

EVOLUTION: THE FOUNDATION OF BIOLOGY*

EVOLUCIÓN: EL FUNDAMENTO DE LA BIOLOGÍA

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ABSTRACT

Evolution is the most comprehensive, unifying theory in biology. It complements studies of how organisms function with “ultimate explanations” of why species have the characteristics they possess, rather than other features. This perspective, in which the principle of natural selection is paramountly important, explains countless features of organisms and their genomes that otherwise would be inexplicable, and provides a scientific explanation, based in a purely mindless process, for features of organisms that look as if they were consciously designed. Evolutionary science not only embraces and extends the other biological disciplines; it is also useful. From pest management to human genetics and the evolution of pathogenic microbes, the principles and methods of evolutionary biology are becoming indispensable.

RESUMEN

La más abocante y unificadora teoría de la Biología es la Teoría de la Evolución. Esta teoría complementa estudios funcionales de organismos con explicaciones distales de por qué esos organismos tienen las características que poseen y no otras. Esta perspectiva, en la cual el principio de selección natural es de importancia fundamental, explica innumerables características de los organismos y de sus genomas, que no podrían ser explicadas de otra manera. Así mismo, provee una explicación científica, basada en un proceso sin diseñador, para características que parecieran diseñadas conscientemente. La ciencia de la Evolución no solamente comprende y amplía a las otras disciplinas biológicas, sino que también tiene aplicaciones prácticas. Por ejemplo la Biología Evolutiva es indispensable en áreas como el manejo de plagas, la genética humana y la evolución de microbios patógenos.

Keywords: antibiotic resistance; Darwinian medicine; evidence for evolution; evolutionary applications; evolutionary history; natural selection; phylogeny; processes of evolution; ultimate explanation.

Palabras clave: Resistencia a los antibióticos; medicina Darwiniana; evidencia de la evolución; aplicaciones de la evolución; historia natural; selección natural; filogenia; procesos evolutivos; explicación distal.

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INTRODUCTION

My intention in this presentation is to provide a portrait of some major aspects of the field of evolutionary biology, and describe a few of the ways in which this subject is important.

Two grand questions are studied in evolutionary biology. First, what has happened in the history of life? Can we determine what has happened, and describe how and when the great diversity of living things, and the great diversity of their characteristics, came into existence? The major fields which undertake this task are paleontology (the study of the fossil record), and phylogenetics (the study of the evolutionary, genealogical relationships among different species). Second, how has evolution happened? What are the causes of evolution, and how have they produced the diversity of organisms and their characteristics? In order to answer this question fully, it will be necessary to draw on many fields of biological science, especially genetics and ecology.

Of course, both of these large questions are still imperfectly answered, and a great deal of research remains to be done. Nevertheless, immense advances in both of these areas have been made since Darwin, and have accelerated in the recent past (Futuyma, 2009; Bell *et al.*, 2010).

INFERENCES OF EVOLUTIONARY HISTORY

One of the most important tasks in the study of evolutionary history is to describe the historical transformations of the characteristics of organism. We wish to know, for example, whether the great changes in organisms, such as those that occurred in the origin of higher taxa such as angiosperms or mammals, happened gradually, by small steps as Darwin suggested, or by “jumps,” meaning large, abrupt changes.

By studying the fossil record, we know that in some instances, transformations have occurred very gradually. A conspicuous and important example is the fossil record of our own lineage. In the hominid lineage, the size of the brain increased since the earliest hominids (e.g., *Ardipithecus* and *Australopithecus*) gradually up to the large brains of *Homo sapiens* and *Homo neanderthalensis* in the very recent past.

When we turn to the origin of higher taxa, we cannot always show each small step by which evolution has happened, but we can often find critical intermediates between very different groups. A dramatic example is the increasing evidence on the origin of birds. We now know, from wonderful new fossils that are found especially in China, that there were diverse feathered dinosaurs, some of which could fly. The first such creature found was *Archaeopteryx*, discovered in the 1860's, but we now also have forms such as *Microraptor*, which had large flight feathers on both the front leg (that is, the wing) and on the hind leg: *Microraptor* was a four winged dinosaur. Another example of a critical intermediate form is *Tiktaalik*, an ancient (Devonian) vertebrate found just a few years ago, that adds to an increasingly complete series of transitional intermediates between the lobe-finned fishes and the tetrapods, the land-living amphibians. *Tiktaalik* demonstrates the origin of important features of the front limb, such as a wrist joint that was indispensable for lifting the body and walking on land.

