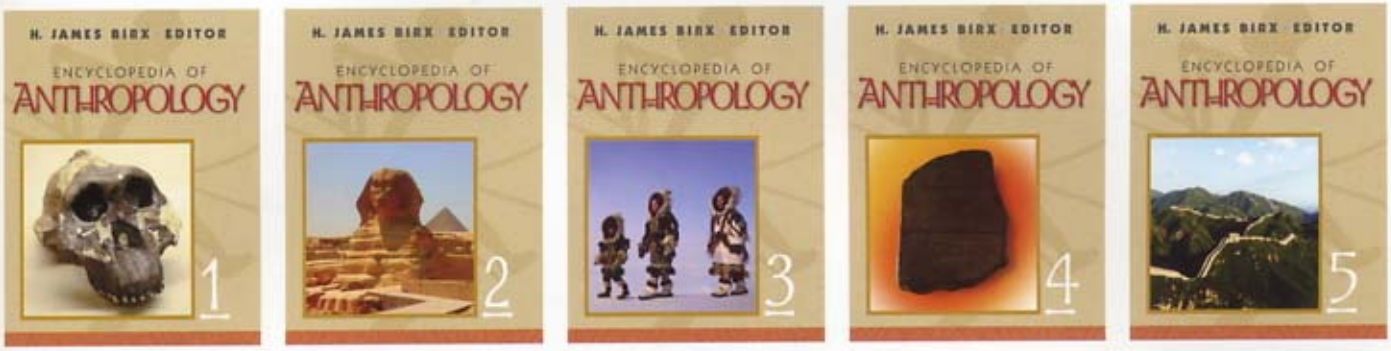

ENCYCLOPEDIA OF ANTHROPOLOGY

(published 2006)

H. JAMES BIRX ▪ EDITOR
Canisius College, SUNY Geneseo

4

A SAGE Reference Publication

SAGE Publications
Thousand Oaks ▪ London ▪ New Delhi

4 years, he traveled throughout the United States and Canada, where he documented information. He distributed questionnaires to collect data within the United States, India, Africa, and surrounding islands. The results showed him that the Tamil people of southern India used the same kinship terminology as the American Indians. Morgan considered this as proof that the American Indians were in fact of Asiatic origin.

Morgan continued to suggest that there was an explanation as to why families within these communities combined their titles of kinship such as calling a mother's sister "mother" and calling a father's brother "father." In *Ancient Society* (1964), he concluded that there must have been an "ancient existence of a consanguine family in which brothers and sisters intermarried in a group . . . and beyond this, in the remotest antiquity of mankind, lay promiscuous intercourse where no customs of marriage existed at all." Although Morgan's theory proved to be inaccurate, he was acknowledged for his extensive data collection and inquiry. This information was used for his book, *Systems of Consanguinity and Affinity of the Human Family.* Morgan gathered a very significant amount of information regarding his travels and experiences within these cultures unlike any other anthropologist from that time.

With origin on his mind, Morgan began to focus on biological and cultural evolution. *Ancient Society* was written to explain the process that cultures went through to evolve into civilized societies. He suggested that a society went through three main stages during its biological and cultural evolution. A culture began at the very bottom of existence as humans in savagery, then moved toward barbarism, and ultimately reached civilization.

Within savagery and barbarism, Morgan created three levels; lower status, middle status, and upper status. Morgan's theory rested on the assumption that through inventions, discoveries, and the growth of ideas, cultures evolved and progressed to the next stratum of human existence. Within the stratum of savagery, people relied on wild plants to survive. There was no working the land or animal domestication. Barbarism was defined by the initial use of agriculture. Civilization involved the use of the written word and the desire for property. In further detail, Morgan suggested that from barbarism, humankind was able to control subsistence use, and this allowed the continuation of the human species. From the cultivation of plants and cereals and the domestication of animals, societies created an abundance of permanent subsistence and therefore reached civilization. Morgan continued to distinguish between primitive and civilized societies when he stated, in *Ancient Society,* that primitive society was "founded upon ties of kinship, and modern, or civil, society is organized upon the basis of property relations and territorial distinctions."

