

On Human Phylogeny and Linguistic History: Reply to Comments

RICHARD M. BATEMAN, IVES GODDARD,
RICHARD T. O'GRADY, V. A. FUNK, RICH MOOI,
W. JOHN KRESS, AND PETER F. CANNELL
*National Museum of Natural History, Smithsonian
Institution, Washington, D.C. 20560, U.S.A. 2 XI 89*

Our contribution to this anthropological debate (CA 31:1-13) was prompted by our perception of Cavalli-Sforza, Piazza, Menozzi, and Mountain's (1988) widely reviewed paper as both biologically and linguistically naive and by our belief that explicit, species-independent methods of reconstructing evolutionary histories should replace more common but less rigorous (and often authoritatively imposed) "special-purpose" studies. We are therefore encouraged by the qualified support offered by all commentators outside the aegis of the Stanford group, and we hope that the interdisciplinary nature of the issues discussed will attract comment from scientists beyond the realms of anthropology.²

Delimitation and characterisation of genetic entities. We plead guilty to Cavalli-Sforza et al.'s (CA 31:16) anthropocentric charge that we are "biologists . . . unfamiliar with the data, methods, and models of human population genetics." We operate on the assumption that *Homo sapiens* is a biological species and that there are no methods or models peculiar to human population genetics. Methods and models of eukaryotic allogamous population genetics are applied with equal validity to humans and fruit flies.

We are especially astonished to learn that the concepts of genodeme (a population possessing genetic cohesion irrespective of cause) and gamodeme (a population possessing genetic cohesion caused by free interbreeding of its constituent individuals) "are impractical to use with

human populations" and that "the definition of a Mendelian population, the evidence of mating patterns, and the nearly continuous nature of spatial variation . . . make it impossible to establish nonarbitrary boundaries" delimiting genodemes. If this assertion is correct, the "statistical and genetic" populations delimited by Cavalli-Sforza et al. are, by definition, arbitrary (i.e., merely "statistical"). Even the incompatibility problems caused by the heterogeneous, gap-ridden nature of Cavalli-Sforza et al.'s data-base of ca. 3,000 populations (which largely reflect its secondary derivation from published literature) are overshadowed if the "populations" themselves are truly arbitrary. What significance can then be attributed to the 42 more inclusive populations created by Cavalli-Sforza et al. as the pivotal entities of their "phylogenetic" analysis?

We believe that Cavalli-Sforza et al.'s dislike of "taxometric classifications" has undermined their research programme. The delimitation of genetic entities is crucial to subsequent phylogenetic interpretation; if the entities are arbitrary, so are the interpretations. As noted by Blount (p. 15), many systematists are experienced at delimiting biologically meaningful intraspecific taxa as well as species. They generate entities that are nonarbitrary and therefore phylogenetically useful.³

Following delimitation of entities, several studies have proceeded to investigate the relationship between genetic variables and geographical distribution and/or linguistic affinities. Here there is an important distinction between studies in which correlations were apparently calculated on the basis of primary data-sets (e.g., Sokal 1988) and those in which aggradation of data-sets prior to final analysis was practiced (e.g., Cavalli-Sforza et al. 1988). We do not, as Cavalli-Sforza et al. claim, deny the "importance [of] the [positive] correlation between geographic and genetic distance"; we merely doubt the value of such correlations when they reflect similarities between genetic entities that were created by aggradation according to the extrinsic property of geographic proximity rather than the intrinsic genetic properties ostensibly under scrutiny (see Bateman and Denholm 1989b). Similar problems of tautology complicate investigation of the relationship between geographical distribution and languages.

Sampling relationships between extrinsic and intrinsic properties of populations are inevitable; demes

1. Permission to reprint items in this section may be obtained only from their authors.

2. We refer readers unfamiliar with phylogenetic terminology to reviews by Wiley (1981), Farris (1983), and Wiley et al. (n.d.). This reply omits two important issues that should be addressed by better-qualified commentators: the validity of Cavalli-Sforza et al.'s (1988) application of the bootstrap test (raised by Oswalt and Nunez) and the problems surrounding the concepts of plesiomorphy and apomorphy at the level of gene-frequency data (raised by Cavalli-Sforza et al. and Mizoguchi). Also, the more philosophical penultimate section of our paper is not pursued, since it has so far failed to elicit serious criticisms or notable additions.

