyman 2000, 2003a; Kuhn 2004; O'Brien et al. 2008). Secondly, that methods and principles drawn from population genetics can provide a fruitful means of testing hypotheses concerning issues such as drift, technological selection and hominin dispersal (Neiman; 1995; Shennan 2000, 2001; Bentley et al. 2004, 2007; Lycett and von Cramon-Taubadel 2008). The following sections of this paper discuss both the use of phylogenetic methods and population genetics principles, as they might be applied to data from these earlier periods.

Phylogeny and Palaeolithic Variability

Phylogenetics: The Study of Historical Diversification and Descent

Darwin's theory of descent with modification transformed Linnaean taxonomy from a mere hierarchical classificatory scheme of intransmutable taxa into an organisational principle for patterns caused by evolutionary change (Mayr 1982; O'Brien and Lyman 2000).

Hence, wherever there is a process of evolution, an understanding of the relationships (i.e. pattern of diversification and descent) between evolving units becomes an essential goal. Under this framework, phylogenetic analysis is a means of organising groups of things (be they species, populations or artefactual assemblages) into a hierarchical pattern that reflects closeness of genealogical relationship based on the attributes (e.g. genes or morphology) exhibited by individuals within those groups (McLennan and Brooks 2001; O'Brien and Lyman 2003a). It is important to emphasise that in a phylogenetic sense, "relationship" refers explicitly to genealogical affinities rather than mere closeness of similarity (e.g. typological resemblance). In essence, phylogenetics is an historical approach to a given data set (Smith 1994; O'Brien and Lyman 2003a; Lipo et al. 2006; O'Brien et al. 2008).

Recognition that many changes in the artefactual record can be seen as resulting from an historical process of descent with modification mediated by social transmission, has led several recent workers to suggest that phylogenetic methods drawn from biology might yield great potential in the case of archaeological data (Foley 1987; Collard and Shennan 2000; O'Brien et al. 2001). In the case of biology, cladistics has been a commonly used method of phylogenetic reconstruction over recent decades (Eldredge and Cracraft 1980; Quicke 1993; Smith 1994; Kitching et al. 1998; Page and Holmes 1998; Gee 2000; McLennan and Brooks 2001). Subsequently, cladistics has also been adopted by many archaeologists and anthropologists in order to investigate historical questions of phylogeny pertaining to archaeological artefacts and other cultural data (e.g. Collard and Shennan 2000; O'Brien et al. 2001; Tehrani and Collard 2002, 2009; Jordan and Shennan 2003; Darwent and O'Brien 2006; Harmon et al. 2006; Jordan and Mace 2006; Buchanan and Collard 2007, 2008; Lycett 2007b, 2009a, b; Lycett et al. 2007).

As is widely known, cladistics emphasises the importance of using uniquely shared (i.e. "shared-derived") characteristics, rather than shared primitive ("symplesiomorphies") or convergences (i.e. "homoplasies") in determining the phylogenetic relationships between evolved units, while at the same time using the principle of parsimony as a means of choosing between hypotheses of phylogeny when faced with several possible alternatives (Sober 1983). Cladistics can be computationally demanding and is also notorious for its association with esoteric terminology. Fortunately, in recent years, several accessible introductions to the principles and terminology of cladistics have become available (e.g. Kitching et al. 1998; McLennan and Brooks 2001), including some written specifically for archaeologists (O'Brien and Lyman 2003a). It has also been noted that despite the use of rather complex computer algorithms to determine the most parsimonious cladograms, cladistics can conceptually be broken down into a small series of fundamental methodological steps (McLennan and Brooks 2001; Buchanan and Collard 2007).

The first step in any cladistic analysis is to delineate the taxonomic units (i.e. identify those units that one wishes to understand the structure of relationships between). These analytical units are referred to as "Operational Taxonomic Units" (OTUs), and in biology might be individuals, species or populations, while in archaeology might be artefacts or assemblages. The second stage is to generate a character state matrix describing the character states for each OTU. Next, the direction

of evolutionary change ("character polarity" in cladistic terminology) is determined, most commonly via comparison with an outgroup. Thereafter, a branching diagram (i.e. cladogram) is constructed that describes the relationships between OTUs for each character. Finally, in accordance with the principle of parsimony, an ensemble cladogram is constructed that is consistent with the largest number of character trees and also, therefore, requires the least number of ad hoc (non-parsimonious) character state changes to be invoked in order to explain the phylogenetic relationships between the different OTUs. This use of parsimony also explains why cladograms are frequently referred to as Maximum Parsimony (MP) trees.

Testing the Utility of Phylogenetic Methods for Palaeolithic Data: A Case Study Using Acheulean Handaxes

Handaxes are defined by the imposition of a long axis on artefact form by means of invasive bifacial knapping around the edge of a core, nodule or large flake blank (Roe 1976; Isaac 1977; Gowlett 2006). Currently, classic Acheulean handaxes of teardrop, triangular or ovate shape are known from sites across Africa, western Asia, Western Europe, and the Indian subcontinent. Such artefacts date from *ca*. 1.7 MYA (in Africa) to less than 200 KYA (Asfaw et al. 1992; Schick and Toth 1993; Clark 1994; Klein 2005). Acheulean handaxes are truly multidimensional in variation of form, shape and symmetry across their large time-span and geographic distribution (Wynn and Tierson 1990; Clark 1994; Vaughan 2001; Gowlett 2006; Lycett and Gowlett 2008; Lycett and Norton 2010). Hence, they seem an appropriate phenomenon to discuss some of the challenges and potential of phylogenetic approaches to Palaeolithic data.

The idea that phylogenetic methods might usefully be applied to Palaeolithic data of this nature has not been without criticism. One such criticism concerns recognition that stone artefacts can be subject to technological convergence (e.g. McBrearty 2003; Otte 2003). However, convergence is also common in biological data, and as one recent case study has demonstrated (Lycett 2009a), hypotheses of convergence are themselves phylogenetic scenarios that – ironically – can only be evaluated formally with phylogenetic methods. A somewhat related idea is the long-held view that much of stone artefact variation is the product of raw material properties (Goodman 1944), and as such potentially swamp any cultural information that might be present. Fortunately, as will be shown below, the degree to which a cladogram of hypothesised stone artefact relationships is influenced by raw material is a factor that may be determined empirically.

A further challenge concerns the relationship between stone artefact form and socially inherited knowledge. At a proximate level, it is not the attributes of artefacts that are themselves transmitted between individuals. Rather, it is the ideas, concepts, skills and actions surrounding the process of manufacture. However, such entities are not directly amenable empirically in the case of archaeological data; all we are left with is the material (artefactual) products of their implementation and application.

