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The pattern of human evolution

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Abstract
The systematic morphological variation between human geographic groups is widely and quite correctly attributed to climatic and cultural adaptations. Certainly, the main distinguishing characters of race as socially defined have clear adaptive significance. These features include skin color, hair color and form, and stature and body proportions. However, the forensic bases for racial identifications involve skeletal features whose variation is often without obvious adaptive significance. The adaptive advantage of prognathism vs. orthognathic faces, shoveled vs. flattened incisors, rounded vs. squared orbits, and others remain unknown.

Multiregional evolution provides an explanation for the distribution of these non-adaptive variants. This paper discusses the Multiregional explanation, focusing on the center and edge hypothesis to account for the initial distribution of regional features such as these, and tracing the evolutionary history of regional continuities in several different areas. The point we wish to establish is that history as well as adaptation is an important cause of modern human variation.

Key words: Multiregional human evolution, Middle & Late Pleistocene, adaptation, social factors

Although detailed, specific, evolutionary patterns are impossible to derive for an entire species throughout all of its existence, understanding of a general pattern is important. This pattern forms a framework for other studies, including adaptive ones, which may lose validity if the underlying evolutionary assumptions for the species are invalid. A variety of influences such as polytypism, genic exchanges, communication, all play a role in the question of how local gene pools respond to selection. Genetic response depends not only on the magnitude and direction of selection, but also on the distribution of alleles in a population and the potential influx of genes during the selection period. For instance, clines created by gene flow and opposing selection may appear no different from clines responding to environmental gradients. Other aspects of modeling are important in reconstructing past changes. Adaptive/-ecological interpretations that rely heavily on analogy with other species that have a punctuated evolutionary pattern with long periods of stasis can inadvertently assume their conclusions - that the pattern of evolution is punctuated and bush-like and that adaptive changes occur with speciations, not between them. The pattern of human evolution is intrinsically no more or less a problem to understand than for other species, but its understanding is complicated by the much greater depth of knowledge we have about human biology, populations, prehistory and social systems. There is much more to account for.

Two periods

Ever since Darwin there has been recognition of divergence of different human groups from a common origin and most questions about human evolution reflect this. The questions still abound - where and when did that divergence occur? Did similar divergences occur before (were there successive replacements)? What kind of divergences have there been: populational? speciations? What is the pattern of those divergences; i.e., what were

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the relationships of the different groups to themselves, their descendants, and us. Were early geographic groups the same "races" as the ones we belong to today as their modern descendants in various regions, or are races temporary ephemera? The pattern of human evolution provides the context in which these questions can be addressed, and reflects the evolutionary processes that shaped our species.

However, there are two very distinct parts to human evolutionary history and the general patterns are quite different for each:

1. In the longer part, for the first two-thirds of their evolution humans were geographically restricted and their evolutionary pattern was similar to that of other species, most of which are adapted to limited ecological niches. Dispersions and the mechanisms of species cohesion are not a difficult issue to understand.
2. In the second shorter and more recent part, which Gamble (1993) refers to as the colonization phase, humans came exist all over the Old World. People already with substantially larger and more expensive brains than their predecessors left Africa with behaviors that allowed them to establish themselves in numerous habitats and environments.

These periods are quite discrete and can be best understood using different criteria. For the first part, when humans were less sophisticated behaviorally and were geographically restricted, hypotheses can be based on general species dynamics formulated for other species in similar ecological conditions. This is when multiple species abounded and the ecological models of workers such as Foley (1987) are most relevant. But for the second part, hypotheses need to be based on models derived from the evolutionary processes at work in modern human populations.

