

Molecular Anthropology

Beginning with the study of serology in the first decade of the twentieth century, molecular genetic data have had an ambiguous role in physical anthropology. Though often attractive for their reductionist nature, molecular data have proved frequently difficult to interpret when applied to anthropological questions.

The term "molecular anthropology" was coined by the American chemist, Emile Zuckerkandl, shortly after the elaboration of the structure of DNA and the genetic code. First isolated by Miescher in 1869, deoxyribonucleic acid was thought to be a large, simple biomolecule, not complex enough to encode genetic information. Though a series of well-controlled experiments indicated by the mid-1940s that DNA was indeed identical with the genetic instructions (Avery et al. 1944), it met forceful opposition from the American biochemist Alfred Mirsky (McCarty 1985). A less clear-cut experiment refocused interest a few years later on DNA, rather than on protein, as the substance of which genes are made (Hershey & Chase 1952).

The structure of DNA was established by James D. Watson and Francis H.C. Crick (1953), based on inferences about its composition derived from the chemical analysis of Erwin Chargaff (1950). As described in Watson's lively and candid memoir, *The Double Helix* (1968), Watson and Crick stayed barely a step ahead of the American chemist Linus Pauling (1901–1994) in their elucidation of the structure, relying heavily on unpublished X-ray diffraction photographs taken by an unpopular colleague, Rosalind Franklin (1920–1958).

Blood-Group Serology

Molecular anthropology, however, long antedates the molecular revolution of the 1950s. "Blood" is a strong metaphor for heredity, and hereditary relationships among organisms could apparently be reconstructed from properties of the blood, as demonstrated by George H.F. Nuttall (1862–1937) (1904).

In the first half of the twentieth century,

when the overarching goal of physical anthropology was to establish the number and identity of the fundamental subdivisions of the human species, the blood groups were recruited in the endeavor. Discovered by the German immunologist Karl Landsteiner (1868–1943) in 1900, the ABO system is now known to be governed by three major alleles (A, B, O), resulting in six genotypes (OO, AO, AA, BO, BB, AB) and four blood-group phenotypes (O, A, B, AB). Most populations have all three alleles; what varies is merely the proportion of the alleles within each population (see Table 1). The major source of variation here, then, is polymorphic (within-population variation), and the nature of the variation across populations is clinal (changing gradually with geographical distance).

Early serological studies, however, failed to interpret their findings this way (see Fig. 1). The first surveys during World War I managed to divide the human species into three groups in accordance with their ABO blood groups: European, Intermediate, and Asio-African (Hirschfeld & Hirschfeld 1919). This fell into strong accord with a worldview that separated Europeans racially or constitutionally from the rest of human populations.

Racial invasions of pure A and B peoples superimposing themselves on a primordially O species were invoked to explain the prevalence of polymorphism. Finding little A and virtually no B among Native Americans, serologists interpreted this not as the random loss of alleles due to genetic drift, but rather as evidence that all Old World populations were more closely related to one another than any was to Native American populations (Coca & Diebert 1923). The American geneticist Laurence Snyder (1926) revised the racial analysis of ABO blood groups, identifying seven racial types in the human species, based on their allele frequencies. These were not, however, at all harmonious with the phenotypic clusters identified in the species, leading the American physical anthropologist Earnest A. Hooton (1887–1954) (1931) to doubt the fundamental utility of serology in physical anthropology as focused on "races."

The American immunologist William C. Boyd (1903–1983) refined the use of blood groups in the study of human diversity, but he continued to interpret his results in the context of races. In 1940, when the most useful traits for racial analysis were considered to be *nonadaptive* traits, Boyd argued for the superiority of serological data on the basis of