This is closely analogous to the situation that palaeontologists routinely find themselves in when attempting to determine the phylogenetic relationships of extinct taxa from fossils. It is genes that are inherited at the proximate level, yet only morphological attributes are available for study, which must be used as a proxy for the genetically transmitted information.

A further potential problem might therefore be a relative paucity of "cultural" information in stone artefacts of Lower and Middle Palaeolithic age. It might, for instance, be suggested that stone is not as "plastic" as the pottery decorations or carpet designs used in cladistic analyses of later artefacts, and thus does not convey cultural information of the type required to give a reasonable phylogenetic signal. Theoretically, some argument can be made against such a line of reasoning from the outset, and it may even be founded on misconceived ideas that for a phylogenetic model to operate stone knappers must have had some preconceived "mental template" and/or been consciously signalling cultural identity. Fortunately, neither of these assumptions is a necessary requirement of phylogenetic approaches to Palaeolithic data. It has long been considered (e.g. Oakley 1958) that certain "traditions" of artefact manufacture result from inherited knowledge about how specific techniques will lead to certain outcomes. However, any culturally transmitted idea or technique surrounding stone tool manufacture – from abrading a platform in a certain type of way with a certain type of abrader, to holding the artefact and/or turning it certain ways during manufacture – may, in principle, result in quantifiable differences in certain attributes of the final product, *whether the knapper is consciously aware of those outcomes or otherwise* (see also Clarkson, this volume). Numerous attributes of manufacture, however subtle, might be applied at the numerous stages of manufacture and result in some unforeseen but quantifiable variable. A corollary of this, is that it is difficult a priori to determine precisely what attributes might be more or less phylogenetically informative in the case of stone tools. Again, it is interesting to note that in palaeontology, systematic morphometric approaches to character acquisition, which explicitly take account of the fact that populations vary in a continuous manner both within and among themselves in terms of their attributes, are increasingly being used in phylogenetic studies (e.g. Adrain et al. 2001). More importantly, as will be shown below, the degree of phylogenetic signal in a resultant tree and the goodness-of-fit to a tree model can be evaluated empirically, once a phylogenetic tree has been constructed.

To investigate these issues in regard to the phylogenetic analysis of Palaeolithic data, a series of analyses were conducted on a data set of Acheulean handaxe assemblages from a series of localities across Europe, Africa, the Near East and the Indian subcontinent (Table 9.1). Quantitative data for a total of 72 characters were collected for each of the ten OTUs (total $n = 255$ handaxes). Information concerning these characters has previously been described in detail elsewhere (e.g. Lycett et al. 2006; Lycett 2007a, b, 2008). However, in brief, the characters comprise a series of data describing overall form (i.e. Characters 1–57), as well as wider attributes such as consistency of complete flake scars, position and percentage of cortex, number of negative flake scars, number of untruncated flake scars and the number of non-feather terminations. In order that morphometric data emphasise shape information rather

Table 9.1 Operational taxonomic units employed in analyses

Locality	*n*	Raw material
Attirampakkam, India	30	Quartzite
Bezez Cave (Level C), Adlun, Lebanon	30	Chert
Elveden, Suffolk, UK	24	Chert
Kariandusi, Kenya	30	Lava
Kharga Oasis (KO10c), Egypt	17	Chert
Lewa, Kenya	30	Lava
Olduvai Gorge (Bed II), Tanzania	13	Quartz, lava
Morgah, Pakistan	21	Quartzite
St Acheul, France	30	Chert
Tabun Cave (Ed), Israel	30	Chert

Total *n* = 255 handaxes

than mere size differences (which might reflect initial blank form and/or reduction intensity rather than socially transmitted factors influencing shape; see also Buchanan and Collard, this volume), variables 1–48 were size-adjusted via the geometric mean method (Jungers et al. 1995; Lycett et al. 2006). The geometric mean removes the confounding effect of isometric scale differences, equalizing the volume of each artefact while maintaining overall shape information (Falsetti et al. 1993; Jungers et al. 1995). Following size-adjustment, character data were converted into discrete states for the cladistic analyses via a statistical procedure termed "divergence coding" (Thorpe 1984). Divergence coding is a particularly useful approach since it not only accommodates the fact that attributes will vary both within and between OTUs (potentially even with some degree of overlap), but also assigns character states on the basis of statistically significant ($p \leq 0.05$) differences rather than arbitrary decisions or untested assumptions of similarity that might apply in the case of qualitative procedures (for further information see Lycett 2007b, 2009a). Screening of character data for non-phylogenetic integration via correlation analyses (see Lycett 2007b, 2009a for details) resulted in the removal of six characters (Characters 7, 11, 16, 35, 40, 43: Table 9.2), leaving 66 characters for the cladistic analyses. Parsimony trees were obtained in PAUP*4.0 (Swofford 1998) via the branch-and-bound algorithm, which is guaranteed to find the most parsimonious tree (Kitching et al. 1998). All characters were treated as ordered and freely reversing, as is appropriate for quantitative data of the type used here (Slowinski 1993; Rae 1997). Handaxes from Bed II Olduvai Gorge were used as an outgroup, since being the oldest artefacts in the data set (*ca.* 1.4–1.2 MYA) are most likely to be informative regarding the plesiomorphic characteristics of the handaxe assemblages used (Smith 1994: 58–59).

Figure 9.1 shows the cladogram produced by parsimony analysis of the handaxe data. An obvious attribute of this cladogram is that non-African assemblages form a monophyletic clade to the exclusion of African assemblages. A further attribute of note is that the two Near-Eastern assemblages of Bezez (Lebanon) and Tabun (Israel) are indicated to be sister taxa. The geographic and probable temporal proximity of these assemblages (Bar-Yosef 1994) intuitively supports the suggestion that the