3. Whether the intraspecific classes are then used to construct formal, Linnean "taxometric classifications" is scientifically irrelevant, though it appears highly relevant to the politically motivated suppression of the "race concept" in anthropology (see commentaries by Cavalli-Sforza et al. and Jacobs).

sampled by biologists for intrinsic properties such as gene frequencies are, in practice, largely delimited by extrinsic properties, usually a combination of restricted spatial distribution and ecological tolerances (i.e., they are ecotopodemes). In the "demographic" systematic procedure advocated by Bateman and Denholm (1989a, b), further aggradation of the ecotopodemes into intra-specific taxa and (eventually) species is achieved using data that reflect their intrinsic properties. Only then should the extrinsic properties of these intrinsically delimited groups be reconsidered and re-evaluated. Cavalli-Sforza et al. reject this "positive-feedback" method in favour of aggradation using the very properties (geographical distribution and/or language) that they use as ostensibly independent measures of the success of their genetic phylogeny. As Oswalt shrewdly notes (p. 21), the degree of coincidence between these criteria partly depends on expectations; however, it also depends on the objectivity of the data collection and analysis. In the absence of feedback and of repeated analysis at different levels in the demographic hierarchy, the procedure employed by Cavalli-Sforza et al. is wholly tautological.

Cavalli-Sforza et al. also appear perplexed by the nature and causes of genetic variation within species. The bootstrap test does indeed "estimate the extent of statistical variation due to gene sampling," but it does not distinguish between the effects of the many potential causes of such variation. That Cavalli-Sforza et al. recognise the existence of at least some of these causes and of the dangers of comparing entities from different levels in the demographic hierarchy is evident from their commentary but not from their methodology or the text of their 1988 study. Recent methodological advances in population statistics (briefly reviewed by Mizoguchi [p. 20]) cannot rescue a study pursued within a conceptually inadequate framework.

Phenetic and cladistic approaches to phylogenetic inference. We agree with Cavalli-Sforza et al. that "concepts and methods for the study of interspecific differences are not necessarily suitable for that of intraspecific ones." However, three issues concerning the historical relationships of the entities have been confused. The first is raised by Armstrong [pp. 13–14], Bayard [p. 14], and Oswalt [pp. 21–22]: Is a tree the most appropriate representation of the historical relationships of intraspecific entities such as Cavalli-Sforza et al.'s "populations"? The second has been a major focus of our disagreement with Cavalli-Sforza et al.: If a tree is most appropriate, should it be phenetic or cladistic, rooted or unrooted? And thirdly, how should the fit of the tree to the original data be assessed?

Cavalli-Sforza et al. have answered the first question to their own satisfaction without seriously addressing it: "the two evolutions [genetic and linguistic] follow in principle the same history, namely, sequence[s] of fissions." If so, a tree is appropriate. Others, including some commentators (Armstrong, Bayard, Oswalt) and some of us, are less confident, given the clinal nature of much of the intraspecific variation under scrutiny (e.g., Wolpoff, Wu, and Thorne 1984).

Both questions are further investigated using figure 1, which illustrates three different historical patterns exhibited by four hypothetical human populations and three different methods of representing these patterns as trees.⁴

Figures 1a and 1b are identical ordinations depicting spheres of variation (circles) and centroids (spots) for four distinct extant populations (1–4), one of which apparently shows incipient divergence (4a, b). Both plots lack a time axis, and the populations are therefore linked by unrooted trees. Figure 1a shows a phenetic minimum-spanning tree (Gower and Ross 1969); branches represent maximum overall similarity, all nodes are population centroids, and the tree need not fork at every non-terminal node. Figure 1b shows an unrooted cladogram; branches represent specific character transitions, only terminal nodes are population centroids, and branching occurs at every non-terminal node. In both cases, the absence of a root obscures deep historical relationships.