To understand the overall pattern of later human evolution we need to test hypotheses with data that attest to population histories. The hypothesis chosen should be the most reasonable one that explains all of the data available with the fewest assumptions. However in paleoanthropology, choice of a null hypothesis is often a bone of contention. In this paper we argue that the Multiregional hypothesis (Wolpoff, Wu & Thorne 1984) is the relevant null hypothesis for the colonizing phase of human prehistory, because it is the model of human evolutionary processes requiring the fewest number of assumptions to account for the paradox of global change and local continuity, as discussed below. In fact, the main assumption it requires is that the evolutionary processes at work in relatively recent modern human populations were in operation in the past. Our species is unusual and difficult to model because it is polytypic, with extremely broad geographic and ecological ranges. Most polytypic animals are so because they occupy an ecological niche that is broadly distributed, but the human pattern of a widespread single polytypic species with many different ecological niches is very rare. The human capacity for information storage and transmission and its associated behavioral flexibility, that are a part of what has been called "Culture", allowed the occupation of so many diverse niches. Furthermore, culture affects evolutionary processes in many other respects; it influences the demography of populations and plays an inestimably important role in shaping the evolutionary histories of human populations. While we do not think that culture appeared suddenly in its present form - its definition and evolution are obviously complex, the behavioral flexibility it allows was clearly significant during the colonizing phase in human evolution. Humans in this later phase should not be expected to follow the species proliferation or extinction patterns of other fauna that lack this degree of flexibility. Because of the lack of adaptively flexible, polytypic mammalian analogies, modern humans themselves provide the best model on which to base the reconstruction of the pattern of recent human evolution.

Present and past

We start, then, with the assumption that we can use relationships between human groups today to serve as a model for those in the Middle and Late Pleistocene. Obviously there are many different relationships between populations, some populations are relatively isolated, some go extinct, some are parts of large scale networks, others are parts of small ones, and no doubt, in the past, a wide variety of relationships also existed. We recognize that it is impossible to come up with *detailed* patterns of human evolution that are not population specific. But so far, we have found no reason to think that this same sort of complicated mesh of human relationships, reflecting a *general* evolutionary pattern of widespread species cohesion, did not characterize the past. This general evolutionary pattern is Multiregional Evolution, a processual model that explains population variation and species cohesion in humans as a polytypic species. It is quite reasonable to proceed cautiously when attributing "human qualities" to our ancestors; while we have been criticized for assuming conclusions when hypothesizing a polytypic pattern for them, we think that it is the simplest null hypothesis to start with. We *don't* know that premodern humans were polytypic - perhaps different regions were home to different species as some workers have proposed (Wood 1992). But, when trying to understand the relationships between geographically dispersed advanced hominid groups (including the question of whether or not they are different species) the theory that requires the least number of assumptions is the polytypic one. The reason for this is quite simple, parallel evolution of distinct species would require the assumption of homoplasy on a scale unknown before now. We do not argue here that Multiregional model is known to be true, only that it is the most reasonable one.

What is Multiregional Evolution?

The Multiregional model of human evolution describes the pattern of population variation and evolutionary change in a widespread, geographically diverse species that is internally subdivided. Assuming, as we argue above, that the present is a valid model for interpreting the past, it attempts to frame how evolutionary change continued in the face of geographic dispersion without speciation - the pattern that seems to characterize the last 2 million years of human evolution. The key elements are:

- the historic and adaptive processes that created and maintained the pattern of variation,
- the dynamics of reproduction, communication, and population movements that link local populations and provide the network for advantageous changes - whether these are based on new gene combinations or new ideas - to diffuse throughout the species.

The human species evolves as various localized advantageous changes spread widely and persist. The Multiregional model is an attempt to account for the combination of long-lasting diversity and species-wide evolution by examining the consequences of the species' internal structure - widespread diversification linked by gradations of continuously varying features that reflect gradients in selection, genic exchanges between adjacent populations, or gradients based on the balance of both. The gradations persist as long as there are balancing opposing forces, for instance directional genic exchanges that often move alleles from the center to the edge of the species range, and local selection that is often most intense in more peripheral populations.

In a nutshell, the Multiregional Evolution model begins with the obvious - humans are a single widespread polytypic species, with multiple, constantly evolving, interlinked, populations whose dynamics can be partially explained by evolutionary processes that pertain to other widespread polytypic species in general. These processes can be understood both through clinal theory and the history and consequences of popu-ation placements relative to other populations - the center and edge mechanism described by Thorne (1981). They have affected humans since humans became a single widespread polytypic species and therefore can explain patterns of morphological variation that we see in prehistory - patterns extending for a long time into the past, to the time when humans first successfully colonized regions outside of Africa. This is when evidence of regional continuities in different places first becomes apparent and convincing.