Table 9.2 Characters employed in cladistic analyses

1. Core left width at 10% of length
2. Core left width at 20% of length
3. Core left width at 25% of length
4. Core left width at 30% of length
5. Core left width at 35% of length
6. Core left width at 40% of length
7. Core left width at 50% of length
8. Core left width at 60% of length
9. Core left width at 65% of length
10. Core left width at 70% of length
11. Core left width at 75% of length
12. Core left width at 80% of length
13. Core left width at 90% of length
14. Core right width at 10% of length
15. Core right width at 20% of length
16. Core right width at 25% of length
17. Core right width at 30% of length
18. Core right width at 35% of length
19. Core right width at 40% of length
20. Core right width at 50% of length
21. Core right width at 60% of length
22. Core right width at 65% of length
23. Core right width at 70% of length
24. Core right width at 75% of length
25. Core right width at 80% of length
26. Core right width at 90% of length
27. Core length distal at 10% of width
28. Core length distal at 20% of width
29. Core length distal at 25% of width
30. Core length distal at 30% of width
31. Core length distal at 40% of width
32. Core length distal at 50% of width
33. Core length distal at 60% of width
34. Core length distal at 70% of width
35. Core length distal at 75% of width
36. Core length distal at 80% of width
37. Core length distal at 90% of width
38. Core length proximal at 10% of width
39. Core length proximal at 20% of width
40. Core length proximal at 25% of width
41. Core length proximal at 30% of width
42. Core length proximal at 40% of width
43. Core length proximal at 50% of width
44. Core length proximal at 60% of width
45. Core length proximal at 70% of width
46. Core length proximal at 75% of width
47. Core length proximal at 80% of width

Table 9.2 (continued)

48. Core length proximal at 90% of width
49. Coefficient of surface curvature 0–180°
50. Coefficient of surface curvature 90–270°
51. Coefficient of surface curvature 45–225°
52. Coefficient of surface curvature 135–315°
53. Coefficient of edge-point undulation
54. Index of symmetry
55. Maximum width/width at orientation
56. Maximum length/length at orientation
57. Nuclei outline length
58. Area of largest flake scar
59. CV of complete flake scar lengths
60. CV complete flake scar widths
61. Total number of complete (i.e. untruncated) flake scars
62. Total number of negative flake scars
63. Number of flakes removed superior and in contact with outline of nucleus
64. Number of non-feather terminations
65. % Cortex 1st superior quadrant
66. % Cortex 2nd superior quadrant
67. % Cortex 3rd superior quadrant
68. % Cortex 4th superior quadrant
69. % Cortex 1st inferior quadrant
70. % Cortex 2nd inferior quadrant
71. % Cortex 3rd inferior quadrant
72. % Cortex 4th inferior quadrant

Six characters (i.e. characters 7, 11, 16, 35, 40, and 43) were not employed due to integration (see Lycett 2009b for further details) leaving a total of 66 characters for the analyses

types of variable being used as characters in the phylogenetic analysis, are accurately determining phylogenetic relationships based on the proximity of socially transmitted information. The robustness of this relationship will be evaluated further below.

As noted earlier, how well a particular data set fits a tree model will depend on how useful the attributes inputted to the analysis are for this purpose, and to what degree they contain a "phylogenetic signal." One means of determining the strength of phylogenetic signal in a data set is to use a procedure termed "phylogenetic bootstrapping." This method involves randomly resampling the original character matrix and replacing some character states with alternatives. Usually a large number (≥1,000) of these pseudoreplicate character matrices are produced, and MP cladograms are determined for each of them. The results of these analyses are typically presented in the form of a majority-rule consensus tree, which indicates how many of the original instances of branching in the MP tree were also found in the bootstrap trees. Most commonly, this
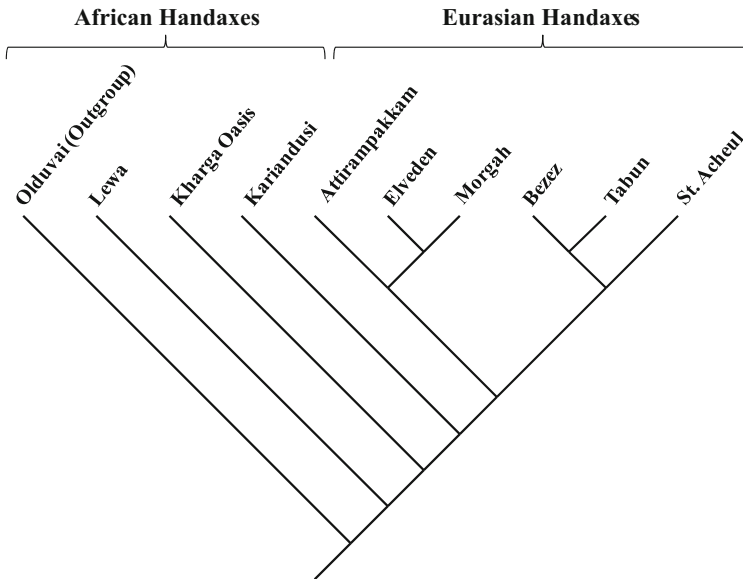
Fig. 9.1 Maximum parsimony cladogram based on 66 characters (Tree length = 1,222, ensemble Retention Index = 0.55)

is indicated by a percentage figure placed next to each instance of branching ("node" in cladistic terminology). The underlying logic here is that more robust data sets will provide a high number of nodes consistent with the original cladogram, whereas data sets containing relatively little phylogenetic signal will have fewer instances of branching consistent with the real MP tree. In the case of biological data sets, it has been suggested that where nodes are supported in at least 70% of the bootstrap trees, they may be considered robust (Hillis and Bull 1993).

Figure 9.2 shows a majority-rule consensus tree of 10,000 bootstrap trees obtained from the handaxe data set. It is noteworthy that the majority of nodes are supported at high levels (average bootstrap value = 87%). It is also important to note that the node indicating the branching of Eurasian handaxe assemblages from African assemblages is supported in 98% of the bootstrap trees, suggesting that the phylogeographic pattern noted earlier is robust. Likewise the sister-taxon relationship indicated by the MP tree for the two Near-Eastern assemblages (Bezez and Tabun) is supported in 100% of the bootstraps. Hence, it appears that the branching relationships of the MP cladogram are robustly supported by the character data.