Morgan died in 1881. Some of his work had since been proven to be false and seen as Eurocentric, but he is still considered as an important anthropologist from his time. Through his timeless research, data collection, analysis, and work with the Iroquois, he is seen as one of the founding fathers of anthropology.

— Simon Brascoupé and Jenny Etmanskie

Further Readings

Ben-Zvi, Y. (2003). National appropriations and cultural evolution: The spatial and temporal U.S. of Lewis Henry Morgan's Native America. *Canadian Review of American Studies, 33,* 211–229.

Morgan, L. H. (1962). *League of the Iroquois.* Secaucus, NJ: Citadel Press.

Morgan, L. H. (1964). *Ancient society.* Cambridge, MA: Belknap Press of Harvard University Press.

Tooker, E. (1994). *Lewis H. Morgan on Iroquois material culture.* Tucson: University of Arizona Press.

Morphology versus Molecules in Evolution

One of the first investigators of the "blood relationship" of organisms was George Henry Falkiner Nuttall. Early in the 20th century, Nuttall sought to demonstrate that the degree of similarity between animals in their blood serum proteins reflected their evolutionary closeness. He produced an antiserum to serum of one animal and combined it with another animal's blood serum, producing a precipitate. The more precipitate that formed, the greater the similarity (due to a greater number of antibody–antigen binding sites) and, consequently, the closer the supposed evolutionary relationship between the organisms

being compared. Nuttall also thought that the reaction rate reflected closeness of relatedness. He concluded in *Blood Immunity and Blood Relationship,* "If we accept the degree of blood reaction as an index of the degree of blood relationship within the Anthropoidea, then we find that the Old World apes are more closely allied to man than are the New World apes, and this is exactly in accordance with the opinion expressed by Darwin." But for the most part, Nuttall's work went unrecognized for decades.

Perhaps the most influential publication of the early 1960s in the area of biochemistry and relatedness was Emile Zuckerkandl and Linus Pauling's 1962 chapter on fetal and adult hemoglobin. They compared human, gorilla, horse, and fish sequences and found that the fish was more dissimilar to the human than to the horse and that the gorilla was most similar to the human. Because this arrangement mirrored the morphologically based phylogeny of these taxa, Zuckerkandl and Pauling believed that their observations "can be understood at once if it is *assumed* that in the course of time the hemoglobin-chain genes duplicate, [and] that the descendants of the duplicate genes 'mutate away' from each other" (emphasis added). From this assumption, they concluded that "over-all similarity must be an expression of evolutionary history," with descendants "mutating away" and becoming "gradually more different from each other." That is, the more ancient a lineage, the more molecular difference its descendants will gradually accumulate. Consequently, evolutionary closeness became equated with molecular difference despite the fact that Zuckerkandl and Pauling's study did not justify assuming that "over-all similarity" is "an expression of evolutionary history," that difference always reflects the same directionality of change, or that molecular change accrues at a constant and gradual rate. Nevertheless, as Adalgisa Caccone and Jeffrey R. Powell wrote in 1989, "Virtually all molecular phylogenetic studies . . . have a major underlying assumption: The genetic similarity or difference among taxa is an indication of phylogenetic relatedness. Lineages that diverged more recently will be genetically more similar to one another than will be lineages with more ancient splits." Embrace the assumption and the rest may follow logically, but not necessarily biologically.

In 1966, Vincent Sarich and Allan Wilson began investigating primate evolutionary relationships using albumin, translating degree of reactivity between albumin and anti-albumin into "immunological distance" (ID). An ID value of 1.0 meant "identical" (as in combining serum and antiserum of the same individual). The closer an ID value was to 1.0, the greater the overall molecular similarity and thus, by extension, the more closely related the taxa under study. As a "check" on the validity of this approach, Sarich and Wilson conceived the "test of reciprocity" (reversing whose serum or antiserum was used), which usually confirmed the initial finding. Because their arrangement of the primates agreed more with than it differed from the morphologically based pattern of primate relationships, they concluded that the "data are in qualitative agreement with the anatomical evidence, on the basis of which the apes, Old World monkeys, New World monkeys, prosimians, and nonprimates are placed in taxa which form a series of decreasing genetic relationship to man."