The addition of a time axis to figures 1c, 1e, and 1f reveals three contrasting phylogenies. Figure 1c shows repeated dichotomous divergence of lineages 1–4 from the single ancestral population I. Thorough characterisation of the four extant populations should allow accurate reconstruction of the order of divergence events and thereby of the phylogeny as a rooted tree (fig. 1d); this could have been generated as a cladogram or, if evolutionary rates remained constant, as a phenogram. Comparison of figures 1c and 1e shows that identical arrays of extant populations could reflect radically different phylogenies. In figure 1e, the number of populations has remained constant; ancestral populations I–IV generate extant populations 1–4 via repeated anastomoses and occasional extinctions, and the partial separation of populations 4a and 4b in figure 1c is perceived as partial fusion in figure 1e. Dichotomous phenograms or cladograms generated from comparison of the extant populations in figure 1e would not accurately reflect their complex historical relationships.

In the third phylogeny (fig. 1f), the populations were never isolated and therefore exhibit overlap of intrinsic properties through time. This hinders recognition of lineages and may prevent their resolution into trees (though if biologically meaningful populations *could* be discerned, their historical relationships could theoretically be reconstructed by tracing their centroids through time).⁵

We should emphasise that only the first of the three phylogenies is readily transformed into a realistic tree and that the time axis crucial for distinguishing between the radically different phylogenies in figures 1c and 1e is wholly inferential unless fossil data are available and can be compared with similar data for extant descen-

4. Although intended to depict intrinsic properties, figures 1a–f could equally well depict an extrinsic property such as geographical distribution.