A further useful means of measuring how well a particular data set fits a tree model is to look at the ensemble Retention Index, or RI value. This descriptive statistic measures goodness-of-fit by determining the number of homoplastic (i.e. non-parsimonious) character changes that occur in the MP tree independent of its length (Kitching et al. 1998). The RI ranges from 0.0 to 1.0, whereby a value of 1 equals a perfect goodness-of-fit, while values approaching 0 indicate poor goodness-of-fit to a tree model. Usefully, the Retention Index is not sensitive to differences
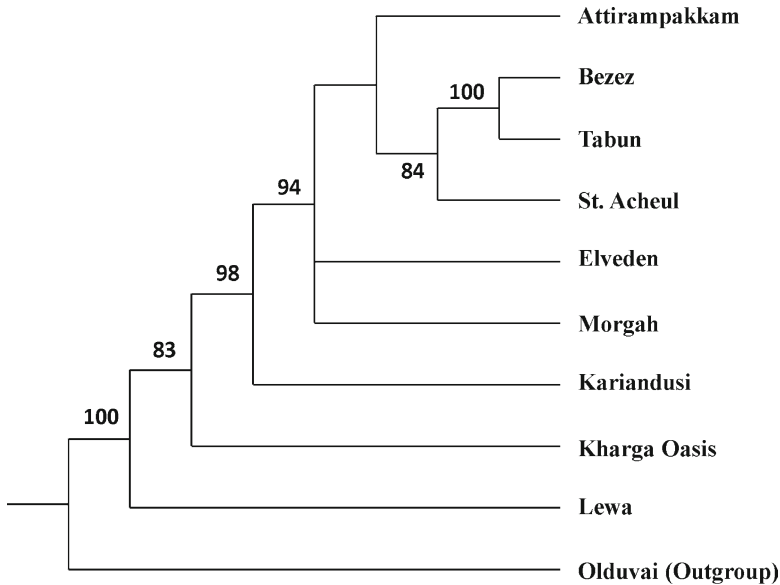
Fig. 9.2 50% majority-rule consensus bootstrap tree (based on 10,000 bootstrap replications). Numbers next to nodes indicate the percentage of bootstrap replications that support that branching relationship

between the dimensions of different character matrices, enabling RI values from different data sets to be compared.

Collard et al. (2006) recently employed the ensemble RI statistic to compare 20 cladograms produced from human cultural data sets of Holocene populations to equivalent cladograms generated for 21 biological data sets drawn from a range of behavioural, morphological and genetic studies of various non-human taxa. Their analyses indicated that, in the case of the cultural data sets, RIs ranged from 0.42 to 0.78 with a mean of 0.59. In the case of the biological data sets, RIs ranged from 0.35 to 0.94 with a mean of 0.61. Thus, contrary to what is often assumed, the human cultural data sets appeared to fit, on average, a tree model equally as well as biological data sets.

An RI value for the handaxe MP cladogram generated here may usefully be compared against Collard et al.'s (2006) results to test the relative goodness-of-fit to a tree model. An RI for the handaxe cladogram was computed in McClade 4.02 (Maddison and Maddison 2000) following importation of the data set from PAUP*4.0 (Swofford 1998). If the handaxe cladogram does not fit a tree model as well as those generated for the human cultural data sets examined by Collard and colleagues, we would expect the RI to fall close toward the lower end of, or even fall outside, the RI range for those data sets.

To the contrary, the RI value for the cladogram of handaxe assemblages was calculated at 0.55. This is well within the range of RI values reported by Collard et al. (2006) for human cultural data sets (0.42–0.78) and is very close to the mean of those data sets (0.59). Likewise, the handaxe cladogram RI falls within

the range of biological RIs reported by Collard and colleagues (0.35–0.94) and is again not drastically below the mean of those data sets (0.61). Hence, it would appear that in a comparative sense the handaxe assemblages fit a tree model equally as well as human cultural data sets from later periods and even biological data.

Even so, it might be argued that inputting a large database of metric characters such as that used here (i.e. 10 taxa × 66 characters) into a cladistic analysis automatically results in a relatively high RI value. To test this contention formally, 1,000 random character matrices of equal dimensions (i.e. an equal number of taxa, characters, and character states) were generated by reordering randomly the character states of the original matrix. MP trees for each of these 1,000 pseudoreplicate character matrices were determined and the RI for each of these trees recorded. It can be reasoned that if simply inputting a large data base into a cladistic analysis automatically results in an RI value similar to that found in the previous analysis, then the mean RI of these 1,000 random trees should be similar to that of the MP tree.

As noted above, the RI of the MP handaxe tree is 0.55. Conversely, the mean RI of 1,000 random trees was found to be only 0.20, with a range of 0.10–0.46. Hence, none of the random trees produced an RI value as high as that of the real data and the RI value of the handaxe cladogram is over twice as high as the mean RI of the 1,000 random trees. This provides strong evidence that the goodness-of-fit found for the handaxe assemblage cladogram is not a random (chance) result produced as a by-product of a relatively large data set of characters, but results from the internal properties of the data set itself.

As noted earlier, a potential concern in the application of phylogenetic methods to stone artefacts is the influence of raw material. The basic raw materials of the (ingroup) handaxe assemblages used here may be assigned to one of three broad categories: chert, quartzite or lava. A statistical test known as the Kishino–Hasegawa (1989) test may be used to determine if the MP handaxe cladogram is statistically different from a "model tree" that has been deliberately constrained by raw material factors. Thus, a model tree was built by first constructing a constraint tree reflecting pure raw material groups. This tree was constructed manually in MacClade 4.02 (Maddison and Maddison 2000). The constraint tree was then imported into PAUP*4.0 and a parsimony analysis conducted to find the cladogram most consistent with these raw material constraints (Fig. 9.3). The Kishino–Hasegawa (K–H) test uses the standard deviation of changes in each character in the cladogram and the t-statistic to determine if the true MP tree is statistically different ($p \leq 0.05$) from the model tree. If it is, then the parameter constraining the model tree (i.e. raw material) cannot reasonably be considered to be a dominant factor in producing the suggested relationships between taxa in the MP tree.

Table 9.3 shows the outcome of the K–H test. Differences between the MP cladogram and the raw material model tree were found to be highly significant ($p < 0.0001$). Hence, it does not appear that raw material is a dominant factor in producing the relationships between different handaxe assemblages in the MP cladogram.
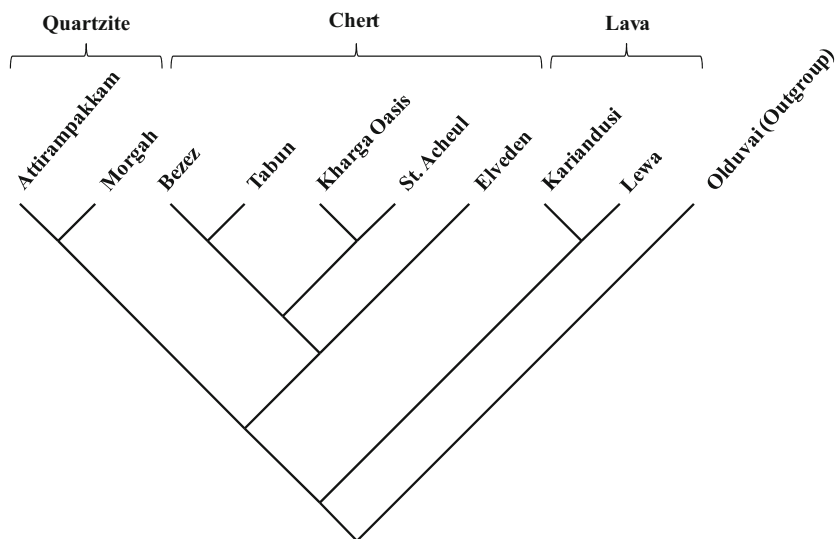
Fig. 9.3 Raw material model tree. The statistical differences between this tree and the Maximum Parsimony (MP) cladogram shown in Fig. 9.1 are highly significant ($p < 0.0001$), indicating that raw material factors do not have a dominant role in producing the relationships shown in the MP tree

