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### Thinking about Evolutionary Change The Polarity of Our Ancestors

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The debate over the origin of modern humans polarizes into two camps: multi-regional (regional continuity) and replacement (restricted origin). Despite the acrimony which has all too frequently attended this debate, it is curious that the differences between the two camps have not always been clearly spelled out; it has at times been easy for upholders of one or the other position to claim that the other camp has misrepresented their position. Each of the two models has a more and a less extreme version, and it is necessary to examine the statements of the protagonists in order to determine just where along the spectrum they really do lie.

#### THE MULTIREGIONAL MODEL

The most extreme expression of multiregionalism would maintain that the earliest population of the genus *Homo* in any given region of the world is exclusively ancestral to all later populations in that region. To my knowledge, no one who claims to be a proponent of multiregionalism would accept this formulation in either its theoretical or its practical aspects. Theoretically—because even Coon, perhaps the most extreme proponent of the model, did not deny that evolutionary change in a given population could have been initiated by gene flow from other regions (Coon 1962:36–37), indeed in all probability there always had been some genetic contact between regional human populations (Coon 1962:369). Practically—because no one seems to regard Lower/Middle Pleistocene Javanese as ancestral to modern *Javanese*, but rather to modern aboriginal Australians and Melanesians (i.e., there have been at least some distributional shifts and “regional” continuity is to be taken rather loosely).

What the multiregional model’s exponents propound, then, is some less extreme form of “weak multiregionalism.” As expressed by Wolpoff et al. (1984) and Frayer et al. (1993), in what may be taken as the definitive expositions, it

involves the maintenance through time of particular morphological complexes in given geographic regions, despite the continuous operation of specieswide evolutionary trends. Gene flow operates, therefore, across both space and time.

But how extreme, or not, is the multiregionalism of this school? When did interregional differentiation start, and were *all* non-sapient *Homo* populations involved in modern human origins, or did some become extinct without issue? Wolpoff and colleagues are explicit: it began with the initial expansion of *Homo* out of Africa (1984:450–451), and all known (morphologically distinct) non-sapient populations left a detectable genetic heritage in their modern vicars—even the neandertals (1984:470–471).

### THE REPLACEMENT MODEL

Stringer does not exclude the possibility of hybridization; he merely relegates to it a minor role, except perhaps for Australasia (1992a:14–16, 20). Bräuer goes further: hybridization certainly did occur, and he identifies certain European specimens as showing its influence but makes it clear that this is in no sense regional continuity (1992a:93); he names his version the “African Hybridization and Replacement model.” On the other hand Bräuer is more extreme than Stringer in that he is sure that modern humans evolved in Africa, whereas Stringer leaves open the Middle East as a possible locus, and even draws attention to certain Chinese fossils as intriguing in this respect (Stringer 1993:91). Perhaps the most extreme version is that of Groves and Lahr (1994), who are as certain as Bräuer is that it was Africa, and as certain as Stringer that we do not have any evidence for hybridization (in fact, not even in the Australasian case).

### WHAT DOES NOT COUNT AS EVIDENCE

We are discussing the origin of modern humans (*Homo sapiens*, as that binomial is increasingly restricted). That category is, and can only be, defined anatomically. Certain technologies, and certain behaviors vis-à-vis neighboring groups, may well have been exclusive to *Homo sapiens* throughout its history, but this is not the heart of the matter. Neither are genetic data central—if human mitochondrial DNA has less variation than that of chimpanzees, orang-utans, or gorillas, this may be because the human species really does have less time depth and really did not incorporate genes from other taxa of *Homo*. But it may not—there may have been a recent selective sweep that got rid of the more divergent variants (S. Easta, School of Medical Research, Australian National University, personal communication 1996), or the molecular clock might be much sloppier

than we thought, or the mitochondria of all the neandertal and *Homo erectus* women who contributed to the modern gene pool might by chance have been lost. It is a common misapprehension that human origins models depend, in whole or in part, on genetic and behavioral (including technological) data, but this is not the case.