The following year, Sarich and Wilson argued that molecular change occurred at a constant rate among all major groups of primates and that, if the small difference between hominoid albumins reflected little molecular change, little time must have elapsed since the hominoid lineages separated. They claimed that because molecular change was constant, IDs represented a "molecular clock," which they calibrated on the fossil-based interpretation of when the Old World monkey and hominoid lineages supposedly split and then calculated that gibbons diverged approximately 10 million years ago, orangutans diverged approximately 8 million years ago, and humans and African apes diverged approximately 5 million years ago. The obvious implication was that fossils older than 5 million years, such as *Ramapithecus* (= *Sivapithecus*) from approximately 12 to 14 million-year-old deposits in Indo-Pakistan, could not, as their morphology indicated, be hominid. In 1971, while defending the correctness of the molecular clock, Sarich rejected as being of any phylogenetic significance the very morphology on which the clock was predicated.

But although all molecular systematists accepted the molecular assumption, M. Goodman and others did not embrace a constant molecular clock. Because Goodman accepted the paleontologically derived date of less than 14 million years ago for the hominid–ape split, he had to offer a different explanation for the small difference between hominoid albumins.

Although similar to other anthropoids in having hemochorial placentation, large-bodied hominoids have longer gestation periods. As such, Goodman argued, whereas in animals with hemochorial

placentation but short gestation periods parturition would occur before the mother's immune system could produce antibodies to any molecular differences in the fetus, in large-bodied hominoids the gestation period is long enough not only for maternal–fetal immunological incompatibility to build up but also for maternally produced antibodies to diffuse through the placenta and attack the fetus. Consequently, selection must have acted to reduce the possibility of maternal–fetal immune interaction by slowing down the rate of molecular change in hominoids with longer gestation periods.

Protein sequences were also used to determine evolutionary relationships. As mentioned earlier, Zuckerkandl and Pauling first sequenced hemoglobin in 1962. In 1973, A. E. Romero-Herrera and colleagues analyzed myoglobin sequences of various taxa. The most "parsimonious" arrangement of hominoids placed the gibbon closer than the orangutan to a human–African clade. The order of the gibbon and orangutan could be reversed only by invoking a more complicated scenario of hominoid myoglobin "evolution," including specifying various "back-mutations" to the presumed primitive state.

But although protein sequences were seen by some, especially Zuckerkandl as late as 1987, as appropriate for analyzing evolutionary relationships, others thought that the "best" systematic information lay at a deeper "genetic" level. Because base differences at the third base position did not produce different amino acids, the concern was that demonstration of similarity in protein sequences could produce "false" phylogenies because the underlying nucleotide sequences could be different. The expectation (based on bacteria and inferred for metazoans) was a direct correlation between specific DNA sequences and specific genes. In addition, because DNA sequences are composed of thousands of bases, there was the appeal of a vast amount of supposedly phylogenetically relevant information. But because DNA sequencing, although possible by the late 1970s, was expensive and laborious, an alternative approach—DNA hybridization—was used.

The justification for using DNA hybridization as an approximation of overall DNA sequence similarity between different taxa lay in the fact that not only will two separated strands of DNA from the same individual reassociate (reanneal) via their complementary bases, but any two single strands of DNA from different taxa will attempt to recombine or hybridize at complementary base positions. The more complementary sites between hybridized DNA strands, the more heat is needed to melt the bonds between them. From the molecular assumption followed the assumption that differences in melting temperatures reflected degrees of molecular similarity that reflected evolutionary relatedness. But because DNA hybridization relied on an assessment of overall similarity rather than the identity of sequences of bases, similar differences in melting temperatures obtained for different pairs of taxa might not be due to hybridization of the same regions of DNA. This is not a trivial concern because, DNA sequences, even if homologous, are not the same length in all animals, large-bodied hominoids included.