Such intermediate forms show that contrary to the claims of creationists, plentiful evidence documents the origins of major new forms of life. (Intermediate fossils and other evidence for evolution are provided on several excellent Web sites, such as “Understanding Evolution” (<http://evolution.berkeley.edu>) and “The talk Origins Archive” (www.talkorigins.org). A rich source of information on all aspects of the conflict between scientists and creationists is the National Center for Science Education (www.ncse.com).

For many groups of organisms, such as those that lack hard parts, the fossil record provides little or no information. Nevertheless, we can infer many aspects of the history of the evolution of such organisms by comparing the characteristics of living species today, in the framework of a phylogeny, a tree that shows the relationships among species. The relationships are postulated from analyses of the similarities and differences among different organisms, in phenotypic characteristics or in DNA sequences. A great deal of research is devoted to improving the methods of determining relationships from such data.

For example, a phylogenetic tree of the major group of vertebrates shows that birds and crocodiles stem from a more recent common ancestor than they, in turn, share with mammals: the common ancestor of mammals, birds, and crocodiles existed further back in

the past. In this case and in many other cases, the hypothesized phylogenetic relationships that were inferred from traditional anatomical, and morphological data are the same as the relationships found by analyzing a totally different kind of data, namely sequences of DNA that correspond among these different organisms. When independent data give the same answer to a question, we gain confidence that we are approaching the correct answer. The correspondence between the traditional morphological interpretation of relationships among groups of vertebrates and the relationships based on DNA provides a great deal of confidence in our ability to infer phylogenies, and of course it also provides confidence in the reality of the historical process of evolution from common ancestors.

A strongly supported phylogeny, one in which we have confidence, enables us to say certain things about the history of the organisms' evolution. For example, we can specify where, on the tree, there evolved for the first time the amnion, the embryonic membrane that is characteristic of reptiles, birds, and mammals. We can infer from the position of birds and mammals, the two groups of homeothermic vertebrates in the tree, that homeothermy, the capacity to maintain constant body temperature, evolved twice, independently. These are simple examples of the many inferences that we can make about the history of evolution, from a phylogeny of this kind.

Let me offer another example. Fifteen or twenty years ago there was a great deal of argument about whether humans are more closely related to chimpanzee (genus *Pan*), or to the gorilla (*Gorilla*), or might be equally related to all of the apes (*Pan*, *Gorilla*, and *Pongo*, the Asian orangutan). That is, all the apes might form a single branch, from the same common ancestor as a separate human lineage. This is no longer a question, because everyone now agrees, based on extensive DNA evidence, that humans are most closely related to the genus *Pan*, the two species of chimpanzees. Both *Pan* and *Gorilla* live in Africa.

This relationship was already suspected by Darwin, long before we had evidence from DNA, and Darwin used this suspicion to make a prediction. In *The Descent of Man*, published in 1871, he wrote: 'In each great region of the world the living mammals are closely related to the extinct species of the same region. It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla

and chimpanzee, and as these two species are now man's nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere.

This was written fifty years before the first fossil hominids were found in Africa. Today, of course, we know that the entire early history of the hominid lineage occurred in Africa, and that the human species spread from Africa across the rest of the world. This is a wonderful example of how a phylogenetic point of view, and understanding of relationships among organisms, makes it possible to predict data that have not been yet found. Any scientific theory has power because it can make predictions about data that we do not yet have. This, indeed, is a test of the validity of the theory.

Knowing that humans must have emerged recently from Africa, we would envision that they spread through Eurasia and then America by successive colonizations, each accomplished by a rather small number of people. Each such group would carry just a fraction of the genetic variation, the variety of different genotypes that were present in the ancestral African population. Consequently, we expect to find that populations which are the farthest away, most distant from Africa, should have less genetic variation than populations that are closer to Africa. Exactly this pattern has been found (Figure 1). Again, evolutionary theory makes predictions that are upheld by evidence.