Table 9.3 Results of K–H test

Tree	Length	Length difference	SD difference	P-value
1.	1,222	178	37.4	<0.0001
2.	1,400			

Tree 1 = Maximum parsimony topology; Tree 2 = Raw material model tree

Summary of Handaxe Cladistic Analyses

A series of analyses using cladistic procedures have indicated that Lower Palaeolithic data sets such as Acheulean handaxe assemblages can possess a strong phylogenetic signal, as predicted by cultural transmission theory. It has also been shown in this case study that the influence of raw material factors can be assessed. Such analyses indicated on this occasion that raw material is not a major determinant in producing the relationships shown in the cladogram. Interestingly, the cladogram appears to show a correlation between geography and phylogeny. Such correlations can particularly be seen in the robustly supported branching of Eurasian OTUs from African OTUs. Such phylogeographic patterning can be explained by dispersal factors as hominins migrated from Africa (Lycett 2009b). It has long been hypothesised that the Acheulean originated in sub-Saharan Africa and subsequently spread across many regions of the Palaeolithic Old World via hominin dispersals (Clark 1994; Carbonell et al. 1999; Goren-Inbar et al. 2000; Bar-Yosef and Belfer-Cohen 2001; Saragusti and Goren-Inbar 2001; Klein 2005). Such a hypothesis is precisely the

sort of question that population genetic approaches might allow us to test further. It is these methods that are discussed in the following section.

Population Genetic Models and Palaeolithic Variability

In biology, patterns of genetic and phenotypic variation reflect neutral forces of evolution (i.e. drift) and selective factors (either natural or artificial) to varying degrees. In the case of neutral evolution, variation is structured by mutation rates, gene-flow and dispersal (Wright 1931). Conversely, selection is reflected in instances wherever specific patterns of variation are related directly to increased survival and fecundity. Population genetics is the study of patterns of molecular variation against this context of selection, drift, mutation and gene flow (Crow and Kimura 1970; Gillespie 1998; Halliburton 2004). As such, population genetic approaches aim to examine the specific factors (e.g. drift, selection and population dispersal) that structure allelic variation.

A further corollary of cultural transmission theory is that many of the factors known to structure population-level patterns of genetic variation (e.g. population size, drift and dispersal) must also be considered when attempting to understand patterns of cultural variation (Neiman 1995; Lipo et al. 1997; Shennan 2000; Shennan and Wilkinson 2001; O'Brien and Lyman 2003b; Henrich 2004; Eerkens and Lipo 2005; Hamilton and Buchanan 2009; Lycett and Norton 2010). Again, it bears emphasising that this does not rely on an assumption that cultural and genetic transmission are identical in all aspects, most notably in regard to strict parent–offspring transmission in the case of genetics, contrasted with a diversity of potential transmission pathways in the case of culture. Rather, it is because both genetic transmission and cultural transmission are mechanisms of information transfer, demographic factors such as shifts in effective population size can have a strong statistical effect on resulting patterns of diversity in the transmitted phenomenon. (Note that the term "effective population size" here refers not necessarily to the total number of individuals in a given population, but to those individuals actually involved in the transmission process.)

As Mayr (1976: 26–28) has pointed out, "population thinking" – or the study of population variation – is yet another of those logical consequences that we owe directly to Darwin's theory of descent with modification and its three key pillars of inheritance, variation and sorting. As with phylogenetics, an implication of this is that principles and methods used to address these factors in genetic data may have utility when addressing analogous questions in cultural data (Cavalli-Sforza and Feldman 1981; Shennan 2001, 2006; Bentley et al. 2004, 2007; Richerson and Boyd 2005; Shennan and Bentley 2008; Mesoudi and Lycett 2009).

Looking at Dispersal, Drift and Selection in Acheulean Handaxes

While artefacts such as handaxes most certainly do not breed, the continued existence of handaxes, and to some extent parameters of handaxe variation through time, will be

influenced by factors affecting the *replicative success* (*sensu* Leonard and Jones 1987) of those ideas, skills, knowledge sets, etc. involved in their manufacture. The replicative success of such phenomena may be influenced by a variety of factors including stochastic processes (drift), natural selection and cultural (i.e. artificial) selection, the latter of which may or may not be intentionally directed by their manufacturers toward the patterns of variation or attributes concerned (for a more extended discussion of such issues in regard to handaxes see Lycett 2008).

Colleagues and I have previously used these principles to address questions surrounding Acheulean handaxes (Lycett and von Cramon-Taubadel 2008; Lycett 2008; Lycett and Norton 2010). In one of these studies (Lycett and von Cramon-Taubadel 2008), a formal population genetics model termed the "serial founder effect model" (sometimes also referred to as the "iterative founder effect model") was used to test the contention that handaxe manufacturing traditions were carried from Africa to wider parts of the Palaeolithic Old World via dispersal of Acheulean populations, as has long been hypothesised (e.g. Clark 1994; Carbonell et al. 1999; Goren-Inbar et al. 2000; Bar-Yosef and Belfer-Cohen 2001; Saragusti and Goren-Inbar 2001; Klein 2005). The serial founder effect model operates on the logic that as populations disperse over long distances, effective population sizes will become somewhat reduced with each episode of dispersal. In cases where the variation in a transmitted phenomenon is relatively neutral (i.e. not under strong selection), this will lead to a reduction of its within-group variance due to repeated instances of bottlenecking (i.e. reduction of effective population size and accompanying drift). Hence, in the case of genetic data, the model predicts a reduction of within-group genetic variance (σ^2) with increased geographic distance from a hypothesised point of origin (Fig. 9.4).

The serial founder effect model has recently been used with genetic data to test hypotheses regarding the dispersal of anatomically modern humans from Africa (Prugnolle et al. 2005; Ramachandran et al. 2005; Linz et al. 2007). These studies demonstrated a statistically significant fit between within-group genetic variance and increased geographic distance from Africa consistent with the predictions of the serial founder effect model. Subsequently, a fit to the model has also been supported using modern human craniometric data (Manica et al. 2007; von Cramon-Taubadel and Lycett 2008), demonstrating that phenotypic data can provide a proxy for parameters strictly transmitted and effected at a more proximate (i.e. genetic) level. In an intriguing application of the model (Linz et al. 2007), a fit has also been demonstrated in the case of human stomach bacteria (*Helicobacter pylori*), suggesting that the demographic consequences of human dispersal also had an effect on the population genetics of these transported populations of reproducing organisms, as humans carried them out of Africa in their stomachs.