In 1968, R. J. Britten and D. E. Kohne first employed DNA hybridization in 1968 and found that the genomes of higher organisms—but not of bacteria or viruses—contained "hundreds of thousands of copies of DNA sequences" (repeated DNA) that not only represented a considerable portion of a genome but also were "trivial and permanently inert." Only a small fraction of a genome was composed of apparently active or functional single-copy DNA. They also argued that theories of genomic change must be considered on two levels: the change in nucleotide sequence (gradually via point mutations) and the origin of new families of nucleotide sequences (suddenly via "saltatory replications"). The former explains only the "divergence of pre-existing families" of nucleotide sequences, whereas "saltatory replications of genes or gene fragments occurring at infrequent intervals during geologic history might have profound and perhaps delayed results on the course of evolution." Although a model of "saltatory replication" is not embraced by molecular systematists, it poses a serious challenge to the "molecular assumption" and appears to have been borne out with the identification during the 1990s of the vertebrate *Hox-a-d* genes as replicates of the *Antennapedia* gene of fruit flies.

During the 1980s, Charles Sibley and Jon Ahlquist questioned previous DNA hybridization experiments due to the limited number of cross-hybridizations that were tested. This, they claimed, was the reason why certain evolutionary relationships could not be resolved. They made a point of the lack of resolution of the relationship between humans and African apes that, although based on little morphology, had become the favored molecular hypothesis. They also argued that one must create hybrids only with single-copy

DNA. And because DNA hybrid strands will link up only along complementary stretches of bases, there should be no question about homology.

Sibley and Ahlquist proposed a uniform average rate of genomic change (UAR), which they believed characterized molecular, and thus evolutionary, change in all taxa. By assuming a UAR, they also sidestepped the molecular clock debate. The power of DNA hybridization in "discovering" the phylogenetic relationships of organisms supposedly came from sampling entire genomes. Because an organism's genome is composed of millions of nucleotides, the "law of large numbers" seemingly eliminated the problem of an analysis being thrown off by "false" similarities or parallelisms.

In 1983, Sibley and Ahlquist converted differences in melting temperatures for DNA hybrids into phylogenetic distances using a procedure called "average linkage," which begins "by clustering the closest pair or pairs of taxa," after which "one links the taxa which have the smallest average distance to any existing cluster" until "all taxa are linked." The underlying assumption is that DNA hybridization "measures the net divergence between the homologous nucleotide sequences of the species being compared."

Many aspects of Sibley and Ahlquist's phylogenetic reconstructions of birds were consistent with theories of relatedness derived from study of morphology. But there were some significant differences, for instance, with regard to the broader phylogenetic relationships of, as well as the details of relatedness among, the flycatchers. However, by the 1980s, it was common practice, when molecular and the morphological phylogenies were in discord, to opt for the former. The molecular assumption demands that a molecular phylogeny be correct in its entirety, even if other information contradicts it.

The appeal of Sibley and Ahlquist's "law of large numbers" and UAR was probably the reason why paleontologists finally gave in to the notion that when molecularly and morphologically based phylogenies were in conflict, the former had greater authority. But not all molecular systematists were convinced. Templeton, for instance, rejected DNA hybridization because one could not determine the polarity of the similarity and thus address the question: Is similarity due to distant or recent common ancestry? He favored studying actual nucleotide sequences. Sibley and Ahlquist countered that there was "no reason to expect data derived from base sequences to improve on those from amino acid sequences, which have produced contradictory results." Nevertheless, the role of DNA sequences in deciphering evolutionary relationships assumed special significance due to the supposed information content of nuclear DNA. As E. J. Bruce and F. J. Ayala wrote in 1979, "Information macromolecules—i.e., nucleic acids and proteins—document evolutionary history. . . . [Thus,] degrees of similarity in such macromolecules reflect, on the whole, degrees of phylogenetic propinquity."

In 1979, W. M. Brown and colleagues found more difference between humans and a sampling of Old World monkeys in their mitochondrial (mt) DNA than in their nuclear DNA. Accepting the paleontologically estimated divergence between the human and Old World monkey lineages as more than 20 million years ago, they calculated that nucleotide substitutions occur 5 to 10 times more slowly in nuclear DNA than in mt DNA; that is, mt DNA "evolves" 5 to 10 times faster than nuclear DNA. From this, Brown and colleagues argued that mt DNA is better for studying evolutionary events that occurred "within the past 3–10 million years." Although their data showed the fewest differences (interpreted as substitutions) between humans and chimpanzees, Brown and colleagues presented humans as being related to an African ape group. Given the molecular assumption, however, the data should have yielded a human–chimpanzee sister group, as M. Ruvolo and colleagues concluded from their 1991 analysis of mt DNA.