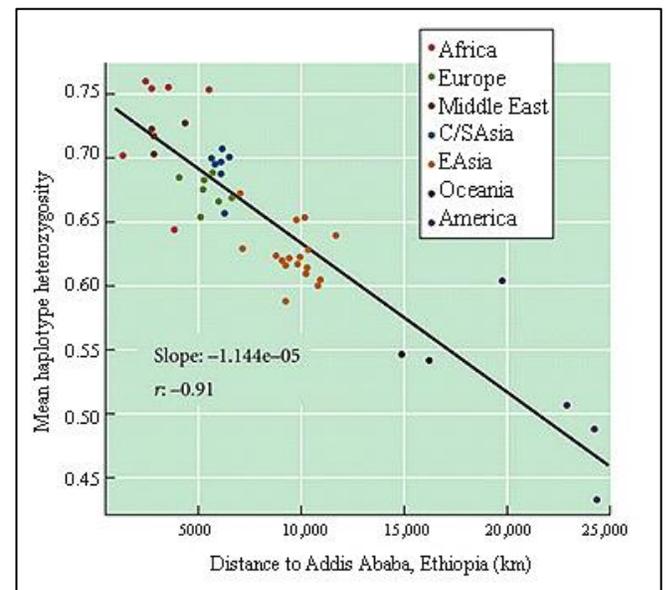


Figure 1. Genetic variation within human populations is lower, the farther they are from Africa.

Just as in human affairs it is often necessary to know history in order to understand why things are as they are today, so it is in biology. There are many, many features and characteristics of animals and plants and microbes that cannot be understood if we do not take the history of evolution into account. Only history can explain why almost every species has some features that are useless: they are vestiges of characteristics that were advantageous to the species' ancestors, but no longer have any function because of a change in the organism's environment or way of life. The human vermiform appendix and coccyx (fused tail bones) are famous examples. And the genome of every species contains thousands of pseudogenes: nontranscribed DNA sequences that resemble functional genes in the same genome or in other species. Evolutionary history also explains many puzzling functional features. For example, what appears to be the flower of the poinsettia, *Euphorbia pulcherrima*, known in Spanish as *noche buena* or *flor de pascua*, is actually a set of red leaves that surround the small, yellow flowers, which lack petals. The leaves have been modified to attract pollinating birds, which is the role of petals in most animal-pollinated plants. Why should this plant use leaves for this function? The entire phylogenetic branch to which this species belongs lacks petals, which must have been lost in an ancient common ancestor. When it became advantageous to attract birds, whatever suitable variations were present at that time were increased by natural selection. Such variations were present in the leaves, but the petals had apparently been irretrievably lost. The peculiar feature of this plant can be understood in light of its evolutionary history. And there are many examples of this kind.

PROCESSES OF EVOLUTION

The most elementary causes of evolution are these. First, mutations occur in DNA, usually during replication. These range from single base-pair substitutions to deletions or duplications of large blocks of genetic material, and even duplication of entire genomes. Each such mutation occurs in a single cell of a single organism, and the same mutation re-occurs very rarely. Therefore, each mutation is initially very rare: it has a low frequency in the species population. All available evidence indicates that mutations are not adaptively directed: the chance that a mutation occurs is not affected by whether or not it would be

advantageous in the organism's current environment.

Second, some DNA sequences affect phenotypic characteristics, such as an organism's biochemistry, morphology, behaviour, or life history. A mutation may or may not alter one or more characteristics. Some genes affect multiple characters (pleiotropy), and most characteristics develop through the action of several or many genes (polygenic traits). Understanding the evolution of phenotypic traits therefore requires us to understand genetics and developmental biology.

Third, newly arisen mutations contribute to genetic variation in phenotype, but evolution occurs only if one or more mutations increase from initially very low frequency, and become more prevalent. Ultimately, a mutation (which we may call a new allele) may become fixed, that is, it completely replaces the previously prevalent allele. The process of replacement is usually caused by one of two factors: random genetic drift and natural selection.