Given the forgoing, an analogous situation in the case of handaxes would predict an inverse relationship between within-assemblage variance and increased geographic distance from East Africa, if the commonly assumed pattern of Acheulean dispersals from Africa is to be supported. Lycett and von Cramon-Taubadel (2008) tested this prediction using the ten handaxe assemblages listed earlier in Table 9.1. Mean within-assemblage variance was calculated using a series of 48 plan form
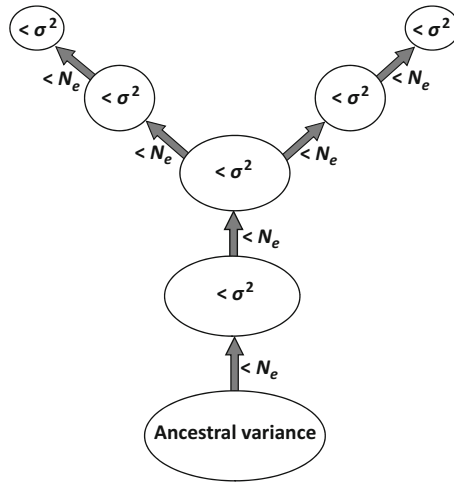
Fig. 9.4 Serial founder effect model. The model predicts a sequential reduction of within-group variance (σ^2) with increased distance from an hypothesized point of origin. This is due to repeated instances of a reduction in effective population size (N_e) along a dispersal route and subsequent drift (bottlenecking)

size-adjusted shape variables (Variables 1–48, Table 9.2). Two measures of geographic distance were used in their analyses: (1) "as-the-crow-flies" distances between East Africa (Olduvai Gorge, East Africa) and each site locality, and (2) the distances derived from a minimum spanning network linking site localities and two "waypoints" (Fig. 9.5). These latter distances were designed to approximate more closely the geographic distances covered by hominins in land-based scenarios of population dispersal(s) from Africa.

Lycett and von Cramon-Taubadel (2008) found statistically significant support for the serial founder effect model, with ~45–50% of within-assemblage handaxe shape variance explained by geographic distance from East Africa. Using a contrasting series of non-African start points, they found that no residual variation could be explained by a significant fit to the iterative founder effect model. Indeed, using non-African start points for the distance calculations did not merely produce non-significant results, but also generated R^2 values (range = 0.001–0.297) markedly different from those using the East-African origin (Lycett and von Cramon-Taubadel 2008: Table 9.3). Hence, using the non-African start points produced both weak and non-significant relationships (neither positive nor negative) between distance and within-assemblage variance patterns. These latter analyses are important since they suggest that the strength of relationship in their primary analysis is due to geographical parameters (i.e. African origin) rather than factors such as sampling bias. In the light of such analyses, it is interesting to reconsider the robustly supported phylogeographic pattern of Eurasian versus African assemblages found in the cladistic analyses presented earlier in this chapter. In combination, these analyses would appear to suggest that hominin dispersal patterns from Africa had an effect on
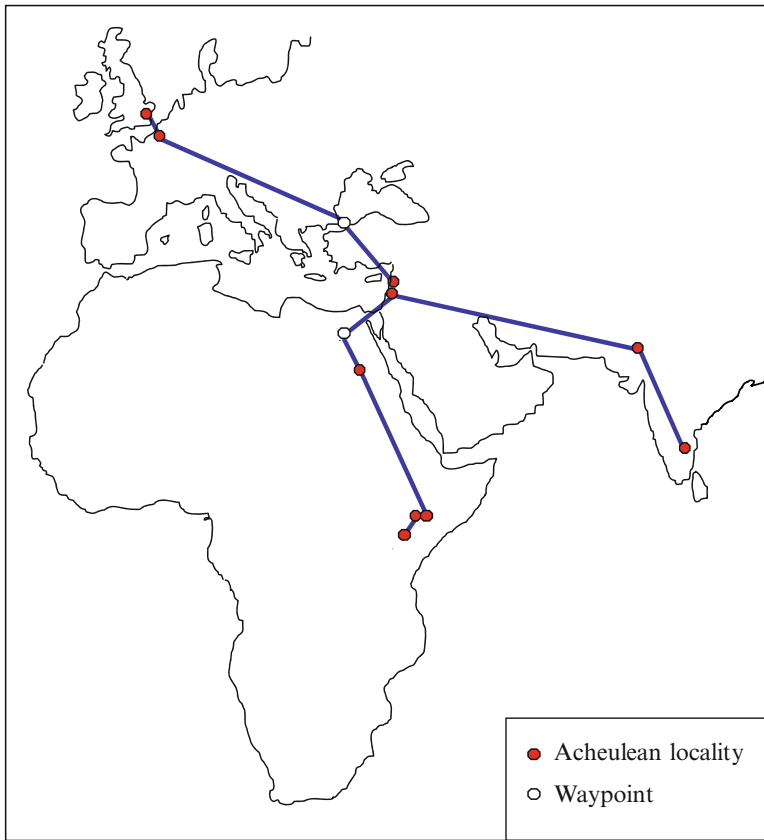
Fig. 9.5 Hypothetical dispersal route based on minimum-spanning network distances between Acheulean localities used in the analyses and two additional waypoints (Cairo, Egypt and Istanbul, Turkey). The waypoints were chosen in order to "anchor" the hypothesised dispersal route to a land-based pattern of dispersal

variation in certain handaxe parameters and, in turn, this led to a set of cladistic relationships that fit a phylogeographic pattern at broad levels.