5. Any phylogenetic tree effectively uses only the centroids, ignoring the surrounding "cylinders of variation."

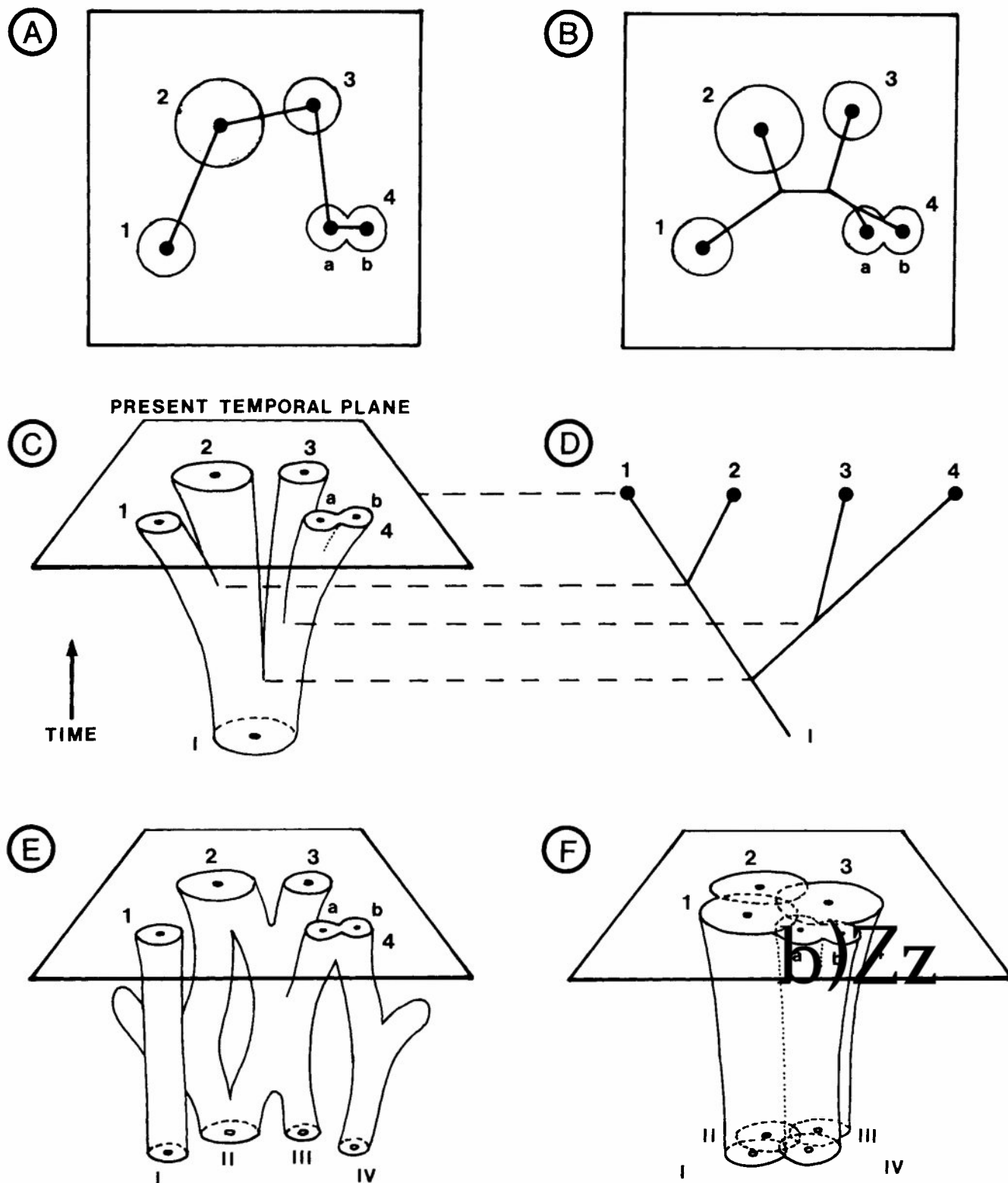


FIG. 1. Different historical patterns exhibited by hypothetical human populations (Arabic numerals, extant populations; Roman numerals, earlier, historical populations). Figures a–e illustrate identical present-day relationships of populations 1–4. Atemporal, two-dimensional plots (a, b) are multivariate ordinations of intrinsic properties such as morphological characters or gene frequencies. Spheres of variation for each population (circles) enclose centroids (spots). An unrooted phenetic minimum-spanning tree is superimposed on a and an unrooted cladistic tree on b. A historical pattern of repeated divergences and no convergences (c) allows translation of the population centroids into a rooted tree (d) that accurately represents the temporal sequence of branching. Application of cladistic or phenetic algorithms to an anastomosing phylogeny (e) would force the anastomoses into falsely dichotomous trees superficially resembling d. In the third phylogeny (f), populations exhibit continuous overlap of intrinsic properties through time, obscuring historical relationships.

dants (cf. Wolpoff, Wu, and Thorne 1984). This raises the question of which of the three types of phylogeny most accurately reflects the history of human genodemes (genetically distinct populations).

We suspect that figure 1c most accurately represents the early history of *H. sapiens*, as groups progressively dispersed from the area of origin. However, once a region of the globe had been colonised by several groups, the anastomosing phylogeny of figure 1e is probably more realistic; the longer coexisting genodemes have been established, the more complex (and less treelike) are their historical relationships.⁶ This scenario underlies two of the most important points in our paper. First, it was during the most recent, least treelike portion of the history of man that languages evolved. Secondly, relatively recently colonised regions of the globe are more likely to exhibit divergences such as those depicted in figure 1c and yield realistic trees, but these divergences will be masked by "noise" if subsumed into overly ambitious global studies.

We will continue the discussion by assuming that meaningful trees *can* be obtained and reconsider the question of which type of tree is most suitable for phylogenetic reconstruction. Cavalli-Sforza et al. have placed us in the unusual position of having to review both phenetic analysis (which they performed) and cladistic analysis (which they apparently thought they were performing). We agree with Sokal and Sneath (1963) that phenograms (trees reflecting overall, phenetic similarity) are primarily stable and potentially objective classifications of organisms rather than estimates of evolutionary relationships (e.g., Wiley 1981, Farris 1983, Kluge 1989). In contrast, cladistic (phylogenetic) analysis was developed by Hennig (1966) expressly to reconstruct evolutionary relationships. Taxa are grouped into assemblages consisting of all descendants of a common ancestor. The tree-building criteria reject overall similarity, filter out similarity from primitive traits (plesiomorphies), and group only by similarity from derived traits (apomorphies); these terms describe the degree of derivation of a character in relation to its level of inclusiveness on a cladogram (Hennig 1966, Wiley 1981, Farris 1983).⁷ For example, passing through increasingly inclusive levels of the vertebrate classification, mammary glands are a symplesiomorphy (shared primitive trait) of the Order Rodentia, a synapomorphy (shared derived trait) of the Class Mammalia, and an autapomorphy (unshared derived trait) of the Subphylum Vertebrata.