In random genetic drift, the frequency of one allele, compared to other alleles, can fluctuate purely at random because the mutation neither improves nor diminishes the fitness of individuals: it is neutral. Rarely, an allele that has arisen by mutation increases to fixation reaching a frequency of 1.0 entirely by random fluctuation. This process occurs more rapidly in small than in large populations.

Genetic drift is the basis of the "neutral theory of molecular evolution", which explains many aspects of DNA sequence variation and the nature of the genome.

For example, if a protein plays a very important function, many of the mutations which would affect its amino acid sequence are likely to interfere with that function; compared to a less important protein, a smaller proportion of mutations would be neutral, and a greater proportion would be eliminated by the death or reduced reproductive capacity of the organisms that carry the mutations. Consequently, the rate of DNA sequence evolution is lower for critically important genes than for DNA sequences that are less important or which lack function altogether. As the theory predicts, pseudogenes and other nontranslated sequences usually have higher rates of evolution: they differ more among species than do important protein-coding sequences (Figure 2).

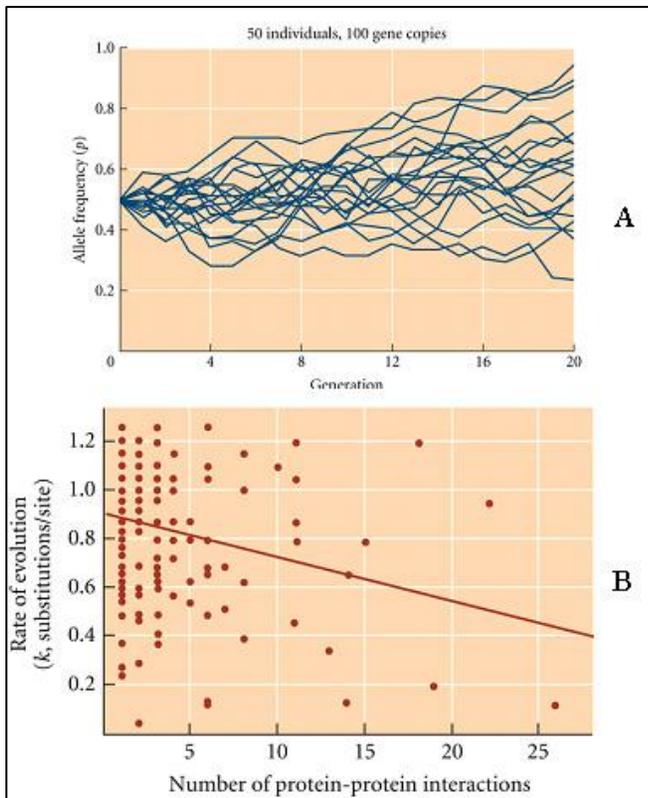


Figure 2. **A.** Genetic drift of neutral alleles. **B.** Proteins with fewer interactions with other proteins have fewer functional constraints, hence a higher fraction of nearly neutral mutations, hence a higher rate of sequence evolution by genetic drift.

Many molecular biologists today actually use this principle to understand whether or not a particular DNA sequence in the genome has an important function. They look for conserved regions of DNA sequence that are very similar among distantly related species, because those are sequences in which many mutations have been deleterious rather than neutral, and so the sequences have not evolved very much. So, the theory of neutral molecular evolution has become crucially important in the field of molecular biology.

I now turn to natural selection: Darwin's most important idea, one of the most important ideas that anyone has ever had in the history of the world. If we understand exactly what natural selection is, we will understand a great deal about biology.

Natural selection is simply a consistent, predictable difference in fitness among genotypes or phenotypes. "Fitness" means reproductive success. Reproductive success includes survival, because you cannot reproduce if you do not survive to reproductive age; so

reproductive success is survival and reproductive rate. Ecologists combine survival and reproductive rate into a single measurement, which is the rate of increase of numbers in the population. In the same way, we can look at the rate of increase in numbers of a genotype, or of a gene, compared to another genotype or another gene, in the same species population (Figure 3).