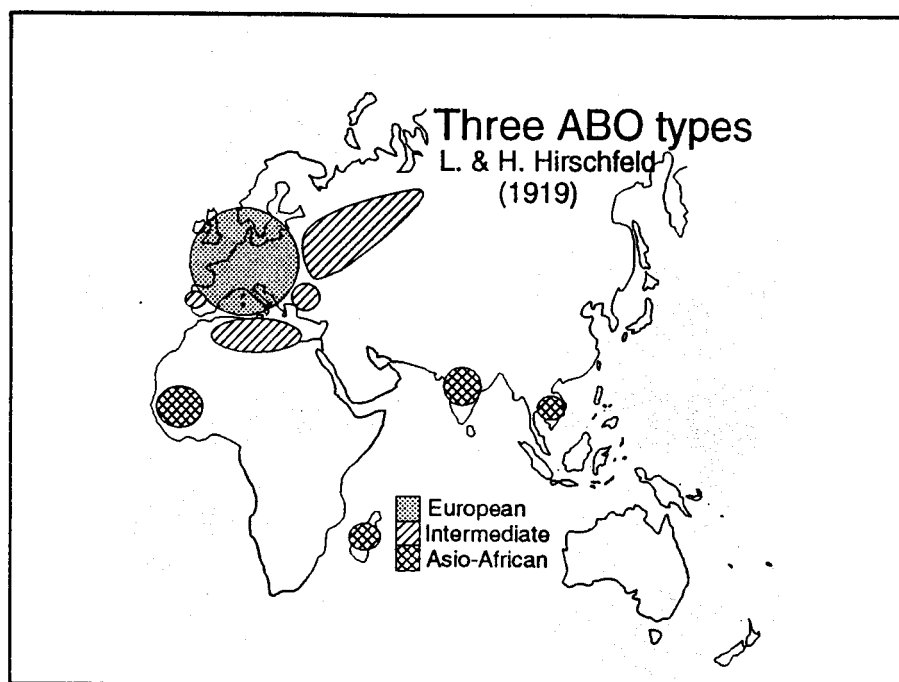


Fig. 1. Geographic samples used by the Hirschfelds (a.k.a Hirszfelf) to separate Europeans from other human populations on the basis of ABO blood group types.

their nonadaptive nature; in 1963, when the optimal racial traits were considered to be *adaptive*, Boyd argued for superiority of serological data on the basis of their adaptive nature. These data, apparently, were the best, no matter what criteria were applied. This reflects not so much the scientific value of genetic data, but the cultural value of hereditarianism—a belief in the simple primacy of genetics.

The Molecular Clock

In 1962, the chemists Zuckerkandl and Pauling analyzed the (sparse) amino-acid sequence data for hemoglobin. Assuming a constant rate of change, they estimated that if humans and horses differed by eighteen amino acids, and shared a common ancestor 100–160 mya, then humans and gorillas diverged about 11.0 mya. An empirical justification for that assumption was given the following year by the biochemist Emanuel Margoliash for cytochrome c. Observing approximately the same number of amino-acid differences between a bird and each of four species of mammals, a fish and each of five species of amniotes, or a yeast and six species of vertebrates, Margoliash inferred that rates of change in different lineages were approximately equal.

With more data available on hemoglobins, Zuckerkandl and Pauling found “an approximate constancy in rate of evolution of different hemoglobin chains” (1965:144) and drew the obvious implication: “*There may thus*

exist a molecular evolutionary clock” (1965:148, emphasis in original). In addition, they noted a great deal of flexibility of structure in relation to protein function and suggested that most amino-acid substitutions had minimal effects on the functional integrity of the protein.

Calculations performed by the Japanese population geneticist Motoo Kimura (1968)

TABLE 1. ABO allele frequencies from representative populations. (From A.E. Mourant, A.C. Kopeć, and K. Domaniewska-Sobczak: *The Distribution of Human Blood Groups and Other Polymorphisms*. 2nd ed. New York, 1976).

Aboriginal population		Allele frequency		
		A	B	O
America	Chippewa	.06	.00	.94
	Kwakiutl	.10	.00	.90
Europe	Denmark	.27	.08	.66
	Bulgaria	.31	.12	.56
	Ukraine	.27	.16	.57
Asia	Kazakhstan	.25	.27	.48
	Pakistan	.20	.25	.55
	Japan	.29	.16	.54
Oceania	Australia	.18	.04	.78
Africa	Efe Pygmies	.26	.21	.53
	Angola	.16	.11	.72
	Sierra Leone	.16	.15	.69

suggested that the high rate of detectable genetic substitutions in proteins might be attributable to the mutations being of roughly equal fitness value, or "neutral." The "neutral theory" gave a theoretical justification for the apparent general constancy of the rate of molecular evolution.