Adaptation and history

The two fundamental reasons why geographically disperse human populations differ are **adaptation** and **history**. Their intertwined role can be seen in the initial colonizations, particularly of the peripheries such as eastern Asia, Australasia or western Europe. Earlier peripheral populations were homogeneous for a number of features. Some of these were adaptive, important elements that helped populations meet the requirements of their environments. These appeared in high frequency in response to changes in the conditions that made them helpful, not always at the time of colonization. Adaptive features are not necessarily long lasting, as environments fluctuate, but initially adaptive characteristics often persist when they form the basis for subsequent exaptations - features that come to change their adaptive role as they prove successful in meeting new selective challenges. In that way previously adaptive explanations become historic ones. Others features common in peripheral populations were established during the period marked by large amounts of genetic drift and bottlenecking at the time of the colonization process. These may be nonadaptive, but more often are anatomical variants that are equivalent adaptive alternatives - one of several equally useful ways of meeting biological or social needs. Drift may come into play during the time that one of the alternatives was established at high frequency. Some of these features no doubt disappeared but others persisted. Certain cases of this persistence reflect an evolutionary momentum. Features initially at high frequencies may remain unaltered because no evolutionary forces change them. They may subsequently become exaptations as they are incorporated in local adaptations. Exaptations can differ substantially between different populations meeting the same adaptive requirements.

Regional continuity

Features with a primarily historic explanation reflect past racial differences. The races themselves are transitory, but in many cases the features have not been. Whether established by adaptation or by other historic processes, the observation that characteristics of both backgrounds persisted for long periods of time, in some cases through the Late Pleistocene and some even to recent and living populations, is called regional continuity. Regional continuity is marked by features that tend to characterize particular areas over time - they are found in high frequency in present and past populations of the same geographic locality and they persist in spite of changes in other morphological features. We want to emphasize that many features do change. Some of these reflect general evolutionary trends, others local adaptations to changing circumstances. But while regional features persevere, that doesn't mean that "races" do. Races are transitory and ephemeral and we are aware of some instances where regional features remain common in an area even as a local race changes. For instance, the H-O mandibular foramen is virtually unique to European Neandertals (it is found in virtually no other fossil remains, including Late Pleistocene Africans and the Skhul/Qafzeh sample), and has a significant frequency in the subsequent post-Neandertal populations of Europe and only decreases to rarity in recent Europeans (Table 1).

We think that features such as these demonstrate some elements of genetic continuity, but they do *not* necessarily reflect populational stasis or any form of racial continuity.

Table 1. Mandibular foramen form in Late Pleistocene and recent Europeans (after Frayer 1993, Table 7).

	Horizontal-oval foramen percentage frequency	Normal foramen frequency
European Neandertals	53	47
Early Upper Paleolithic	18	82
Late Upper Paleolithic	7	93
Mesolithic	2	98
Medieval	1	99

Finally, understanding the mechanisms that explain observations of regional continuity is a different proposition than "proving" genetic continuity in a region through time. The nature and consequences of regional continuity can be examined for single traits, as in the example above, but genetic continuity between successive populations can probably never be *established* by examining single features, or features one-at-a-time, as Habgood (1989) has argued. There is simply too much normal variation for this to work - it's that partitioning of genetic variation again, there is much more variation within populations than between them. Habgood shows that as far as the *demonstration* of this continuity is concerned, complexes involving combinations of several features must be examined to focus through the blurred picture that normal variation creates. This is not an aspect of the process but of its identification.

There can be selection on populations and considerable gene flow, without a concomitant change in all regional features. Even with large scale migrations and population replacements such as those in Holocene Southeast Asia, we ex-pect to see gradually shifting frequencies and continued reflections of the old complexes in modern populations. The *explanation of regional continuity* in *Homo* is found in the Multiregional Evolution model.