Given these well-established principles of phylogenetic reconstruction (e.g., Futuyma 1986), we are be-

lived by Cavalli-Sforza et al.'s (1989:1128) equation of phenetic similarity with phenotypic similarity (physical expression of the genotype) and by their subsequent argument (p. 17) that their phenetically constructed tree (phenogram) gives a "cladistic answer" because it depicts sequences of forking lineages whose branch lengths are regarded as proportional to time elapsed since separation. Phenograms do not depict the sequence of lineage divergence. In contrast, cladograms have dimensionless branches that only indicate nested groups of descent; they are not proportional to time or to degree of anagenetic (non-branching) microevolution. The two types of tree are not interchangeable, despite their superficially similar repeatedly dichotomous branching. Regrettably, Cavalli-Sforza et al. have used a phenetic tree-building method but then discarded the corollaries of that method, imposing on the resulting tree an ad hoc evolutionary interpretation that is inconsistent with both phenetic and cladistic principles.

Cavalli-Sforza et al. continue to sit on the fence over the contentious issue of constancy of evolutionary rates; they "distrust the uncritical assumption of constant evolutionary rates" but claim that "for the major fissions [between human populations], genetic distance is proportional to the time [elapsed] since separation" (p. 17). In other words, they reject the constant-rate theory that their empirical data ostensibly support. Either the premise is correct or it is not; either the phenogram should be partitioned strictly according to genetic distance or it should not. Abandoning strict partitioning "for expository purposes" defeats the main advantage of a phenogram: the comparative objectivity of its clusters (Sneath and Sokal 1973).

Even if evolutionary rates *were* constant, this would not allow reconciliation of genetic and linguistic histories unless genetic and linguistic divergence commenced *simultaneously* (i.e., at the same basal node for all human "populations"). If genetic divergence predated linguistic divergence, languages are, by definition, polyphyletic (CA 31:10, fig. 3). There cannot be a single global linguistic phylogeny, and congruence with human phylogeny cannot be fully established; each separately evolved lineage must be considered in isolation. This is one of the key factors underlying our recommendation that regional studies be used to develop a general methodology based on sound phylogenetic principles. Attempts to reconcile genetic and linguistic history on a global scale require monophyly of human language, an extremely contentious hypothesis that cannot be satisfactorily tested using present data.

Congruence of the genetic tree and linguistic phyla. Despite our discussions of the consistency index (see, in addition to our CA paper, O'Grady et al. 1989), Cavalli-Sforza et al. continue to misapprehend its application. By measuring the historical persistence of characters on a tree, the consistency index tests empirical support of groupings. It is calculated as the ratio of the minimum number of necessary hypotheses of character evolution to the number of hypothesised character transitions required by their arrangement on a particular tree (fixed for

6. Perception of phylogenetic relationships, especially when employing phenetic methods, is influenced by the nature and number of attributes measured. For example, studies of overall morphology or genotype would probably reveal sufficient overlap of genodemes to generate the poorly resolved type of phylogeny shown in figure 1f. A more specific study of multiple alleles for an adaptively significant locus might reveal a better-resolved phylogeny resembling those shown in figures 1c or 1e.

7. Hennig (1966) coined the terms plesiomorphy ("near the form") and apomorphy ("away from the form") to avoid the anthropocentrism of "primitive" and "advanced" respectively.

a given data-matrix; the presence of every character state must be explained at least once). When the character distribution on a tree shows multiple origins and/or single or multiple losses (termed homoplasy), the denominator exceeds the numerator. When the distribution of all character states can be attributed to single origins with no subsequent losses, the denominator and the numerator are equal and the consistency index indicates a perfect (100%) fit, regardless of the number of taxa and characters involved.

Cavalli-Sforza et al. cite Archie's (1989) unpublished study, which assesses cladograms generated by 28 real data-matrices and shows that larger cladograms tend to produce lower consistency indices.⁸ This is not surprising, as larger data-matrices incur increased probability of encountering homoplasy. Ongoing research into the negative correlation of the minimum possible consistency index value (it cannot reach zero) with data-matrix size will provide a null hypothesis for testing cladistic analyses (e.g., Sanderson and Donoghue 1989). Empirical reasons that a perfect consistency index cannot be achieved differ between data-matrices, confounding attempts to establish additional statistical limits on consistency index values.