One assumption about mt DNA is that, because it is single-stranded, it is not subject to the complexities that occur through recombination of maternal and paternal DNA; it is supposed to be inherited clonally only through the maternal line. Another assumption is the existence of a "hotspot" (the "hypervariable zone") in the D-looped configuration of mt DNA that is the primary site of molecular activity and, therefore, the source of evidence of evolutionary change. The introduction of paternal mt DNA into fertilized eggs has been reported, however, and according to Erika Hagelberg, there is increasing indication that mt DNA is not as exempt from paternal inheritance and recombination as was initially believed. Hagelberg also pointed out, in a 2003 article, that "there is no direct evidence of hypervariability," although "most researchers believe that anomalous patterns of DNA substitution are best explained by mutation." Indeed, "because the notion of hypervariability fits with the

received view of mt DNA clonality, anomalies are seldom questioned."

Questions also arose concerning the comparisons of sequence data, especially with regard to alignment. Because compared DNA sequences are usually not the same length, decisions must be made about subdividing the shorter sequence to align its nucleotides with those of the longer sequence. Typically, sequence alignment is presented in the literature without justification and then is used in phylogenetic analysis. But as J. A. Lake warned in 1991, "The order of sequence alignment can bias the selection of tree topology." In addition to assumptions of alignment are those of whether, for one or another sequence, bases were inserted or deleted or one base was substituted for another.

In 2003, in *What It Means to Be 98% Chimpanzee*, Jonathan Marks gave an example of these problems with DNA sequences from a human and an orangutan by showing three different ways in which their bases can be aligned. Of course, one must first assume that the 40 bases in the human sequence have homologous counterparts in the 54 bases in the orangutan sequence:

Human: CCTCCGCCGCGCCG CTCCGC GCCGC-CGGGCA CGGCC CCGC

Orangutan: CC GTCGCCTCCGCCACGCCGCGC-CACCGGGCCGGGCCGGCCCGGCCCGCCCCGC

Human: CCTCCGCCGCGCCGCT CCGCGCCGC-CGGGCACGGCCCCGC

Orangutan: CCGTCGCCTCCGCCACGCCGCGC-CACCGGGCCGGGCCGGCCCGGCCCGCCCCGC

Human: CCTCCGCCGCGCCG CT CCGCGCCGC-CGGG CAC GGCC CCGC

Orangutan: CCGTCGCCTCCGCCACGCCGCGC-CACCGGGCCGGGCCGGCCCGGCCCGCCCCGC

Marks commented,

> The top one invokes five gaps and six base substitutions; the middle has only two gaps but nine base substitutions. And the bottom one has five gaps and only three base substitutions. The three pairs of sequences differ in the assumptions about which base in one species corresponds to which base in the other. While we might . . . choose the alignment that invokes the fewest inferred hypothetical evolutionary events, we still have to decide whether a gap "equals" a substitution. Does the bottom one win because it has a total of only eight differences? Or might the middle one win because a gap should be considered rare and thereby "worth," say, five base substitutions?
>
> We cannot know which is "right," and the one we choose will contain implicit information about what evolutionary events have occurred, which will in turn affect the amount of similarity we tally. How similar is this stretch of DNA between human and orangutan? There may be seven differences or there may be eleven differences, depending on how we decide the bases correspond to each other across the species—and that is, of course, assuming that a one-base gap is also equivalent to a five-base gap and to a base substitution.
>
> In a more general sense the problem of taking *quantitative* estimates of difference between entities that differ in *quality* is prevalent throughout the genetic comparison of human and ape. The comparison of DNA sequences presupposes that there are corresponding, homologous sequences in both species, which of course there must be if such a comparison is actually being undertaken. But other measurements have shown that a chimpanzee cell has 10% more DNA than a human cell. . . . But how do you work that information into the comparison?