Paradox

How did humans retain geographic distinctions and yet evolve together? This is the apparent paradox that Multiregional Evolution addresses. If it is true that isolation is necessary for long term geographic differentiation, wouldn't that eliminate any common patterns of evolution unless they were fortuitous? If genic exchanges are required for common evolutionary directions, wouldn't they eliminate geographic distinctions? How could we possibly expect these two contradictory processes to be of just the right magnitude to allow both persisting regional distinctions and common evolutionary changes? Part of the resolution of this paradox lies in the incorrect assumptions above. Isolation is not essential for maintaining geographic distinctions. Many variants are found in broad gradients. Some of these form simply as a response to selection that differs over a wide geographic range, for instance skin color that usually corresponds to the amount of solar radiation that skins are exposed to. These gradients are particularly expected to characterize the distribution of skeletal features that can reflect climatic adaptation, such as relative limb lengths or nasal form. However, their interpretation is complex because many, perhaps most, adaptive characteristics *function in several different adaptive systems*. Therefore the distribution of these features may respond to different evolutionary pressures. Relative limb length, for instance, is also important in different patterns of mobility. Clines based on gradients between various evolutionary forces, more important to the multiregional model, are discussed below.

Another invalid assumption is that genic exchanges are necessary for there to be common directions to evolutionary changes in different human populations. Exchanges do create these commonalties, of course, as advantageous alleles would spread widely because of the advantages they confer and result in the same evolutionary changes in different places. Human populations are particularly receptive to this process because communication systems could disseminate the very behaviors that make some of these alleles advantageous, such as new hunting technologies, improved organizational skills, or important changes in the communication systems themselves. Yet at the same time communication, the exchanges of ideas, information, and technology, could become independent causes of a common evolutionary direction. Disseminating ideas can create changes in selection, and populations with similar gene pools may respond in the same manner. The similarities between human gene pools are more pervasive than one might imagine. Geneticists such as Lewontin (1984) have long argued that the vast majority of human genetic variation is within populations and not between them, and it is commonly quipped that virtually any two fruit flies have more genetic differences than the most extreme two people. There is ample opportunity for similar selection to cause similar changes. These two processes are not independent. When ideas and artifacts spread, genes frequently spread as well.

However, a more important resolution to the paradox lies in the affects the contradictory elements of gene flow and selection have on each other. They are both part of a single process - clinal variation. Gradually varying distributions of a feature can develop when the source of selection it responds to varies gradually, such as skin color corresponding to differences in solar radiation as noted above. But, clines will also form when there are contradictory evolutionary forces affecting a feature, for instance, genic exchanges and selection. This forms a gradient that in itself is a cline, that can be independent of the environment. Populations are usually more numerous and denser toward the center of a species range, sparser and less common toward the edge. Population movements are usually from denser to sparser regions, and advantageous new alleles or allele combinations are more likely to first appear in the center as there are bigger gene pools there, and then spread outward because of the advantages they confer. Toward the peripheries, however, there may be opposing forces. Selection may oppose novel incoming alleles or allele combinations because:

- conditions affecting selection are different at the periphery;
- novel genetic material disturbs local adaptive valleys on the genetic landscape comprised of stable coadapted genetic combinations (Lande 1986);
- the changes interfere with local kin or mate-recognition systems (see below).

Genic exchange acting on the distribution of a feature in one way and selection acting in the other will create a cline, even if the source of selection is not distributed along a gradient.

Balance of forces

The opposing forces created by genic exchanges and selection will invariably form a balance. Similarly, genic exchanges and genetic drift can oppose each other and create a balance. Especially when the genic exchanges come from individual or population movements, many alleles introduced into more peripheral populations by successful immigrants are unimportant, minimally advantageous or neutral to selection in a peripheral environment. Disadvantageous alleles, of course, would disappear. Because peripheral or ecologically marginal populations are more subject to drift there is a second possibility for balances to form. This is because drift often leads to the loss of rare or infrequent alleles. The balance creating a cline is between the source and loss ends of an allele's distribution. As evolutionists such as Charlesworth, Lande & Slatkin (1983, 476) have pointed out, these balances control how much genetic differentiation appears between populations. In discussing the mechanisms that cause geographic variation they assert "the extent of genetic differentiation between two or more local populations is determined by the balance between gene flow and natural selection or random genetic drift".

Thus there are two sources of clines:
- geographic gradients of selection,
- opposing evolutionary forces.

