

1

A Brief History of Evolutionary Thinking

Summary

Evolution is as close to a general theory of biology as we have. Remarkably, the central tenets of the theory can be traced back to the nineteenth-century work of Charles Darwin. Darwin was influenced by his predecessors and by the social and political currents of his time. Darwinian evolution can be summarized as “heritable variation subject to natural selection.” Darwin’s avowed goal was to counter the theory of special creation. Nevertheless, his theory was not widely embraced. Where did variation come from? How was it inherited? Darwin had no answer to these questions. One class of answers to these questions was provided by the rediscovery of Mendel’s work in the early twentieth century and the development of the science of genetics. The merging of Darwin’s theory and Mendelian genetics into the Modern Synthesis led naturally to the search for the chemical basis of heredity and the founding of molecular biology. Evolution was reconceptualized as changes in allele frequencies in populations over time. Among other advances, the development of rigorous, sequence-based phylogenetic methods greatly enhanced our understanding of the history of life. Nevertheless, as the modern synthesis emerged in the early twentieth century, the darkest chapter in the history of evolutionary thinking unfolded. Eugenics – controlling breeding to improve the human race – took hold throughout the world. Yet Darwin himself was not a eugenicist. By arguing that controlling

breeding might be favored at the level of individuals but not at the level of tribes or societies, Darwin both refuted the intellectual basis for eugenics and anticipated the development of a multilevel theory of evolution.

Introduction

As Dobzhansky [1] famously pointed out, “Nothing in biology makes sense except in the light of evolution.” Evolution, the closest to a general theory of biology that we have, thus provides common intellectual ground for all biologists. For instance, consider the growing field of genomics. When biologists seek to identify portions of genomes that are functionally important, they compare genomes of different species. Areas that are conserved between species likely reflect such functional importance [2, 3]. The thinking here is entirely evolutionary. Shortly after two species diverge from a common ancestor, their genomes are expected to be highly similar. As time passes, mutation acts to break down this similarity. In species that share a distant ancestor, parts of the genome may show little similarity. However, purifying selection will remove organisms whose genomes contain deleterious mutations in areas that are functionally important. To the extent that deleterious mutations commonly occur, these areas of the genome will thus appear conserved relative to areas that lack functional importance. Genomic studies routinely take advantage of these consequences of evolution.

A cynic, however, might suggest that evolutionary biologists traditionally focus more-or-less exclusively on organisms and genes (and now genomes). Evolutionary theory thus has had little impact on many fields of biology. As Wilkins [4] notes:

The subject of evolution occupies a special, and paradoxical, place within biology as a whole. While the great majority of biologists would probably agree with Theodosius Dobzhansky’s dictum that ‘nothing in biology makes sense except in the light of evolution’, most can conduct their work quite happily without particular reference to evolutionary ideas. ‘Evolution’ would appear to be the indispensable unifying idea and, at the same time, a highly superfluous one.

Wilkins [5] later elaborated on these remarks: “...many biologists who investigate proximal causes in various biological processes (in, for instance, biochemistry, physiology, development) often have little or no recourse to evolutionary ideas or explanations.” Such statements from the founding editor of the notably interdisciplinary journal *BioEssays* suggest that while evolutionary theory may have the potential to unite all biological disciplines, it has not yet done so. At least some biology continues to be conducted with no particular reference to an evolutionary framework. The role that evolution could play in uniting biological disciplines has thus not yet been fully realized.

Yet this is changing. Minimally, since biology must embrace the history of life, virtually all biologists recognize the need for a historical framework. Further, the tools for providing this framework are increasingly well developed. Modern techniques of phylogenetic systematics analyze increasingly massive nucleotide sequence datasets with more and more sophisticated models of mutational change. As a result, we are progressively better able to apply evolutionary thinking to biological data of all sorts. The promise of over 150 years of evolutionary thinking is beginning to be realized.

Darwin

Remarkably, even in the age of genomics, evolutionary theory can be traced relatively intact back to the work of a nineteenth-century individual, Charles Darwin. The year 2009 was the 200th anniversary of Darwin’s birth and the 150th anniversary of publication of one of his most important works, *On the Origin of Species by Means of Natural Selection*. Of course, Darwin built on earlier ideas. In particular, we will mention two.