Sequencing proteins, however, was costly and difficult. An estimate of genetic differences between taxa could be made using the vertebrate immune system. The significance of this approach lay in the close association between the immunological reaction and the genetic material itself. A foreign protein can stimulate an immunological reaction in a different species. Vertebrate blood, immunized against a protein derived from a particular species, can distinguish that protein from its homologue in a different species. The immunological reactions could thus measure differences in protein structure, which were a reflection of differences in genetic structure.

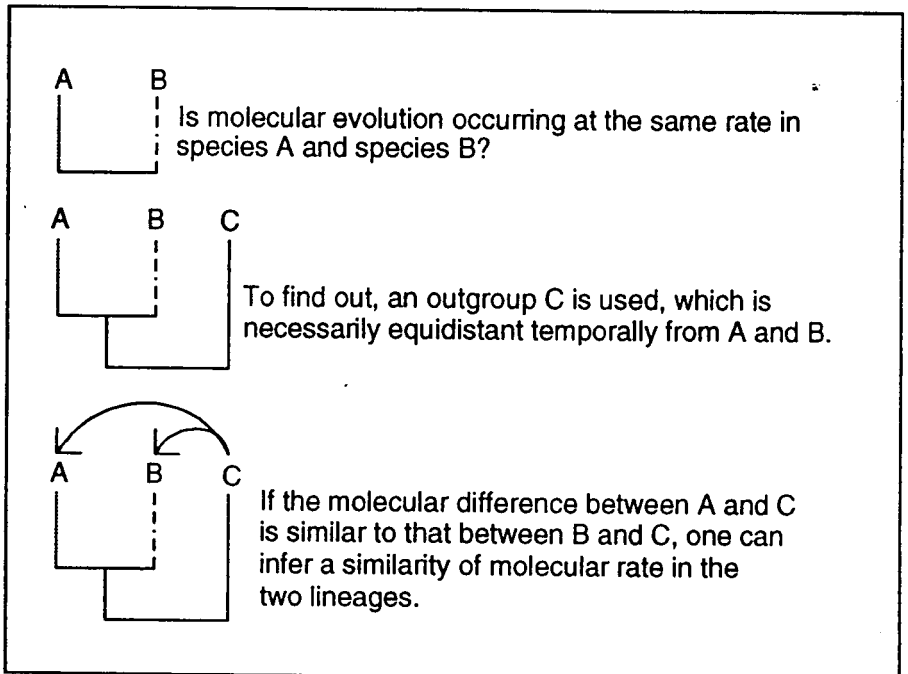
Serological Macroevolution and Molecular Systematics

Two major studies in the 1960s brought the application of serological techniques to the forefront of physical anthropology. Nuttall (1904) had shown that the extent of immunological cross-reactions roughly re-create the taxonomic affinities of primate species, though with notable exceptions, such as failing to detect that prosimians are primates. In 1962 the American molecular biologist

Morris Goodman (1925–) demonstrated a major taxonomic paradox: Serologically, chimpanzees and gorillas clustered with humans (as an African group) rather than with orangutans (as a "great ape" group). As the serological data were arguably tracking genetic affinities more closely than traditional phenotypic analyses were, the phylogenetic conclusions gained widespread acceptance (Simpson 1963). Goodman further maintained that this necessarily implied a revision of primate classification based on the phylogenetic revision, but most systematists chose to retain the paraphyletic family Pongidae. The school of systematics known as cladism had not yet come into existence; years later, it would provide a retroactive validation for Goodman's viewpoint.

Technical modifications to the immunological studies permitted the results to be quantified by the mid-1960s, and were applied to the primates by the American bioanthropologist Vincent Sarich and New Zealand-born biochemist Allan Wilson (1934–1991) (cf. Sarich & Wilson 1967a, 1967b). The physical anthropologist Sherwood L. Washburn (1911–) had maintained a recent common ancestry of humans and apes, as recent as 1.0 mya (Washburn 1960, 1963). Application of the quantified immunological data to anthropoid evolution showed that immunological differences tended to accumulate in lineages at about the same rate, via the relative-rate test (see Fig. 2). Having estab-

Fig. 2. The relative rate test.