Our calculation of a consistency index of 48% for Cavalli-Sforza et al.'s (1988) study was not kept artificially low by "choosing" to omit autapomorphic linguistic phyla. There is no choice: cladistic procedure dictates that non-homoplasious autapomorphic characters (in this instance, a language spoken only by one population) must be omitted from consistency-index calculation because their single occurrence cannot conflict with any hypothesis of relationships and would therefore incorrectly inflate the value (e.g., Kluge 1989:9). As a hypothetical example, a consistency index of 4/9 (44%) is artificially inflated to 7/12 (58%) if three autapomorphies are included, even though their inclusion does not increase the empirical support for any groupings on the tree. In stating that the consistency index for their tree can be increased to 56% by lowering the level of analysis to tribe-language associations (p. 17) Cavalli-Sforza et al. inadvertently demonstrate the cladistic principle that apomorphy is a relative concept; an autapomorphy for a taxon (e.g., a phylum) can be a synapomorphy of less inclusive groups within that taxon (e.g., families). Thus, the new value of 56% may be valid at the new, lower level of analysis, but this has little bearing on the higher-level analysis of population-linguistic-phylum associations presented by Cavalli-Sforza et al. (1988). Moreover, lowering the level of analysis increases the probability of encountering contradictory data and therefore requires re-assessment and re-analysis. If Cavalli-Sforza et al. have simply summed the tribes contained within each population prior to comparison with the linguistic groupings, then the test and the resulting consistency index of 56% are

invalid because they are erroneously including non-homoplasious autapomorphies.

Similarly, our decision to treat each language-replacement event as two steps was not a device to minimise the consistency index; it is a standard requirement of the method. As noted by Cavalli-Sforza et al. (1988), the 16 linguistic phyla are independent lineages; this is clear from the polytomous nature of the language "tree" in their figure 1. Only if one language changes into another along a single evolutionary lineage should the transition be treated as a single step.

We emphasise that we are not arguing that Cavalli-Sforza et al.'s (1988) study is a failure because their consistency index is only 48%; rather, we believe that they have demonstrated that over half of their population-language associations cannot be attributed to coevolution of human genodemes and languages.

Linguistic analysis. Our main objectives in discussing languages were (1) to emphasise that the classification of linguistic phyla⁹ used by Cavalli-Sforza et al. is controversial¹⁰ and (2) to compare and contrast the historical-linguistic methodology with those of evolutionary biologists.

Greenberg implies that we fail to explain how to distinguish historical from ahistorical resemblances (pp. 18–19), yet we state that the former are identified using the well-established methodology of historical linguistics to construct hypothetical models of linguistic history. This contrasts sharply with Greenberg's massive superficial comparisons of words and grammatical elements. Many critics have argued that Greenberg's method of "multilateral comparison" yields empirically incorrect word equations and note that he ignores the elevated error rates that undermine his deep-level classifications.

We accept that Greenberg (1987:24) correctly classifies the languages of Europe using valid data (Indo-European and Finno-Ugric languages are grouped and sub-grouped correctly and separated from each other and from Basque), but we regard these relationships and groupings as unusually obvious. European languages have been diverging for only a few thousand years, insufficient time to mask their similarities but sufficient to allow the development of clear-cut differences among their sub-branches. The key question in assessing the validity of the linguistic classification used by Cavalli-Sforza et al. is whether "multilateral comparison" can correctly recover and rank language relationships at time depths much greater than the ca. 6,000 years of Indo-European using inferior data. Greenberg's ability to present sets of linguistic forms that appear "similar in sound and mean-

9. Our use of the linguistic terms "family" and "phylum" followed that of Cavalli-Sforza et al. (1988), who in turn followed Ruhlen (1987a). Although these terms are poorly defined, some form of hierarchy of linguistic entities is useful, for example, to distinguish the status of Indo-European and Amerind.

10. We are unimpressed by Cavalli-Sforza et al.'s (p. 18) argument that conflict among linguistic classifications is unimportant because "fully congruent hierarchies will eventually arise." It is their current analysis that we are assessing, not their future work.