Fruyer et al. (1993) fall into this error when they list a behavioral criterion as the very first of their "predictions" for what they dub the "Eve theory."<sup>1</sup> They consider that there should have been a technological advantage in order for replacement of one population by another to have occurred, that archaeology does not demonstrate this, and that the replacement model is therefore refuted.

Such an argument is not relevant: it is about *how* it occurred, not *whether* it did. If replacement of other species by *Homo sapiens* occurred, only the fossil evidence itself can demonstrate it. Clearly there was some "how" involved in the replacement process. If archaeology fails to document a "spreading technological advantage," then new stone tool types were evidently not part of it. Mechanisms of replacement might or might not include extermination, global competitive superiority, local competitive advantages, greater fertility and/or longer reproductive span, increase in the population of a key resource, some disease affecting the non-*sapiens* taxa, or even just pure chance. Or *Homo sapiens* might really have been more sapient, and the other people couldn't stand it and died of shame.

*Why* one anatomical type should replace another is a very interesting question, but that one cannot think of *how* it could have happened is not evidence that it did not happen.

#### WHAT CONSTITUTES EVIDENCE FOR REGIONAL CONTINUITY?

Support for the claim that there has been genetic continuity, from then to now, in a given region is based on features (in cladistic terms, character states) that occur within that region throughout that period. In what sense the features invoked in support of continuity are "regional" is not made clear by Wolpoff et al. (1984) but is spelled out in more detail by Fruyer and colleagues (1993): the features do not have to be exclusive to the region (1993:21), merely in their highest frequency (1993:17) and found in distinctive combinations (1993:21–22) there.

These two aspects—highest frequency and combination—will be briefly considered in turn.

*Highest frequency.* Samples of modern crania are large enough that one can calculate accurate frequencies of occurrence of particular features, and so claim confidently that in some regions a certain feature occurs at significantly higher frequencies than elsewhere. The fossil record, though by now respectable in

many respects, is still not sufficient to enable us to give accurate frequencies for the occurrence of features, yet one can certainly say that a particular feature is "commonly" seen in one regional sample but "rarely" in others. If the two features in the same region are the same, ancient and modern, then multiregionalists may have a point. Maybe. But first calculate the frequencies on the modern samples and make sure they are correct. Lahr (1994) claims that they have not always been correctly assessed, and if she is right the consequences for multiregionalism are rather serious.

*Combinations, not individual features.* Why do clusters of features occur in combination? There are several possible reasons: (a) they are consequences of a single pleiotropic gene, or tightly linked genetically, (b) they form part of a developmental complex, (c) they form part of a functional complex, (d) they are selected for by common environmental factors, and (e) they occur together by chance. As far as I can see, in the first three cases there would be no option but for the features to co-occur, so the fact that they are found in combination is of no special significance. If they are selected for by common environmental factors, there would be some significance in their co-occurrence only if at least one of the features was *exclusive* to that region at that time (i.e., it was not part of the specieswide genetic heritage). If they co-occur by chance there is much more likely to be some special significance (in terms of regional continuity) to the combination. In other words, common high frequency could well be an indicator of regional genetic continuity; co-occurrence may or may not be.

### THE IMPORTANCE OF POLARITY

If two taxa share a certain character state absent from a third, what can we deduce about their relationship? It depends on the *polarity* of that character state: whether it is *apomorphic* (derived) or *plesiomorphic* (primitive).

Suppose we have three groups (or taxa), A, B, and C (Figure 23.1), and they differ from one another in various character states. Let us call them lungfish (A), lizard (B), and dog (C). In one character, integumentary covering, A and B are alike, C differs (Figure 23.1, right or top): lungfish and lizard both possess scales, dog has hair. Is this evidence that lungfish and lizard are more closely related to each other than to dog? No, because scales are plesiomorphic, hair is apomorphic. We know this by taking into consideration an *outgroup*, a taxon known to be, phylogenetically, not a part of the group under consideration. In this case, say, salmon. Salmon, like lungfish and lizard, are scaly; scales, therefore, simply persist from a more remote common ancestor, while a change has occurred during the evolution of dog to produce hair.