One of the very powerful ideas that developed in the nineteenth-century Europe was the “uniformitarian” view of the Earth’s geology. Developed by James Hutton and others, this view, summarized by “the present is the key to the past,” eventually led to the geological time scale, which is central to our understanding of the history of life and is shown in Figure 1.1. Hutton was unfortunately so brilliant that no one could really understand a word he said, and his theory was popularized and

EON	ERA	Period	Epoch	AGE mya
Phanerozoic	Cenozoic	Quaternary	Holocene	66
			Pleistocene	
		Tertiary	Pliocene	
			Miocene	
			Oligocene	
			Eocene	
			Paleocene	
	Mesozoic	Cretaceous		252
		Jurassic		
		Triassic		
	Paleozoic	Permian		541
		Carbon-iferous		
		Devonian		
		Silurian		
		Ordovician		
		Cambrian		
Proterozoic				2500
Archaean				4000
Hadean				4600

Figure 1.1 *The geological time scale.* Originally based on relative time derived from uniformitarian principles, radiometric dating of geological strata now allows both relative and chronological time measures. Newly ratified periods of the Proterozoic (e.g. the Cryogenian) are based not on stratigraphic events but on measures of chronological time.

made more accessible by Charles Lyell's *Principles of Geology*, which had a lasting influence on Darwin.

Other political and social developments in the nineteenth-century Europe include the Communist Manifesto, published in 1848. Communism closely identifies with the evolutionary theory of Lamarck, a predecessor of Darwin. Lamarck's theory of evolution – usually summarized as “the inheritance of acquired characteristics” – emphasizes that the organism must strive for the acquisition of novel characteristics. For instance, a giraffe with a short neck must struggle to lengthen its neck, stretching it every day, year in, year out. Only then will it acquire and pass on the longer neck. Thus, the parallel to the dialectic of communist ideology is clear.

Darwin's theory, on the other hand, was strongly rooted in capitalistic society. Darwin was from the English middle classes in the nineteenth century. This was Victorian England. Class structure was still very strong in England at this time, although the hereditary English nobility had lost a lot of its power to the English middle classes. This was a very gradual process; there were no revolutions. Numerous vestiges survived from earlier times – the House of Lords in Parliament and Queen Victoria, herself. At the same time, England was carving an empire out of the rest of the world. There was perhaps the need to justify this process in terms of the “natural order.” The assumption that because something is natural it is also morally right was widely embraced.

At the same time that English society was changing gradually, and England was conquering much of the world, there was the prevailing view that change was progressive; the world was getting better. The gain of power of the middle classes led to economic advances, industry, science, medicine, and so on; the conquering of other countries was alleged to have a “civilizing” influence, although perhaps those conquered countries would have debated this.

These societal influences were no doubt important, particularly for young Charles Darwin when he set off on his voyage around the world on the HMS *Beagle*, 1831–1836. On this trip Darwin examined various aspects of geological and natural history – coral reefs, finches, tortoises, and so on. Darwin would ask himself: Why were areas of South America that were

climatically similar to England nevertheless populated by distinct flora and fauna? And why when he unearthed South American fossils were they more similar to the modern South American creatures, while English fossils were likewise similar to modern English creatures? These were daunting questions to an inquiring mind.

Darwin's Theory

After his return to England, Darwin thought about these and other questions for a number of years and eventually came up with the theory of evolution by natural selection. After resisting publication for some time, a paper by Alfred Russell Wallace forced his hand. Darwin published a short paper in 1858 with Wallace and then in 1859 published *On the Origin of Species*. His goal in the *Origin* was to convince readers that there was no need for "special creation" of each species by God, hence the title "*On the Origin of Species*." It is also noteworthy that he did allow a role for the Creator in the origin of life. While this was implicit in the first edition of the *Origin* [6], it became considerably more explicit by the 6th edition [7]:

There is grandeur in this view of life, with its several powers, having been originally breathed by the creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Darwin most clearly and succinctly describes his theory in the opening paragraphs of perhaps his greatest work, the *Descent of Man* [8], first published in 1871:

He who wishes to decide whether man is the modified descendent of some pre-existing form, would probably first enquire whether man varies, however slightly, in bodily structure and in mental faculties; and if so, whether variations are transmitted to his offspring in accordance with the laws which prevail with the lower animals...The enquirer would next come to the important point,

whether man tends to increase at so rapid a rate, as to lead to occasional severe struggles for existence; and consequently to beneficial variants, whether in body or mind, being preserved, and injurious ones eliminated.

Darwin's theory thus consists of three principles:

- 1) organisms vary
- 2) this variation is inherited
- 3) this variation is subject to natural selection

The cause of the variation is completely unspecified; the existence of variation need only be demonstrated empirically. The mechanism of inheritance is also unspecified and could be entirely unknown as long as parent–offspring correlations can be demonstrated empirically. Darwin's theory is thus compatible with genetic or epigenetic mechanisms of inheritance, or even cultural inheritance. The actions of natural selection are often thought of as differential mortality; however, differential reproduction with no mortality is equally effective.