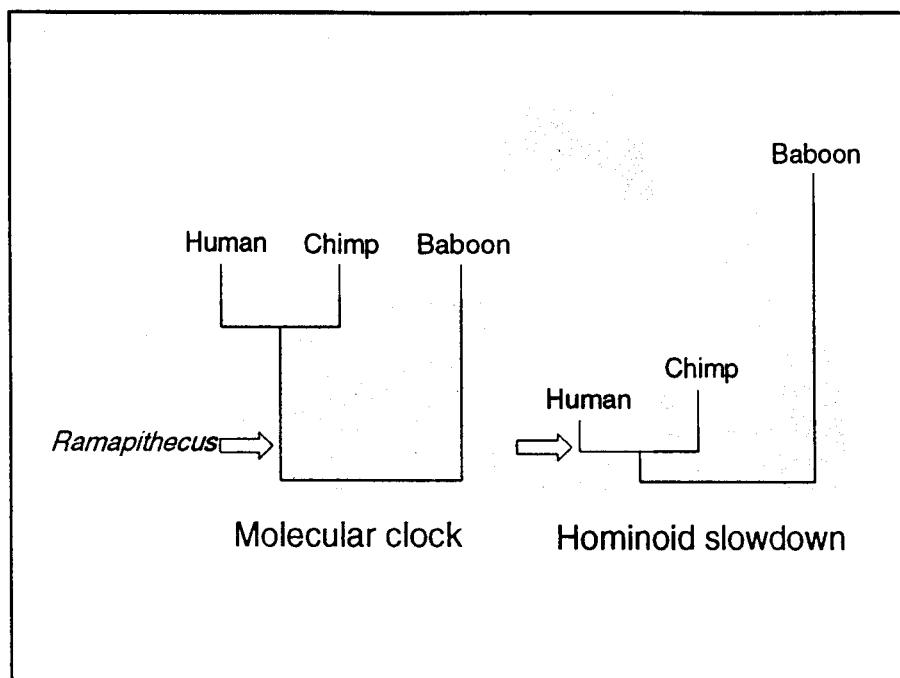


Fig. 3. The rate of molecular evolution could influence the phylogenetic placement of *Ramapithecus*.

lished this, Sarich and Wilson calculated that, given equal rates of change across lineages, the amount of change that had accumulated between humans and chimpanzees, relative to that which had accumulated between apes and Old World monkeys, implied a divergence date between humans and chimps of about 5.0 mya (Sarich & Wilson 1967a). This was later refined to 3.5 ± 1.5 my (Sarich 1968).

At the same time, however, certain features of the dental anatomy in the fossil genus *Ramapithecus* were being invoked to establish its presence on the unique evolutionary line ending in our species. Since this genus (being synonymized with *Kenyapithecus*) appeared to be present in East Africa 14.0 mya, it implied a human split from the apes prior to that date. The molecular data, in undermining the date, appeared to undermine the hominid allocation of *Ramapithecus* as well. If there was no uniquely human line until 3.5 my, obviously *Ramapithecus* could not have been on it at 14.0 my. Thus, argued Sarich, even given some play in the molecular dating, "one no longer has the option of considering a fossil specimen older than about 8 million years as a hominid *no matter what it looks like*" (Sarich 1970:199, emphasis in original).

Alternatively, it was conceivable that molecular evolution had proceeded at an aberrantly slow rate in the human lineage, such that a relatively long time elapsed with little molecular change (see Fig. 3). This could preserve the hominid allocation of *Ramapithecus*

by retaining an ancient separation for human and chimpanzee, with anomalously little detectable genetic change having occurred since that separation. Such a hominid slowdown, however, was not detectable by the relative-rate test.

Though few genetic regions have been analyzed, studies since the late 1980s have found a slower rate of molecular evolution in the human line, but of insufficient magnitude to have a major effect. And the anatomy of *Ramapithecus* has been reinterpreted, based on subsequent discoveries in Turkey and Pakistan.

The Trichotomy

The widely publicized success of the molecular clock resulted in a period of less critical acceptance of other biochemically generated results. Where earlier molecular studies had found humans, chimpanzees, and gorillas to be genetically so similar as to form a trichotomy, or three-way split, C.G. Sibley and J.E. Ahlquist (1984) claimed to have "resolved the trichotomy" into a human-chimpanzee association, with gorillas a distant third. Again, this appeared to conflict with most interpretations of the anatomy. David Pilbeam (1986), formerly a leading advocate of *Ramapithecus* in opposition to the molecular evidence, now vigorously promoted the new DNA hybridization work. This new-found advocacy, however, was now insufficiently critical of the molecular claims: it was found in short measure that the human-

chimpanzee linkage was not, in fact, sustained by those data, which was subsequently conceded (Marks et al. 1988; Sibley et al. 1990).