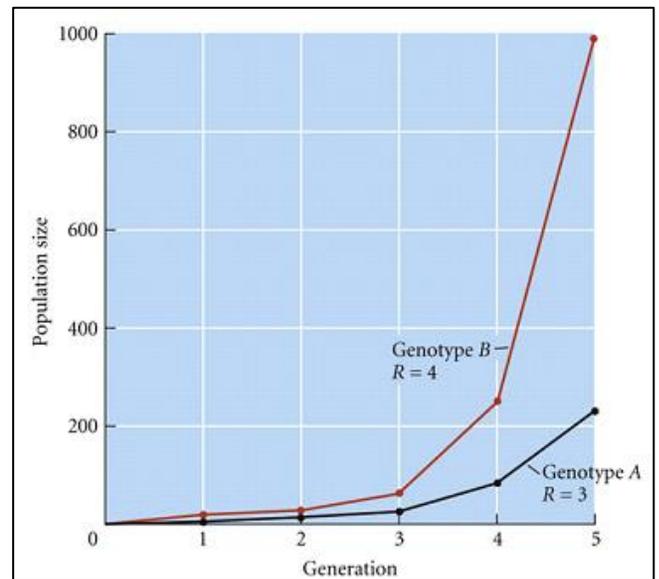


Figure 3. Natural selection is a consistent difference among genotypes or phenotypes, manifested as differences in reproductive success. (Components of reproductive success include survival and reproductive rate).

If, therefore, two genotypes differ in their rate of increase, because they differ in their survival or their rate of reproduction, either by males or females, that is natural selection. Natural selection is occurring because *individual genes* that are carried by *individual organisms* alter the survival or the reproduction of those individual organisms. This is not a process that can anticipate the future. Therefore, it cannot provide insurance against the possible extinction of a population or species, because that is a future event. The alleles that enhance the fitness of individual organisms might reduce the likelihood of species extinction – or they might not.

Natural selection is the mechanism that Darwin proposed to explain the wonderful adaptations of organisms, some of which are simply astonishing. For example, some tropical grasshoppers (Tettigoniidae)

look exactly like a dead leaf that has been damaged by insects and fungi. Vipers (Crotalidae and Viperidae) have an exquisite mechanism for attacking prey and defending themselves - poison glands connected to long, hollow teeth that are rotated against the roof of the mouth when not in use. These complex adaptations may look as if they have been designed, but the “designer” is a completely nonintelligent process. The discovery that design for a function can arise without an intelligent designer is one of the triumphs of science.

Because natural selection involves the survival or reproduction of individual organisms, natural selection “can honestly be described as a process for maximizing short-sighted selfishness,” as my late colleague George Williams wrote (Williams, 1989). This may not be an appealing perspective, and indeed, it should remind us never to look to “nature” for moral or ethical guidance, or to justify any code of human behaviour. But this view of natural selection explains many selfish characteristics. For instance, very often a young male lion will replace an older male by combat, take over a group of females, and kill all the babies of those females. This may not be good for survival of the species or the population as a whole, but that is not what natural selection is about. Natural selection is not the survival of species; it is the survival or reproduction of individuals that differ in their characteristics. If a gene disposes a male lion to kill the babies of the females that he now has obtained, and if the females then become sexually receptive sooner than they otherwise would, this action enables the male to become a father sooner, and to pass on that gene in greater abundance. So, infanticidal behaviour will evolve. Similarly, in some birds, such as boobies (Sulidae), one of the two chicks typically evicts its sibling from the nest while the parents stand by, without interfering. This may be adaptive for both the surviving chick and the parents, if the parents can bring enough food to raise only one offspring (Mock, 2004).

Organisms have countless characteristics that can be understood only as products of natural selection. For example, the males of many species of animals have bizarre characteristics, such as the very long front legs of the Neotropical long-horned beetle *Acrocinus longimanus* (Cerambycidae) and the very long tail feathers of many species of hummingbirds. In *The Descent of Man*, Darwin explained such characteristics by a form of natural selection that he called sexual selection: these features evolve because they enhance

the ability of males to fight for the possession of females or make the male more attractive to females. In either case, genes that enhance the feature will be passed on to the offspring. Today, there is extensive evidence for both of these hypotheses (Andersson, 1994).