Long lasting genetic differentiation created by clinal balances is commonly thought to be the main cause of human racial variation (Livingstone 1962; Brues 1972; Birdsell 1972). It is the central contention of Multiregional Evolution that these shifting balances extend far into the past, for most of the Pleistocene and that the balances transcend the populations with which they are associated. While the populations changed and the details of the balances varied with the ongoing process of evolution, local continuities for certain features lasted for long periods of time. *These account for the observations of regional continuity, and at the same time create the potential for historical depth to join the two dimensional clinal model of modern population variation. Now, the clines themselves take on a dynamic historical dimension.*

The most important characteristic of these clines is in how they relate the conflicting causes of variation. When there are clines, the *balance of forces* define the *steepness of the gradient*. Just as a see-saw can balance children, clinal balances are independent of the absolute magnitude of the forces and depend only on their *relative* sizes. The comparison of magnitudes creates the slope of the gradient - whether a feature varies a lot or a little from one place to another. But once there is a cline it means that one of the forces cannot overwhelm or swamp out the other - they will always form a gradient.

Why should some clinal patterns be long lasting? Why long-term continuity in some features, especially at the peripheries? Three factors come into play. The first of these is the homogeneity within peripheral populations that is:
- more common in subdivided species (Wahlund effect, discussed in Ridley 1993),
- more prevalent in small populations because of genetic drift (marginal populations are smaller than more central ones),
- more often found in the colonizing populations (and their descendants) of colonizing species.

Homogeneous features, once established, will not change unless they become disadvantageous.

The role of adaptation

The other two factors are long lasting adaptations and exaptations. They differ mainly over the role of history, as exaptations are adaptations that rely on anatomy already present and can only be readily identified when there is the potential for equivalent adaptations. For example, western European and eastern Asian populations probably came to differ in the elements contributing to maxillary incisor shoveling quite by accident, as a consequent of the colonization process or of small peripheral population effect. According to T. Crummett, in Europe crown curvature became a more important element than marginal ridges, while in Asia the marginal ridges were more prominent and the crowns straighter. When both came under selection to increase incisor strength and cross-sectional area in a limited space due to decreasing jaw size, European crowns became more curved and Asian crowns more heavily ridged. The contrasting exaptations are important markers of regional continuity in the two areas.

Discussions of Multiregional Evolution appear to ignore adaptation. This is *not* because adaptation is unimportant, but comes from its potential to confuse the identification of historic processes. Adaptation is a critical component of the evolutionary process. But the problem is that long-lasting features could potentially represent the consequences of history or of adaptations that remain the same because the need for them never changes. The distinction is important in understanding how evolution has proceeded, but it is also important in diagnosing whether the Multiregional pattern accounts for observed variation. For instance, the Bergman/Allen rule predicts that cold adapted humans need relatively short limbs to retain body heat. A succession of unrelated populations over a long period of time may retain relatively short limbs in a cold climate because of this adaptation alone. A succession of related populations may also retain short relative limb length both because of the requirements of adaptation and the influences of history. One cannot be distinguished from the other, and therefore clearly adaptive features may *reflect* an evolutionary continuity *but they cannot be used to prove it.* None the less, continuities in adaptive characteristics are an expected product of the evolutionary pro-cess and may well be the most common form of regional continuity.

Exaptations are quite different as markers of regional continuity, since by their very nature they are dependent on history as well as the adaptive process. The adaptations influenced by already existing morphology have the potential of equivalence - the same requirements met in different ways. Long-term equivalent exaptations are strong indications of genetic continuity. The other place to seek evidence for regional continuity is in nonadaptive features. These are very unlikely to persist if the history of a region is marked by population replacements.

Social factors

We believe that social factors, such as kin identification and mate selection, provide local sources of selection for unique features that have the potential to produce long-term continuity, but only when there have not been significant population replacements. Cues for recognizing potential mates are very important in maintaining reproductive boundaries between species, and mate recognition is of particular importance among sibling species, or when an adaptive radiation brings closely related species into competition. Reproductive boundaries are an important element in maintaining a species' cohesion and establishing its unique evolutionary pattern. However, within internally subdivided species, and especially humans, these cues play a somewhat different role, influencing mate selection within species. Now these factors don't just indicate interfertility, but are associated with complex social issues. In humans, physical characteristics can reinforce social elements of interpopulational relations.