DNA studies have revealed considerable ambiguity in the relations of the African apes and humans, due to (1) their very close phylogenetic relationship; (2) the typological nature of these studies, sampling the relict remains of an originally diverse Miocene gene pool and generally reconstructing phylogeny from a single representative of each taxon; and (3) the extensive parallel evolution (homoplasy) that occurs in DNA.

What is clear is that if any pair of human, chimpanzee, and gorilla are closest relatives, the third is very close by. The complex gene pool of the Late Miocene hominoids appears to have been partitioned into three surviving taxa in a manner that is best described as a three-way split, or as two effectively contemporaneous speciation events (Rogers 1993).

Mitochondrial Eve

The pace of change in the determinants of serological specificity—presumably genes—precipitated the conflict over *Ramapithecus*. Cast in terms of the opposition of molecular data to morphological data, only one set was apparently able to yield an accurate phylogenetic inference. The promotion of DNA hybridization was able to capitalize on the newfound faith in molecules over morphology, while maintaining the same antagonism.

A somewhat different approach was taken by Rebecca Cann and her colleagues at Berkeley in a landmark paper (1987). Where two conflicting hypotheses existed in the paleoanthropological literature on the origin of modern humans, molecular data could now be applied to distinguish between them. The first, known as the regional-continuity model, implied deep local ancestries for genetic variation in the human species, while the second, known as the Out-of-Africa model, suggested a shallow ancestry traceable specifically to Africa. Cann and colleagues, analyzing differences in specific DNA marker sequences, found that the patterns of genetic diversity they encountered supported the latter model. Rather than take a hegemonic approach to the traditional avenues of anthropological research, this work was presented as complementary to them—a radical change in style. The precise relationship between patterns of modern genetic variation and the reconstruction of human prehistory is no longer clear, however.

Gene and Genome Structure

The study of physical anthropology is predicated to some extent upon genetics, for evolution is ultimately a genetic process. Little was known about gene structure and function until mid-century, when it was established that genes were composed of DNA, and the structure of DNA was elucidated.

In the phrase "one gene—one enzyme," G.W. Beadle and E.L. Tatum (1941) encapsulated the inference that at the primary level of function, a gene is responsible for the production of a single operational macromolecule. Following the work of Watson and Crick, the cellular role of nucleic acids became the central focus of molecular genetics. In the classic metaphor of the 1960s, the genetic "code" was broken, and the rudiments of transcription (making an RNA copy from a DNA template) and translation (making a protein from the RNA) led to a recognition that the DNA, RNA, and protein molecules were colinear—that is, their polymeric sequences were direct reflections of one another (Judson 1979). The 1970s yielded the recognition that the RNA transcript is extensively modified prior to being translated.

Perhaps the most fundamental revision of molecular genetics in the latter half of the twentieth century, however, has been in our understanding of the structure of the genome, the entire DNA complement of a cell. The pioneering work of the American geneticist Thomas Hunt Morgan (1866–1945) and his coworkers at Columbia University established that genes (i.e., functional hereditary units) were found in a characteristic fixed sequence, each in a specific location on a linear chromosome. The metaphor used to represent the relationship between genes and chromosomes was that the genes were "beads on a string" (Morgan et al. 1915).

By the 1960s, however, it was becoming clear that there was far more DNA in a cell than could be accountable by recourse to genes. In other words, there was a great deal of string linking relatively few beads. Further, there seemed to be a great deal of variation in genome size without apparent relationship to organismal complexity, producing a "C-value paradox," where the C-value is a measure of genome size (Mirsky & Ris 1951; Thomas 1971).