Natural selection explains many strange characteristics of not only organisms, but also genomes. For example, a very large fraction of the genome of humans and of almost every other eukaryote consists of transposable elements which make copies of themselves that become inserted elsewhere in the genome. For the most part, these pieces of DNA are not useful for the organism; they are like parasites within the genome that reproduce and make more of themselves. But any process by which a gene can make more copies of itself leads inevitably to increasing numbers, even within a genome. Replication of “selfish” transposable elements within genomes epitomizes the simple dynamic of natural selection.

THE IMPORTANCE OF EVOLUTIONARY SCIENCE

Evolutionary biology provides understanding in every area of biological science. I have described examples of evolutionary insights into molecular biology, genomics, behaviour, and anatomy. There are other whole disciplines, such as evolutionary developmental biology and evolutionary ecology.

Evolutionary biology is also useful: it has wide-ranging practical applications and implications (Mindell, 2006).

We must, however, understand that we will not be able to apply evolutionary biology to socially useful ends if we do not have the foundation of basic science: a fundamental understanding of evolution and of the diversity of living things. In every area of science and engineering, the basic science, pursued without reference to its utility, is the foundation on which any kind of useful application rests. In biology, as in other sciences, a great deal of research may not have immediate utility, but is nevertheless important, for it contributes to a deeper understanding of the subject, which is necessary for intelligently applying biology to the needs of society.

Our knowledge of evolution enables us to understand many phenomena that are important to us. For example, humans, by exploiting or harvesting natural populations, sometimes cause rapid evolutionary changes that are contrary to our interests. Darwin thought that evolution by natural selection would always be so slow that it could never be detected, but this was one of the few points on which he was wrong. We now know that very often evolution of some characteristics can often be very rapid.

The Atlantic cod (*Gadus morhua*) at one time was one of the most important commercial fishes, in the northern Atlantic ocean. However, the population has been so overexploited that it became necessary to close the fishery. During the period of great overfishing, there has been an evolutionary change in the size and age at maturity. The fish now become reproductive at a younger age and smaller size, simply because the individual fish that were most likely to be taken by commercial nets were the largest ones. The fish that could succeed best in reproducing were smaller and younger: an instance of human-imposed natural selection that has resulted in an evolutionary change. Similar changes have occurred in other fish species, and in game animals such as wild sheep, in which horn size has become smaller because hunters preferentially shoot the animals with the largest horns.

Hundreds of species of pest insects and weeds have evolved resistance to chemical pesticides, and can no longer be controlled by them. This has occurred because rare mutations are present in the population of many kinds of plants and insects that fortuitously provide resistance to the novel chemicals we have invented. Individuals with these resistance factors are prone to survive and to increase prolifically, so the chemical treatment becomes less effective. So, we are in an “evolutionary race” to control these pests.

One of the most damaging pests of potato is the Colorado potato beetle (*Leptinotarsa decem-lineata*). Some populations of this insect have evolved to be resistant to almost every kind of insecticide. One alternative method of growing potatoes might be to develop strains that have their own resistance to the insect. We know that almost every species of plant, through evolution, has various kinds of chemicals which provide some defense against insects and other natural enemies. (The alkaloid caffeine, in coffee, is one such chemical.) One possibility would be to transfer natural chemical resistance from some kind of

wild plant into potato. Until recently, however, the only way to introduce a gene from one plant into another was to hybridize them, form fertile hybrids, and backcross the desirable trait into the crop.

Out of the thousands of species of plants that might have useful natural chemicals, which might we be able to cross with the potato? Obviously, we would say, the species which are most closely related. But then we need a method for determining which species are most closely related. This is an evolutionary problem. We need to know about the phylogenetic relationships among plant, and we need a reliable method for assessing relationships. Systematists have developed such methods, because they are interested in evolutionary relationships. Plant systematists have determined that potato is related to hundreds of species that constitute the genus *Solanum*, and they have determined which species within this genus are most closely related to *Solanum tuberosum*, the potato. Among them is *Solanum berthaultii*, which is resistant to the beetle. It has been possible to backcross this resistance from *S. berthaultii* into potato.