More recently I extended these analyses to determine whether adding the property of handaxe symmetry to the data set either increased or decreased the fit to the serial founder effect model (Lycett 2008). As noted by Lycett and von Cramon-Taubadel (2008), their results imply that a high proportion of handaxe (plan-form) shape varies according to the principles of neutral drift, rather than being under strong directional selection. Again, drawing on principles applied in population genetics, it has recently been recognised that neutral (i.e. random) drift can provide a powerful null hypothesis for understanding patterns of artefactual and cultural change through time (see e.g. Bentley et al. 2004, 2007; Shennan 2006; Shennan and Bentley 2008; Mesoudi and Lycett 2009). In essence, if the null model of neutrality cannot be rejected, there is no requirement to invoke more complex selective

scenarios to account for particular patterns of artefactual variation and change. Thus, the results of Lycett and von Cramon-Taubadel's (2008) initial analyses provide a baseline of comparison against which other aspects of handaxe variability might usefully be assessed for their relative goodness-of-fit to a neutral model. Since it has often been suggested that handaxe symmetry may have been under selection for aesthetic, functional and/or adaptive reasons (e.g. Schick and Toth 1993; Kohn and Mithen 1999; Le Tensorer 2006), it was predicted that adding symmetry to the data set would decrease or possibly even destroy the fit to a serial founder effect model (Lycett 2008). Conversely, if handaxe symmetry variation was neutral, an equal or increased fit to the model would be expected. Such analyses demonstrated that adding the single variable of symmetry to the data set did indeed allow rejection of a null hypothesis of neutral variation, providing strong evidence that the property of symmetry variation in Acheulean handaxe was under strong influences of selection (Lycett 2008). Taken together, these nested analyses imply that different outline forms or "types" of handaxe (e.g. "cordiform," "pointed," "ovate," etc.) vary in a neutral manner, whereas regardless of which particular means (i.e. shape) a broadly symmetrical biface is achieved, the property of symmetry varies in a non-neutral manner and thus can be seen as subject to stronger selective forces. A neutral pattern of variation for handaxe outline shape would also be consistent with McPherron's (1999, 2003) assertion that a prominent source of variation in outline form is reduction intensity, although the neutral pattern is not mutually exclusive to additional sources of variation.

Using Population Genetic Principles to Determine the most Probable Route of Acheulean Dispersal

Here, I am going to apply these same general population genetic principles to determine whether one particular route of Acheulean dispersal from Africa is more probable than another. As noted earlier, Lycett and von Cramon-Taubadel (2008) found the strongest fit to the serial founder effect model when using a minimum-spanning network that linked Acheulean assemblage localities and two "waypoints" (Fig. 9.5). These two waypoints (Cairo, Egypt and Istanbul, Turkey) were chosen to deliberately "anchor" the hypothesised dispersal route to a land-based pattern of dispersal. However, alternative routes for Acheulean dispersal(s) have been hypothesised. In particular a "southern" route across the Arabian Peninsula has been suggested for populations dispersing into the Indian subcontinent (e.g. Whalen et al. 1989; Bar-Yosef and Belfer-Cohen 2001; Petraglia 2003; Derricourt 2005).

In order to assess the relative goodness-of-fit to this alternative dispersal route, a new minimum spanning network was constructed. This network linked the ten Acheulean localities and waypoints used by Lycett and von Cramon-Taubadel (2008), but also included two additional waypoints that constrained the dispersal of Acheulean hominins into southern Asia via a route across the Arabian Peninsula. The two waypoints chosen were Perim Island, Yemen (12.7N, 43.4E) and Dubai, United Arab

Emirates (25.3N, 55.3E). As shown in Fig. 9.6, this constrained the hypothesized dispersal pathway to a southern route, crossing what is currently the Bab al Mandab Strait between Djibouti and Yemen, and the narrowest point of the Arabian Gulf (i.e. the Strait of Hormuz). For purposes of direct comparison, the ten Acheulean artefact samples employed by Lycett and von Cramon-Taubadel (2008) were used here (Table 9.1), from which 48 plan-form variables were extracted (Variables 1–48, Table 9.2) and size-adjusted via the geometric mean method mentioned previously. Geographic distances were calculated in kilometres using great circle distances based on the haversine (see Lycett 2008). As a basic prediction it can be stated that if the southern dispersal route (Fig. 9.6) is more probable, then it should exhibit a higher relative goodness-of-fit to the serial founder effect model compared with the northern route going solely through the Sinai Peninsula (Fig. 9.5). This prediction was evaluated using least-squares regression, whereby the independent variable of mean within-assemblage variance was regressed on the dependent variable of geographic distance from East Africa (Olduvai Gorge). Hence, relative goodness-of-fit may be assessed
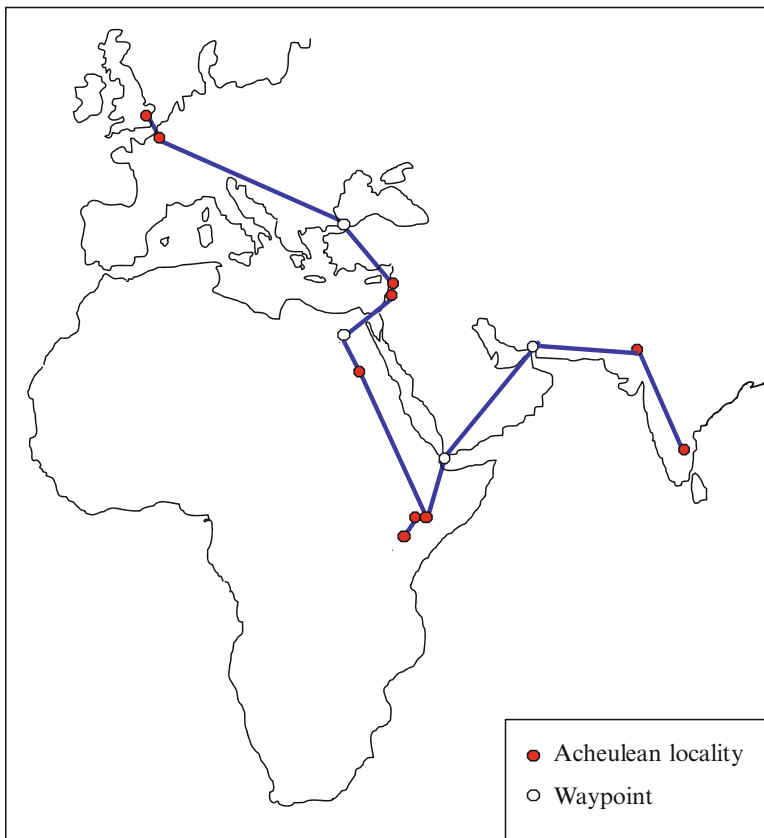

Fig. 9.6 Hypothesized dispersal route involving a "southern dispersal" of Acheulean populations across the Arabian Peninsula toward the Indian Subcontinent

for each route by direct comparison of the resultant coefficient of determination (R^2) values.