An understanding of the roles of recognition in internally subdivided species has never been intensively examined. Certain mechanisms of mate recognition, balancing learned behavior and genetic predisposition to recognize key resemblances, have evolved to meet this problem in polytypic species where migrations and mate exchanges provide special opportunities for interactions with unrelated individuals. The complex nature of one recognition role derives from the fact that choosing mates based on simple similarity would maximize matings with sibs, or other very close kin. Yet ignoring any similarities could result in mate choice outside the species. How a balance is reached is suggested by Bateson's (1982) study of Japanese quail. These birds show a clear preference for first cousins, remaining in their proximity significantly more often than in proximity to birds with other degrees of relationship (including sibs) and to unrelated birds. In fact, the quails spent the *least* time in the proximity of their sibs. Time spent in proximity is directly related to mate choice in this species. Bateson posits that they are poised to prefer mates who are slightly different from the individuals they are familiar with in early life.

In humans and other social species, there are more complex problems of interactions between related or potentially related individuals. Recognition comes to play a double role in humans, where systems of kinship and alliance are of significant importance, not only in mate choice but other interactions where genic level selection plays a part. M. Flynn suggests that recognizing related individuals might be of particular consequence in peripheral populations, during periods when there were influxes of new people. Identification of related people is an important prerequisite for the ability to maximize inclusive fitness. Many workers have suggested an explanation involving genic level selection for some aspects of human social evolution, as well as for the evolution of human language because it requires shared syntactic laws for speaking and understanding. These considerations stem from the fact that related individuals are much more likely to share genetic variations, and one function of society, from a biological perspective, is to help related individuals help each other. Recognition, in the quails, is based on their plumage. In humans recognition of related individuals is largely based on features of the face. It is almost certainly not a coincidence that the face is where many of the externally visible features showing regional continuity are found, as facial characteristics play an important role in helping to recognize those related by systems of kinship or alliance.

The role played by features that promote recognition is therefore potentially important. Supporting this idea is the fact that at the neuroanatomical level the mechanisms of facial recognition are quite complex and distinct. Information is extracted from faces in specific parts of the brain, mostly in the right hemisphere (the non-dominant hemisphere for right handed people). There are three important regions that correspond to the way in which facial recognition proceeds. At the base of the visual cortex at the back of the head, one area processes the visual input and keys onto the unique features of the face. The second region, at the tip of the temporal lobe and well in front of the first, stores information about individuals. Names are stored separately from other biographical information which is why it is possible, if not common, to recognize individuals and associate them with particular times or places but not remember their names (the scourge of college professors!). A third area, positioned between these, is a secondary association area that links the recognition and information storage regions. It is here that the question of "familiar or not?" is settled. The neuroanatomy of this facial recognition system is unique to humans, and seems to be the consequence of the kind of mental mapping important in the neural reorganization posited by Holloway (1981). As in so many other reorganized neural pathways, the earlier limbic links between the recognition are storage regions remain, providing an emotional association for each recognition process. Clearly this is a neural processing system with unique importance in human evolution.

Conclusion

Multiregional Evolution is a model of how evolution works in a widespread polytypic species. It stems from the basic observation that some of the features that distinguish major human groups such as Asians, Australians, and Europeans evolved over a long period of time close to or at the places these people are found today. The model was developed for our own species because more is known about its prehistory than any other. It is predictive (and thereby has the potential of being disproved) over the issue of pattern. For instance, if it could be shown that human evolution preceded as a series of sweeping population replacements by successively better adapted forms, each with their own separate origin (something like what the late P. Teilhard de Chardin proposed), Multiregional Evolution would be clearly disproved, wrong. But unlike theories such as the "Eve theory" or the "Single Species hypothesis" it is not a focused theory about or interpretation of particular evolutionary events (modern human origins or australopithecine species in these cases). Multiregional Evolution is an explanation of the pattern of Middle and Late Pleistocene human evolution, based on the precept that the present is the best basis for modeling the past, which teaches us that populations in polytypic species such as ours remain differentiated for the same reason that they evolve without speciation - because of the matrix of genic exchanges (and in the human case information exchanges) they establish. Human evolution, as our colleague A. Thorne wrote, happened everywhere because every area was always part of the whole.

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