One of the largest fields, and surely the most important, in which evolutionary biology is important is human health (Stearns and Ebert, 2001; Nesse and Stearns, 2008; [http:// evmedreview.com](http://evmedreview.com)).

In the United States, basic research on biochemistry, physiology, genetics, and development is supported by the National Institutes of Health, in the expectation that such knowledge may prove useful in medicine and public health. Enormous sums are spent on research - on *Drosophila* fruitflies, on nematode worms, on *Saccharomyces* yeast, on zebra fish, and on rats and mice. The administrators of NIH are not interested in the biology of flies or worms, so why do they support this research?

It is because we presume that what we learn from studying these model organisms can be applied to the human species. The only scientific justification for this presumption, the only scientific reason to think that we can learn something about human beings from studying mice, flies, or worms, is that we are part of one large family, that we are all descendants from common ancestors, and therefore, that we share some fundamental biological characteristics in common.

We now know that we share even more fundamental features than we used to imagine. Walter Gehring and

collaborators provided a spectacular example (Halder *et al.*, 1995). They induced the “ectopic” development of eyes in fruit flies, eyes growing in abnormal places such as on legs, by inserted into the genome an extra copy of one particular fly gene, known as *eyeless*. This is a master gene, a switch that initiates the action of many other genes, which are required to form an eye. The astonishing part of their work is both mouse and human have a homologous gene, called *Pax6*, that also evokes the development of perfectly formed ectopic fly eyes when it is inserted into a fly’s genome. Mutations of this same gene cause abnormal eye development in humans. So the development of eyes is triggered by the same gene in mammals and insects, after more than five hundred million years since their common ancestor. The genes controlled by the *Pax6* gene are different in insects and mammals, because the structure of insect and vertebrate eyes is very different. Nevertheless, the fundamental developmental pathway has remained the same, so that the insect’s genes are able to respond to the signal, the instructions from the master gene, even if it comes from a mammal.

Of course, the species with the most similar genes to humans, the species that should teach us the most about the human body, are the mammals, and in particular our closest relatives, the chimpanzees. Only about 1% of the nucleotide base pairs differ between DNA sequences of humans and chimpanzees. Of course, some genes are more similar between human and chimpanzee than others are more different. Why, we may ask, are some genes more similar? As I described earlier, similar genes, those which have evolved less, are likely to have very important functions, which could be disrupted by many of the possible. These, then, are genes that, when mutated, are likely to cause inherited human diseases of various kinds. (There are hundreds of human genes in mutations that cause malformations or disease. These genes are the major topic of study in human genetics).

And so, evolutionary theory predicts that mutations in slowly evolving genes are likely to cause human disease. This is exactly what Carlos Bustamante and his colleagues (2005) found when they compared many genes. The greater the similarity of a gene between human and chimpanzee, the more likely the gene is to cause a serious problem in the human being when it is mutated (Figure 4). This remarkable finding suggests that if we wish to find and understanding the function of unidentified genes that cause human malformations and malfunctions, we should be looking at genes that

are most similar to those of chimpanzees or other mammals.

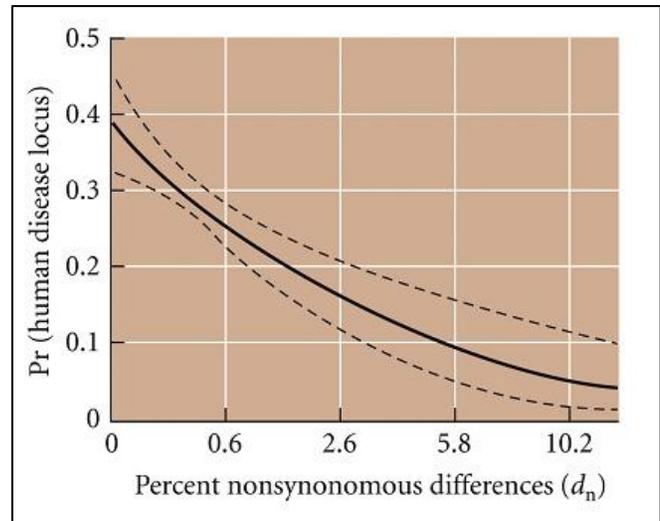


Figure 4. Mutations in slowly evolving genes are likely to cause human disease, as predicted by Evolutionary Theory.