These concerns have not, however, been widely appreciated by molecular anthropologists, who portray the analysis of DNA sequences as neutral and objective but still use an assumption of relatedness to inform the way in which they analyze the sequences they have aligned according to certain assumptions. Exemplary is the 1997 multiple DNA sequence analysis by Ruvolo, who sought to resolve the supposed dilemma of which African ape humans are more closely related to by assuming that humans and African apes were indeed a clade and that the orangutan was its sister taxon. Consequently, whatever differences were found in the orangutan data had to be considered primitive relative to any similarities that were delineated between humans and one African ape or both African apes.

In using the popular parsimony-based phylogenetic computer program PAUP (phylogenetic analysis using parsimony), it is common practice to "root" a phylogenetic analysis in a taxon that is chosen as the primitive sister taxon or out-group. But although rooting any analysis in a particular taxon may be

necessary for the algorithm to "work," this procedure artificially determines character polarity given that the taxon in which the tree is rooted is defined a priori as being primitive in its entirety. In turn, the taxa to which this taxon is the supposed primitive sister taxon are predetermined as being derived in whatever ways they differ from it.

This approach to analyzing nuclear DNA, mt DNA, and protein sequences (and most recently to hominoid morphology) presents its own set of problems. Consider the molecular assumption: Because molecular change is supposedly ongoing and accumulated in a succession of descendants, the degree of molecular similarity should reflect the antiquity or recency of lineage divergence. Accordingly, each lineage acquires its own unique array of molecular changes, which should make it increasingly different the longer it is in existence. On the other hand, by rooting an analysis in a particular taxon, one assumes that this taxon is totally primitive relative to the taxa whose sister taxon it is presumed to be. Yet the molecular assumption validates the use of overall similarity as the key to resolving phylogenetic relationships by contrasting it with the unique differences that earlier divergent lineages accumulated along their own and distinct evolutionary trajectories. Clearly, both assumptions cannot be correct at the same time. Either the earlier divergent taxa or lineages did not change but rather remained primitive (which is the logical extension of identifying a taxon as the outgroup in which to root a computer analysis), or they did change by accumulating their own suites of molecular difference (the basis of the molecular assumption), in which case they are at least in some aspects derived (and uniquely so, for that matter, due to their distinctive molecular histories) and not primitive relative to the taxa being compared with them.

In the realm of morphological systematics, according to Hennigian or cladistic principles, overall similarity is not de facto a clue to evolutionary relatedness. Similarity must be sorted out into features that reflect a hierarchy of inheritance—primitive features from ancient ancestors and derived features from more recent ancestors.

Because the pattern of life is a hierarchy of nested sets of smaller and smaller clades, interpretation of primitiveness versus derivedness depends on the hierarchical level that one is investigating. Primitive features (those retained in descendants) do not elucidate the relationships of taxa sharing them. Only derived features (those more recently emergent) can. Furthermore, one must understand that a derived feature at one level is a primitive retention at another level of the hierarchy. As Templeton suggested, theoretically at least, this approach should be applicable to molecular data. But to be cladistic, the comparison must embrace a wide range of taxa because this is the only way in which relative primitiveness and derivedness can be determined. It cannot be justified by a priori assumptions of directionality (i.e., the molecular assumption) or of relatedness or by comparison with a taxon that is defined from the beginning as primitive. In addition, one cannot assume that shared similarity translates directly into a theory of relatedness. Taxa may be similar not because they inherited changes that distinguished a recent common ancestor but rather because they share features that did not change from the ancestral condition.

Nevertheless, molecular studies are increasingly being identified as "cladistic." One argument is that nucleotide bases—C, G, T, and A—represent alternative character states. This might seem logical but is incorrect because bases are characters. Alternative molecular character states would be better represented, for example, by different arrangements of "gene" sequences with regard to *cis, trans,* and interchromosomal elements; patterns of introns and exons and of methylation of transposons or other elements; or pathways of molecular communication. Molecular systematists also claim that their analyses are cladistic because "shared molecular similarity" is supposed to equate with "shared derived." This, of course, reflects the molecular assumption, namely that recently diverged taxa share recently accumulated (and thus supposedly derived) molecular states. Thus, one identifies shared derived molecular states a posteriori, *after* one's chosen algorithm clusters taxa on the basis of their being more or less similar and also typically after rooting one's tree in a particular taxon. But this is not a cladistic analysis. The hypothesizing of primitive versus derived character states (themselves testable hypotheses) occurs *prior to* generating theories of relationship, and this is the only way in which the results of this can be testable.