By the late 1960s, satellite DNA (with a slightly different composition than the bulk of genomic DNA, thus appearing as a "satellite" peak on a densitometric tracing) was recognized to be a significant portion of the genome. Satellite DNA consists of simple

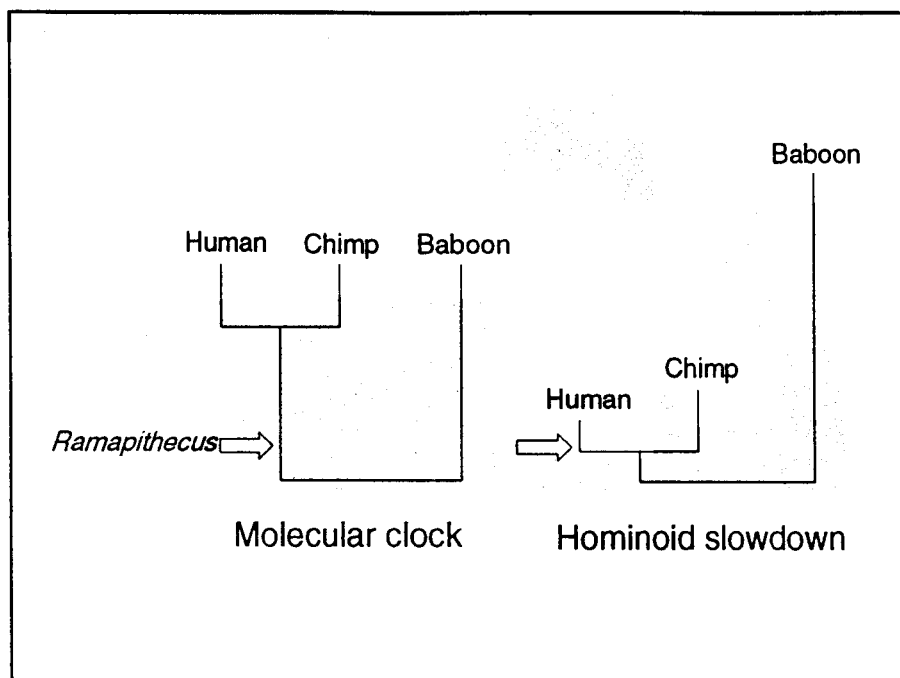


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DNA sequences tandemly repeated millions of times; it is transcriptionally inactive and localized in its chromosomal distribution. In addition, it appeared to be phylogenetically unstable, for closely related species differed markedly in the proportion of the genome taken by the same class of satellite DNA (Flamm et al. 1967; Britten & Kohne 1968).

But a simple dichotomy of localized "repetitive" DNA, distinct from "unique-sequence" DNA, was undermined by the discovery of a large class of repetitive DNA that was not localized, but rather was interspersed within the "unique-sequence" DNA. The largest class of these interspersed elements is known as *Alu* repeats, and they probably occupy as much of the genome as the informational, coding fraction (Schmid & Jelinek 1982).

It also became apparent that genes themselves were not the solitary isolated entities they had been imagined to be, but were structurally related to other DNA sequences (Ingram 1961). Most genes were found to be members of families, and most gene families exist as localized gene clusters, of which the hemoglobin genes are paradigmatic (see Fig. 4).

Apparently, the genome has a battery of evolutionary modes by which DNA segments of varying lengths can become tandemly duplicated (Ohno 1970). If they happen to contain functional units (i.e., genes), the units are duplicated as well. The duplicate gene can then accumulate degenerative mutations (with no ill effect to the organism, for it still has a functional copy), or acquire a new func-

tion through mutation, or be maintained as a second copy if this is to the organism's advantage. Clearly, all three processes have occurred throughout the evolution of the vertebrate globin genes.

Thus, the dichotomy established between "unique-sequence" and "repetitive" DNA emerged to be false. Virtually all DNA is to some extent repetitive. What varies are the extent and the pattern of the redundancy.

Principles of Molecular Anthropology

Since the genome consists of mostly non-coding DNA, it follows that most genetic change is not expressed as phenotypic change. It also follows that the primary agent directing molecular evolution is genetic drift, a constant stochastic spread of adaptively equivalent variants. Consequently, genetic and phenotypic evolution are now approached in conceptually different ways. A researcher focusing on organismal phenotypes endeavors to explain why two taxa are phenotypically different from each other, and does so by recourse to directional selection. Genotypically, by contrast, two taxa are expected to differ, by virtue of the constant pressure of mutation and drift, and what requires explanation are *similarities*—why two DNA sequences are not as different as they might be, explained by recourse to stabilizing selection. This underlay the initial interest in homeoboxes, regions of DNA strongly conserved between flies and humans, unlike virtually any aspect of the bodies of those organisms.