Evolutionary biology makes major contributions to understanding infectious disease, that is, disease caused by other organisms. Phylogenetic analysis is a major tool for tracing the origin and spread of many kinds of many pathogens. The most famous example is the immunodeficiency virus HIV that is the cause of AIDS. HIV is related to simian immunodeficiency viruses (SIV) that occur in various other primates. Phylogenetic analysis has shown that HIV-1 entered the human population from chimpanzees at least three times, and that HIV-2 came from an SIV carried by mangabey monkeys.

Unfortunately, we are now very familiar with one of the most important consequences of evolution. The evolution of resistance to antibiotics by diverse pathogenic bacteria, viruses, protists (e.g., the malarial organism *Plasmodium*), and other disease organisms has created a crisis in public health. As the use of an antibiotic increases, it necessarily imposes increasing natural selection for resistance mutations in the pathogen. As the frequency of resistance increases in the pathogen population, higher levels of antibiotic often are used, exacerbating the problem. For every kind of antibiotic that has been introduced, resistance has been found in some kind of bacteria or other

disease organism, often within ten years and sometimes much sooner. Meanwhile, there is pressure to develop new antibiotics, at great expense, but then a new episode in the “arms race” is triggered. Strains of the tuberculosis bacterium and of *Staphylococcus aureus* that are resistant to multiple drugs pose extreme danger. There can be no more urgent reason to educate doctors - and everyone else - about the reality and importance of evolution.

CONCLUSION

Evolution is a profoundly important topic. The principles of evolution – a history of common ancestry and change, brought about by genetic drift and the natural selection of genetic variation that originates in random mutation – illuminate every subject in biology, and have immense implications for our understanding of the human organism and its variations. Many aspects of living beings are inexplicable unless viewed in an evolutionary framework. Like all sciences, moreover, evolution has practical implications, many of which are only now being developed. As Theodosius Dobzhansky, one of the great evolutionary geneticists of the twentieth century wrote, “nothing in biology makes sense except in the light of evolution.”

In *On the Origin of Species*, Darwin often referred to “my theory”. Today, people still speak of “the theory of evolution”, and biologists often refer to “evolutionary theory”. We must be aware that the word *theory* has a variety of meanings. The colloquial meaning is a speculation, a hypothesis that is open to doubt and argument. This is what many people think of when they refer to the “theory” of evolution. But when philosophers or physicists refer to “quantum theory”, or chemists to “atomic theory,” or biochemists to “metabolic theory”, they intend a very different meaning, namely a hypothesis that has been well supported by evidence, a powerful explanation of many observations and many kinds of phenomena, that is accepted with high confidence, even if it may be incomplete. In science, a theory is the highest contribution that a scientist can aspire to make. *Theory*, in science, is a term of honor.

When Darwin wrote of “my theory” in reference to natural selection, he spoke of a hypothesis that had almost no evidence at that time. When he used “my theory” in the broader sense of descent from common ancestors, with modification, he described an

explanation for which he presented massive amounts of evidence. Today, the evidence for descent with modification is so diverse and so voluminous that we must consider evolution a *fact*, just as the “Copernican hypothesis”, the revolution of planets around the sun, is a fact. For biologists, “evolutionary theory” today is the body of statements about mutation, genetic variation, genetic drift, natural selection, and some other factors that together constitute a causal explanation of how evolution occurs. These statements are not mere speculation; they are embodied in mathematical models and have all been verified by extensive evidence. For biologists, “evolutionary theory” is a solid, well supported explanation. We cannot claim that we have complete understanding of the causes and processes of evolution; for this reason, research on evolutionary processes is probably more active today than ever before. But we can have strong confidence in the processes we claim to be among the causes of evolution. Together, the fact and the theory of evolution are a foundation of biology and its applications to human affairs.

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