8. This trend is not especially strong; our own research often generates small cladograms with low consistency indices and large cladograms with high consistency indices.

ing" (Ruhlen 1987b:6) merely demonstrates that his method reveals many sets of ostensibly similar words. The basic classificatory principle of Greenberg's method is delimiting language groups so that each possesses more internal similarities than it shares with other groups at the same hierarchical level. Greenberg generally fails to demonstrate that his deep-level groupings have this property.¹¹

Greenberg apparently introduces a new evaluatory principle into his methodology when he implies that he would be saved from connecting the second-person prefixes Cheyenne *ne-* and Sioux *ni-* because his methods would identify Cheyenne *ne-* as "deviant" within Algonquian (p. 19). Although the accuracy of an inspectional method of classification would be greatly improved by the use of a reliable procedure for eliminating "deviant" resemblances, Greenberg does not provide an operational definition of this concept. His American Indian word equations show that he does not infer disqualifying deviance from appearance in only one language of a family, since families are often connected on the basis of a form appearing in a single language. For example, in four of his first nine equations between Algonquian and other "Almosan-Keresiouan" languages, Algonquian is included on the basis of a single unanalysed form in a single language (Greenberg 1987:165-66). Such isolated resemblances provide the crucial links between families (and more inclusive groupings) that determine the deeper levels of his classification. Our example was intended to show that phenetic comparison of linguistic elements that are "similar in sound and meaning" is insufficient to identify historically related elements or to eliminate ahistorical resemblances.

Greenberg also uses our reference to "Na-Dene *s.l.*" to restate his belief in the existence of Na-Dene as originally proposed by Edward Sapir: Athabaskan (plus the later rediscovered Eyak), Tlingit, and Haida. The classification of Haida is especially controversial, being included in Na-Dene by some authorities (Na-Dene *s.l.*) and excluded by others (Na-Dene *s.s.*). Given the ambiguous nature of this and many other phyla (see e.g., commentary by Callaghan [p. 16]), qualification is necessary to convey a particular usage.

Greenberg reiterates his earlier claim (1987:321-30) that the historical-linguistic methods used to question the inclusion of Haida in Na-Dene would falsely refute the Indo-European membership of Albanian, Armenian, and Celtic, ignoring the fact that the same historical-linguistic methods were used to establish the Indo-European affinity of these languages. What Greenberg actually demonstrates is that data assembled by multi-lateral comparison provide an inadequate basis for the application of historical-linguistic methods.

11. For example, Greenberg's (1987:63-180) ability to present sets of linguistic forms ostensibly similar in sound and meaning for each of the proposed deep-level sub-groups of "Amerind" does not provide direct support for his classification; he does not attempt to validate his own criteria by demonstrating that each sub-group exhibits more internal similarities than it shares with the other ten.

Conclusions. We share Armstrong's disappointment concerning the reluctance of Cavalli-Sforza et al. to publish details of the nature and pre-analytical manipulation of their data-base, given that explicit reporting is the foundation of science as a progressive, collaborative venture. Cavalli-Sforza et al. and we have each made three contributions to this debate, yet we still have only a vague impression of their methods. We recognise the complexity and difficulty of the problems that Cavalli-Sforza et al. are addressing and accept the arguments advanced by some commentators that there are several potential approaches to their solution, each of us would probably adopt a somewhat different strategy. But we are united in our opinions that the origin, configuration, and manipulation (including imperfections) of any data-base should be clearly stated and that the conceptual framework in which a project was formulated and data interpreted should be unambiguously explained in accordance with conventional scientific practice.

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On Hunter-Gatherers and Their Neighbors in Prehistoric India: Contact and Pathology

JOHN R. LUKACS

*Department of Anthropology, University of Oregon,
Eugene, Ore. 97403, U.S.A. 13 IX 89*