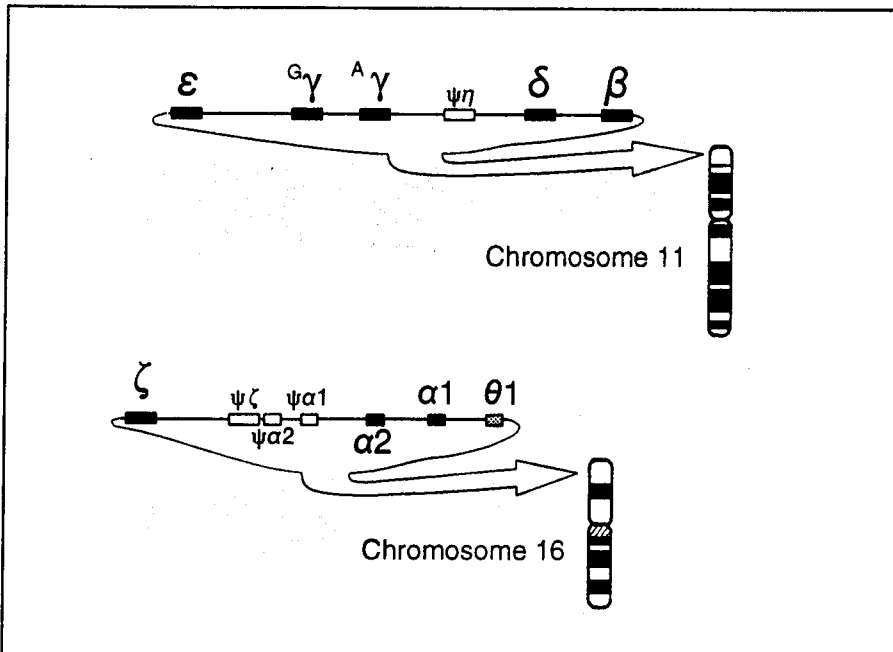


Fig. 4. The β -globin gene cluster, located on chromosome 11, contains an embryonic (ϵ) globin gene, two fetal (γ) genes, a non-functional "pseudogene" sequence ($\psi\eta$), a minor adult gene (δ), and the major adult gene (β). On chromosome 16 lie the structurally related α -globin genes: embryonic (ζ), a pseudogene of the embryonic gene ($\psi\zeta$), two pseudogenes of the adult genes ($\psi\alpha 2$ and $\psi\alpha 1$), the two adult genes ($\alpha 2$ and $\alpha 1$), and another gene of unknown function ($\theta 1$).

Another difficulty in reasoning from molecular to phenotypic evolutionary changes is the fact that they can occur largely independently of one another. The growing organism is both phenotypically plastic and developmentally canalized. As a consequence, except in rare pathological mutations (genetic diseases) it is very difficult to trace specific genetic variations to specific phenotypic variations. Recent conceptions of evolution have, consequently, tended to present changes in DNA or proteins as a basic "level" in an evolutionary hierarchy, in contrast principally to changes in organismal phenotypes (King & Wilson 1975; Gould 1980).

Finally, the most appropriate manner of extracting phylogeny from DNA sequences that has emerged is far from self-evident. DNA sequences are attractive by virtue of their amenability to quantitative treatment. But since there are only four nucleotides, a 25 percent similarity in DNA sequence is random—in contrast to the anatomical comparison, in which comparisons may be more qualitative but there is no obvious limit to how different two organisms may be. Studies of the primates also reveal high levels of parallel evolution (homoplasy) in DNA sequences, which complicates the reconstruction of phylogeny.

In addition to phylogenetic reconstructions, molecular data are now being used to study microevolution, population structure, and demography; paternity diagnosis in non-human primate populations with promiscuous matings; and forensics, where DNA can be extracted and amplified not only from crime scenes, but from historic and prehistoric burials as well.

Molecular evolution has become an exciting research area, particularly because technology has outpaced theory. Generating creative explanations for the abundant data being collected will most likely be the source of the major breakthroughs for this field in the next generation.

Jonathan Marks

See also African Apes; Hooton, E(arnest) A(lbert); Landsteiner, Karl; Mutation; Paleoprimateology; *Ramapithecus*; Systematics (1960s–1990s); Washburn, Sherwood L.

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