In the case of the northern (Sinai Peninsula) dispersal route, regression analyses produced an R^2 of 0.50 ($p = 0.023$). Conversely, the southern dispersal route produced an R^2 value of only 0.445 ($p = 0.035$). Hence, when using the northern dispersal route as much as 50% of within assemblage variance could be accounted for by the serial founder effect model, whereas in the case of the southern dispersal route less than 45% of within assemblage variance was explained by the model. Indeed, the goodness-of-fit in the case of the southern dispersal route was actually less than that obtained by Lycett and von Cramon-Taubadel (2008) when using crude "as-the-crow-flies" distances ($R^2 = 0.452$, $p = 0.033$), which we know to be improbable as routes for hominin dispersal.

The results of this comparative analysis thus appear to indicate that the southern route for Acheulean dispersals was less probable than that of a northern dispersal route via the Sinai Peninsula. Interestingly, Derricourt (2005) has previously suggested that the most parsimonious scenario for Plio-Pleistocene hominin dispersals is one that does not require an ability to make water crossings. Current evidence suggests that well before the appearance of Acheulean technologies in Africa, land-bridges across the Bab al Mandab Strait would have ceased to exist (Fernandes et al. 2006), thus requiring the crossing of a waterway by Acheulean hominins if used as a dispersal route. The analyses undertaken here support the view of Derricourt (2005) that in the absence of strong evidence to the contrary, dispersal routes not involving the crossing of waterways should be treated as a null hypothesis.

Discussion

In this paper I have attempted to show how principles and methodologies derived from biology (descent with modification, population thinking, phylogenetics and population genetic models) can profitably be employed in lithic studies, particularly in the case of Lower and Middle Palaeolithic data where, currently, such theoretical and methodological approaches appear to be less frequently applied. A series of phylogenetic analyses applied to a database of Acheulean handaxes revealed a phylogeographic pattern. It was also shown via bootstrap and randomization procedures that this relationship was robustly supported, and that the handaxe data fit a phylogenetic model equally as well as a comparative set of later human cultural and biological data sets. It was also demonstrated via statistical procedures that raw material was not a dominant factor in producing the relationships indicated by the cladogram. Population genetic approaches confirmed that the source of this basic phylogeographic pattern appears to have been mediated by patterns of hominin dispersal. These latter analyses also showed how formal models drawn from population genetics can provide explicit and testable predictions for lithic artefactual data sets, including what might be expected under alternative potential routes of hominin dispersal. Of course, there are doubtless ways in which the resolution and

quality of the empirical data employed here might be bettered. Indeed, future studies might refine, improve upon, or even refute some of the results and conclusions presented here: such is the nature of scientific progress. However, these scopes for improvement lie more in the realm of empirical parameters rather than with the general theoretical and methodological framework advocated.

One potential area that might provide particular scope for expansion in future studies is in developing a greater understanding between artefact life history and technological evolution. As Shott notes elsewhere in this volume, the breakage of stone is an absolute prerequisite to the manufacture of any knapped lithic artefact. As such, a stone tool's "life-history"[2] extends from the first flake removed from a core through to any potential resharpening and usewear that occurs prior to final discard. As noted here and elsewhere (e.g. Buchanan and Collard 2007) those advocating the application of phylogenetic and population genetic models to lithic data have not been entirely ignorant of such matters, employing sophisticated methods of size-adjustment to remove the confounding effect of size differences that might occur through reduction and resharpening, especially toward the end of an artefact's life history (Lycett et al. 2006; see also Buchanan and Collard, this volume). However, there may be a possibility to more actively integrate artefact reduction sequences (ontogeny) and patterns of technological evolution (see also, Riede 2006), in a similar manner to the way in which evolution and development (so-called "Evo–Devo") studies in biology have embraced both individual life histories and an understanding of long-term evolutionary trajectories (e.g. Raff 2000; Telford and Budd 2003).

Elsewhere, I have shown that the long-held view that Mode 1 style cores became elaborated into bifaces, and that ultimately bifaces are close technological relatives of Levallois cores, can be demonstrated through the use of phylogenetic methods (Lycett 2007b). As such, there is some "recapitulation" of the ontogenetic development of a Levallois core in the phylogenetic relationships between Mode 1, Mode 2, and Mode 3 style artefacts. I mention this here not because the ontogeny of lithic artefacts will always recapitulate their phylogeny any more so than in the case of biology, where it has been recognised that this will occur in some cases but not others (Gould 1977). (Although it is in itself a valuable exercise to document where this does and does not occur.) Rather, it is because the "Evo–Devo" approach has shown that major episodes of evolutionary change are frequently brought about by manipulation of specific developmental stages (Raff 2000; Arthur 2004). Over recent years, there has been much debate as to whether the study of reduction sequences and the *chaîne opératoire* of lithic artefacts are of strong analytical use or more descriptive and typological procedures (e.g. Shott 2003; Bar-Yosef and Van Peer 2009). Combining insights from experiment, refitting, reduction, morphometrics and phylogeny might provide equivalent insights as to how the manipulation of specific ontogenetic stages in reduction led to changes in lithic technological evolution.

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[2] In the case of stone tool "life history," a useful distinction may be made between "ontogeny" (the reduction process leading up to the point of first usage) and "senility" (factors such as resharpening and use wear that take place following first use).

Conclusion

The late Glynn Isaac (1977: 207) once commented that:

> Most Palaeolithic archaeologists in general, myself included, tend to believe that the assemblages of humanly flaked stones that we recover in quantities from sites such as Olorgesailie preserve a great deal of valuable information about the craft traditions, the cultural affinities, and the economic life of the hominids who made them ... It sometimes appears that all of us treat stone artefacts as infinitely complex repositories of palaeocultural information and assume that it is only the imperfections of our present analytical systems that prevent us from decoding them. But is this really so?

Analyses such as those presented here might go some way to reaffirming that this indeed *is* so. Yet, Isaac's remark that it might be "the imperfections of our present analytical systems that prevent us from decoding" such cultural information is particularly interesting in regard to the issues discussed in this paper, and more widely in the present volume. Some of the data accumulated by archaeologists and the way data accumulation is approached may not currently be in a format that is most suitable for addressing questions of this nature. Similar concerns were, of course, also stated by David Clarke (1968) who, as noted in the introduction of this volume, urged archaeologists to find more detailed means of extracting information from their available data. Nevertheless, recent developments (e.g. Tostevin 2003; Buchanan 2006; Clarkson et al. 2006; Lycett et al. 2006; as well as several papers in this volume) suggest that large and detailed comparative multivariate data sets can be obtained. Armed with the ontological framework provided by cultural transmission theory, its associated battery of analytical techniques, and by the rich data that such new methodological developments provide, we may be on the brink of some exciting discoveries regarding the evolution of Palaeolithic technologies.

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