The recent article by Headland and Reid (CA 30:43-66) provides a timely reminder of the inappropriateness of viewing all hunter-gatherers as primitive isolates. Its subtitle, "From Prehistory to the Present," suggests that archaeological evidence bearing on the interdependence of hunter-gatherers and their neighbors will constitute a substantial segment of their discussion, but except for the case of the Philippine Negritos archaeological evidence plays a minor role. Further, the biological implications of trade contact—for diet supplementation, disease transmission, and gene flow—are overlooked here as in most studies of hunter-gatherer exchange systems (Bicchieri 1972; Bird 1983, 1986; Leacock and Lee 1982; Lee and DeVore 1968; Meyers 1988; Schrire 1984; for notable exceptions, however, see Altman 1984, Hart and Hart 1986, and Nurse and Jenkins 1977). This communication calls attention to an archaeologically documented case of economic interdependence between hunter-gatherers and urban agriculturalists in prehistoric India and demonstrates how economic interdependence can have biological as well as socioeconomic consequences for the groups involved. Human skeletal remains from the prehistoric sites of Langhnaj and Lothal in Gujarat State suggest the possibility of changes in morbidity and gene flow as a consequence of interaction between nomadic hunter-gatherers and sedentary agriculturalists.

Langhnaj was discovered in 1941 by H. D. Sankalia, who subsequently conducted several seasons of excavation (1942-63) at the site (fig. 1, Sankalia 1965). While the human remains from Langhnaj are not all contemporaneous (11 of the 14 skeletons are derived from Mesolithic horizons), they have served as an important basis for documenting the biological features of the Mesolithic inhabitants of northwestern India (Ehrhardt and Kennedy 1965, Karve and Kurulkar 1945). Variations in burial position and biological characteristics have

been attributed to cultural and ethnic mixing. A copper knife recovered from the site is interpreted as evidence of contact between its nomadic inhabitants and technologically more developed people settled in urban centers (Possehl and Kennedy 1979). The antiquity of microlithic levels at Langhnaj has not been precisely determined, though Sankalia proposed a date prior to 2500 B.C.

The prevalence of dental caries at Langhnaj, 8.0%, is exceptionally high in comparison with that reported for skeletal series from other South Asian Mesolithic sites, where it varies from 0.0% (at Bellanbandi Palassa in Sri Lanka [Kennedy 1965] and at Sarai Nahar Rai) to 0.9% (at Lekhahia) and 1.2% (at Mahadaha) (fig. 2; Lukacs and Hemphill 1990). In preagricultural groups elsewhere it is uniformly low (Cassidy 1980, Cohen and Armelagos 1984). These low rates are consistent with the caries rates for peoples practicing a nomadic hunting-gathering subsistence strategy (Turner 1979). In contrast, at Harappa, an agrarian Bronze Age site in Punjab Province, Pakistan, the caries rate is 12.8% (Lukacs n.d.), a figure that includes a correction factor for high rates of antemortem tooth loss due to caries. The 8.0% caries rate for Langhnaj falls above the mean caries rate—4.8%—for mixed subsistence economies and cannot be adequately explained by either demographic differences or sampling error affecting these skeletal series (Lukacs 1981, Turner 1979).

Sites of the semiarid region of Gujarat and Rajasthan such as Langhnaj and Bagor differ from the Ganga Valley sites (Lekhahia, Mahadaha, and Sarai Nahar Rai) in their proximity to intensive agriculturalists. Contemporaneous with the late Mesolithic occupation of Langhnaj and 100 km to the south is the Harappan town of Lothal (Rao 1973). Interpreted variously as a port and as a gateway town, Lothal was clearly a technologically developed agricultural settlement on the southeast margin of the Harappan civilization (Leshnik 1968, Possehl 1976). The occurrence at Langhnaj of a 98.12%-pure copper knife, black-and-red ware typologically similar to sherds from Lothal, and Harappan disk beads strongly suggests interaction in the form of exchange between the occupants of these two sites. This interpretation views Langhnaj as a campsite of nomadic hunter-gatherers or pastoralists whose movements brought them into repeated contact with the urban agriculturalists (Possehl and Kennedy 1979). A close biological relationship between the inhabitants of Lothal and Langhnaj has been documented craniometrically (Kennedy et al. 1984), suggesting that in addition to the exchange of goods and supplies, genes may have flowed between these two populations. If this thesis, elaborated by Possehl and Kennedy (1979), is correct, then the greater prevalence of dental caries at Langhnaj than at other South Asian Mesolithic sites and in Mesolithic skeletal series in general (Cohen and Armelagos 1984) may be attributed to the periodic inclusion of agricultural foodstuffs in the Langhnaj diet. These foods could have been obtained in the course of exchange or trade contacts with agriculturalists at Lothal and/or Kalibangan. Nomadic hunter-gatherers or