In another character, limb type, B and C are alike while A differs (Figure 23.1, left or bottom): lizard and dog have legs while lungfish has fins. Is this evidence

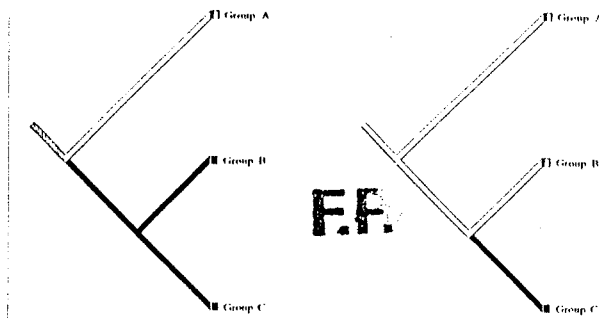


Figure 23.1. Character polarity and its consequences. The apomorphic (derived) character state is shown in black.

that lizard and dog are more closely related to each other than to lungfish? Yes, because legs are apomorphic, fins are plesiomorphic. Our outgroup comparison shows this clearly; lizard and dog share a common ancestor (which had evolved legs) subsequent to the separation of the line leading to lungfish (which retained [primitive] fins).

Now, of course, these two respective explanations are not absolutely certain: they are the most probable ones, because they are the most parsimonious. As Felsenstein (1983) puts it, evolution is relatively improbable; therefore it is more likely that any given evolutionary change has happened only once. It might have happened that legs evolved twice, once in the ancestors of lizard, once in those of dog, in which case their common possession of legs would not, after all, indicate a more recent common ancestry, but this is unparsimonious. It might also have happened that scales had evolved three times (separately in the ancestors of salmon, lungfish, and lizard), but this is even less parsimonious. Despite Felsenstein's claim, cladistic analyses have shown that homoplasy (parallel and reversed evolution) is a common event; the popularity of cladistic analysis in recent years has shown this quite clearly, as reviewed by Groves (1989b; cf. Clark 1988). Parsimony is not an iron law of nature, it is a rule of thumb (Cartmill 1981), a "most probable" scenario.

The cladistic method does suffer from this drawback: parsimony is assumed, but it is merely the most probable condition, rather than the inevitable one. (Biological relevance does not have to be demonstrated for the employed traits, contra Trinkaus 1992c; neutral characters, uncontaminated by selective advantage, will do just as well.) But in the present case the implication is clear and has nothing to do with parsimony: plesiomorphic character states are absolutely not evidence for common ancestry.

An example will show the significance of this drawback. Kramer (1991) examined modern human mandibles from East Africa and from Australia, and Pleistocene (*Homo erectus*) mandibles from Java. In seven character states the

Australians, but not the Africans, resembled *Homo erectus*. Kramer deduced regional continuity from this—the Australians had inherited their mandibular features from Pleistocene Javanese ancestors—but it does not follow, because the polarity of the characters was not tested. East African pre-*sapiens* mandibles might show either the character states of the modern East Africans, in which case regional continuity would be strongly supported, or they might show the same states as the Australians and Javanese *Homo erectus*, which would thereby be shown to be plesiomorphic and so of no value for the question at hand. But since no such investigation has been made, no conclusion can be drawn either way.

Groves (1989b) made the case that, when polarities are known, most (all?) of the features that have been cited as evidence of regional continuity—those that are truly comparable—are found to be plesiomorphic, and thus not relevant. The question arises, of course, whether outgroups were chosen judiciously. If the earliest non-African *Homo* are on the order of a million years old (Hyodo et al. 1993), then *Homo ergaster*, as represented by such well-preserved specimens as ER-3733 or WT-15000, would be a suitable outgroup. If, however, the earliest Javanese *Homo* (marking the initiation of the Australoid lineage) are ca. two million years old (Swisher et al. 1994), then the *Homo ergaster* fossils could be part of an already separated African lineage. In that case, we could be rather stuck for an outgroup!