Also deserving of comment is the assumption of continual molecular change that Zuckerkandl and Pauling used to explain their data: "over-all similarity *must* be an expression of evolutionary history" (emphasis added), with descendants "mutating away" from each other, becoming "gradually more different

from each other." Molecular clocks and UAR, for example, are predicated on this notion. Nevertheless, this is not a demonstration but rather an extrapolation of how something might occur.

The contradiction is that although the molecular assumption also predicts that constant molecular change will occur during gametogenesis, the only physical source of molecular change is ultraviolet radiation, which produces a very low mutation rate of 10^{-8} to 10^{-9} that is random with regard to affecting somatic or sex cells and specific molecules. Thus, any apparent concordance between the reality of the physical world and the concept of a constantly changing molecular world is an illusion.

The notion of constant and accumulative mutation affecting sex cells (the only way in which molecular change can be transgenerational) also contradicts the tendency of cells to be homeostatic, for example, via heat shock proteins that maintain cell membrane physical states through lipid transport, eliminate reading errors that occur during transcription and translation, chaperone other proteins, and ensure proper folding of other proteins such as transcription factors. This makes sense because unabated molecular change would undermine the integrity of cell function and would more likely lead to death than to organismal change.

It may be widely believed, and even true at some level, that "genomes diverge as a function of time," as Sean Carroll recently reiterated. But the fact that genomes differ (in whatever way in which difference, or similarity, is identified) does not inform how this difference arose. No doubt, some difference is due to the rare and random effects of ultraviolet radiation. Genomic difference may also be due to failed DNA repair or, as Britten and Kohne offered, saltatory events. Sibley and Ahlquist's "law of large numbers" may have an intuitive appeal; organisms are closely related because they share "lots" of their genome. But as Marks pointed out, humans share approximately 25% of their genome with bananas. Essentially, there is nothing in the detection of genomic difference or similarity that demands the "molecular assumption" or a theory of evolutionary relatedness.

How might we think about "morphology" and "molecules"? Is there really an evolutionary gulf between the two?

A major area of inquiry in developmental biology is how cells acquire positional information with regard to entire structures (e.g., where limbs will grow) and their components (e.g., limb segments). Morphological differences may be considered in light of differences in regional and overlapping domains of regulatory gene expression as well as in fields of molecular gradients (morphogenetic fields). As C. O. Lovejoy and colleagues hypothesized in 1999 with regard to the emergence of human pelvic shape,

> If a particular PI [positional information] gradient were to span *n* cell diameters, and those cells defined the ultimate anteroposterior dimension of the presumptive ilium (superoinferior in the adult human), then a slight increase in the steepness of its slope would cause that signal to span fewer cells, "distorting" the presumptive anlagen and substantially altering downstream adult morphology.

In other words, although traditionally conceived as involving myriad steps, "the transformation of the common ancestral pelvis [in its entirety] into that of early hominids may have been as 'simple' as a slight modification of a gradient." Thus, morphological novelty can arise via differences in gene expression and pathways of molecular communication and shifting domains of morphogenetic fields in conjunction with the physical and mechanical consequences of cellular organization—and it is at these levels of molecular interaction, not the accumulation of point mutations, that one should address questions of phylogenetic relatedness and also seek a connection between molecules and morphology.

One must realize that there is a difference between change at the genetic level and perceived phenotypic change. Common in the literature on the genetics of evolution is mistaken conflation of the two as constituting macromutation, the origin of species. Nevertheless, especially with increasing awareness from molecular biology that there are not "genes for" features, we must distinguish between what appears morphologically to have been the result of a macromutation (e.g., developing feathers instead of scales) and the underlying genetic–epigenetic interactive pathways.