I conclude that the case for regional continuity must be much more tightly and logically presented than has so far been the case. To carry conviction the case should be put somewhat as follows:

1. The character states defining the australoid lineage (or mongoloid, etc.) are A, B, and C.
2. They are defined *thus*.
3. They occur at frequency  $x$  in aboriginal Australians, at frequency  $y$  in New Guinea Highlanders (and so on), but at no higher frequency than  $z$  in non-australoid populations (always provided that sample sizes are adequate, and frequencies are statistically meaningful).
4. The characters can be observed in the following presapiens fossils [list] from the region, of which the following specimens [list] possess the “australoid lineage” states of the characters.
5. The characters can be observed in [list] from elsewhere, of which only a very few [list] possess the “australoid lineage” states.
6. And finally—absolutely critically—the character states in question are apomorphic, and here is the evidence that they are.

#### WHAT WOULD BE EVIDENCE FOR REPLACEMENT?

The same stipulations demanded of the multiregional model must also apply to the replacement model: archaeology and genetics offer at best indirect evi-

dence, and character state polarity must be demonstrated. I would present the case somewhat as follows:

1. The apomorphic character states of *Homo sapiens*, relative to (say) *Homo ergaster*, are as follows [list].
2. The distribution of these states in Middle and Lower Pleistocene *Homo* is as follows [list those that possess the states in question, and those that do not even though the characters can be observed].
3. The greatest number of these states occurs in fossil group A (regional and chronologically circumscribed), which is thereby identified as the cladistic sister-group of *Homo sapiens*.
4. The next greatest number occurs in fossil group B, which is therefore the sister-group of the A + *sapiens* clade—and so on, until we have constructed a cladogram that is as complete as the evidence permits.
5. Next, examine the non-*sapiens* clades to see if any apomorphic states can be found in them.
6. Finally, focus on *Homo sapiens* itself, identify character states within modern populations that are of regional significance (exactly as for the multiregional procedure, steps 1–3), and document their distribution in fossils assigned to the species.

My version of the replacement model predicts that the Middle Pleistocene African fossil group is group A, the sister-group of *Homo sapiens*; that the neandertals and Middle Pleistocene Europeans are group B, the sister-group of *sapiens* + A; and that East Asian *Homo erectus* is the sister-group of all of these. It further predicts that group A and group B have their own apomorphic states, which can be tracked in the same way as those of *Homo sapiens*. (A taxonomy at species level can then be drawn up as it is felt appropriate.) It predicts finally that the earliest fossils of *Homo sapiens* in Africa will have none of the character states that are of regional significance, that the earliest non-Africans will have few or none, and that regional character states will develop within each region once it is settled (by *Homo sapiens*), such that the earliest fossils of a given region show them incipiently, the later ones more definitively.

## CONCLUSIONS

The multiregional/replacement debate has generally been carried out with more heat than light up to now—shall we say, with a low “signal-to-noise” ratio. This chapter examines the premises and finds that they are often insubstantial or irrelevant. The crucial criterion, which must not be lost sight of, is polarity; using this, both parties to the debate can draw up a research program which has every prospect of finally resolving the problem.

### ACKNOWLEDGMENTS

First let me thank Geoff Clark and Cathy Willermet for their invitation to contribute to this unusual, intriguing, and worthwhile enterprise. I am presently involved in a research project to study original fossils with another contributor, Alan Thorne, and would like to go on record that it is possible for colleagues who differ profoundly in their views to travel and study together with pleasure and without rancor. Despite extensive discussions with Alan and others, notably Chris Stringer, Marta Lahr, Jonathan Kingdon, David Dean, and Dan Lieberman, the ideas put forth in this paper, and especially the way I have expressed them, are all my own.

### NOTE

1. "Eve theory" is an inaccurate designation for the replacement model for two reasons: First, in science a theory is a highly corroborated, robust model of the universe (theory of evolution, quantum theory, etc.). I do not think that many multiregionalists would concur that the replacement model has this character. Secondly, "Eve" is a construct—a publicity stunt, perhaps—of geneticists to designate the coalescence point of the human mitochondrial tree. It does not truly describe the entire replacement model.