As M.-C. King and A. C. Wilson alluded to in 1975, it is not through determining overall molecular or genomic similarity of organisms that we will understand their biology; rather, we will understand through delineating the development of their biology. This makes sense. If the inactivation or deletion of a transcriptional enhancer can shift sacral position caudally, or if expansion of a morphogenetic gradient

can fully transform a primitively narrow pelvic girdle with tall, thin ilial blades into a hominid's broad, deep, and squat structure, it is by studying these molecular events that we may profitably explore the molecular basis of morphology and consequently, through the analysis of both, the evolutionary relationships of complex organisms.

It is, then, appropriate to both question and expand our perceptions of what is or will be evolutionarily revealing at the molecular level. There has been a steady increase in the number of studies that demonstrate virtual molecular identity between taxa that are morphologically very different and then express astonishment at this apparent contradiction. As Carroll pointed out with regard to expectations of the human and chimpanzee genome projects, demonstrating molecular similarity is not equivalent to deciphering the pathways that make these hominoids so different in hard- and soft-tissue anatomy, physiology, reproductive biology, cognitive abilities, and behavior. Here, the "law of large numbers" fails to enlighten. Unlike in bacteria, in metazoans there is not a strict correspondence between a "gene" (a sequence of nucleotides bound by start and stop codons) and a "gene product" (a protein). In multicellular animals, RNA essentially directs the "show," for example, in reading select bases and splicing specific introns as it composes different proteins from the same stretches of DNA. The surprise that the International Chimpanzee Chromosome 22 Consortium had on comparing human chromosome 21 with its apparent chimpanzee counterpart chromosome 22—finding that these hominoids differ by 83% in their amino acid sequences but that this significant difference derives from very similar DNA sequences—provides a lesson: It is time to go beyond mechanically comparing molecular sequences or entire genomes and fanning the flames of a "molecules versus morphology" debate in seeking insight into evolutionary relationships. In light of molecular and developmental biology, the former is naive and the latter is certainly artificial.

— *Jeffrey H. Schwartz*

Further Readings

Brown, W. M., George, M., Jr., & Wilson, A. C. (1979). Rapid evolution of mitochondrial DNA. *Proceedings of the National Academy of Sciences USA, 76,* 1967–1971.

Goodman, M. (1962). Immunochemistry of the primates and primate evolution. *Annals of the New York Academy of Sciences, 102,* 219–234.

Hagelberg, E. (2003). Recombination or mutation rate heterogeneity? Implications for mitochondrial Eve. *Trends in Genetics, 19,* 84–90.

International Chimpanzee Chromosome 22 Consortium. (2004). DNA sequence and comparative analysis of chimpanzee chromosome 22. *Nature, 429,* 382–388.

Lake, J. A. (1991). The order of sequence alignment can bias the selection of tree topology. *Molecular Biology and Evolution, 8,* 378–385.

Lovejoy, C. O., Cohn, M. J., & White, T. D. (1999). Morphological analysis of the mammalian postcranium: A developmental perspective. *Proceedings of the National Academy of Sciences USA, 96,* 13247–13252.

Marks, J. (2003). *What it means to be 98% chimpanzee* (rev. ed.). Berkeley: University of California Press.

Romero-Herrera, A. E., Lehmann, H., Castillo, O., Joysey, K. A., & Friday, A. E. (1976). Myoglobin of the orangutan as a phylogenetic enigma. *Nature, 261,* 162–164.

Ruvolo, M. (1997). Molecular phylogeny of the hominoids: Inferences from multiple independent DNA sequence data sets. *Molecular Biology and Evolution, 14,* 248–265.

Ruvolo, M., Disotell, T. R., Allard, M. W., Brown, W. M., & Honeycutt, R. L. (1991). Resolution of the African hominoid trichotomy by use of a mitochondrial gene sequence. *Proceedings of the National Academy of Science USA, 88,* 1570–1574.

Sibley, C. G., & Ahlquist, J. E. (1983). Phylogeny and classification of birds based on the data of DNA–DNA hybridization. In R. F. Johnston (Ed.), *Current ornithology* (Vol. 1, pp. 245–292). New York: Plenum.

Morris, Desmond (1928–)

Desmond Morris has been referred to as a Renaissance man. He is widely known in both scientific and artistic circles. He has been a prolific author of children's and adult books, nonfiction and fiction. He has made films and hosted television programs on animal behavior and other zoological topics. He has also been a successful surrealist painter for over 50 years.