The core of Darwin's theory of evolution is thus: "Heritable variation is subject to natural selection." Yet Darwin's theory was unconvincing to many. Where did variation come from? How is it transmitted? Darwin had no good answers to these questions, and in later editions of the *Origin*, he came up with increasingly fanciful ideas in this regard.

The Modern Synthesis

Meanwhile, in 1865, Gregor Mendel, a German-speaking, Augustinian friar, first presented his experiments that addressed exactly these questions, but the significance of his work was not immediately apparent. Mendel's data were "discovered" in about 1900 and quickly led to the science of genetics. In 1910, Thomas Hunt Morgan began his studies of fruit flies. In the 1930s and 1940s, led by Theodosius Dobzhansky, a student of Morgan's, and a number of other prominent scientists, the modern synthesis of Darwin's theory and Mendel's genetics was conceived. This led naturally to the search for the chemical nature of heredity, the discovery (in 1953) of the structure of DNA, and the founding of the field of molecular biology.

Molecular biology has roots perhaps best described by Francis Crick [9], one of the discoverers of the structure of DNA:

I myself was forced to call myself a molecular biologist because when inquiring clergymen asked me what I did, I got tired of explaining that I was a mixture of crystallographer, biophysicist, biochemist, and geneticist, an explanation that in any case they found too hard to grasp.

The real focus of molecular biology, however, is on biological information, and great advances have clearly been made in this area. Related to the abundance of biological information now available, there have been correspondingly great advances in phylogenetic methods. Darwin himself recognized that his theory implied that all organisms were connected within a phylogenetic tree. Indeed, the only illustration in the *Origin* was one such tree. Such a tree suggests the history of life as implied by the fossil record (Figure 1.2). At the bottom are the oldest

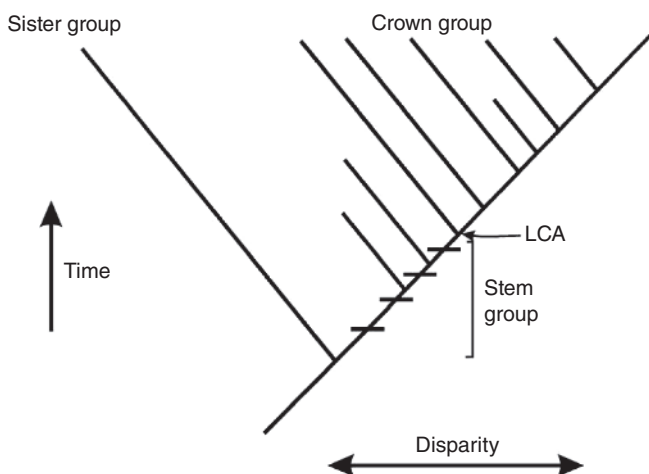


Figure 1.2 A *phylogenetic tree*. Analogous to the fossil record, time proceeds from bottom to top, while diversity and disparity are measured on the x-axis. A stem group diverges from its sister group while deriving novel character states (horizontal bars). The stem group taxa are entirely extinct. The last common ancestor (LCA) shares all the derived character states with the crown group, which includes all living and some extinct members of the group or clade.

strata containing the oldest taxa. These taxa diversify along the x -axis, while time proceeds on the y -axis. Today, such trees are typically built with nucleotide sequence data using statistical and mathematical theory to model mutation rates.

Perhaps the least durable aspects of Darwin's theory relate to gradual, progressive change. Evolution can proceed at various rates, and for some lineages there may be long periods of "stasis," in which little or no change occurs. While complexity does tend to increase during the history of life, secondary simplification also occurs constantly: some eukaryotes have lost their mitochondria, bivalves have lost their heads, snakes have lost their limbs, some birds have lost their wings, and so on.

Evolutionary theory continues to be central to biology in the age of genomics. Finding functional areas of genomes is entirely based on evolutionary thinking. As mentioned above, genomic areas that are conserved in different taxa are typically found to be functionally important. When a mutation occurs in these functional areas of the genome, the mutation is usually detrimental, and the individual containing the mutation is removed by selection or fails to reproduce as rapidly as those without the mutation. Evolutionary thinking has also shown that most large genomes, far from being a "blueprint" of the organism, are actually the evolutionary playground of little bits of DNA called mobile genetic elements, which due to their incessant replication now make up the bulk of the human genome and the genomes of other eukaryotes as well [10]. While Darwin proposed his theory over 100 years before mobile genetic elements were discovered, this theory – heritable variation subject to selection – nevertheless perfectly explains the evolutionary success of mobile genetic elements. Modern evolutionary biology thus encompasses studies ranging from molecular biology to organisms, to human culture and psychology, and everything in between.

The Darkest Chapter

In the glow of the successes in the study and analysis of biological information, it is easy to forget that early twentieth century geneticists and evolutionary biologists embraced the science of

eugenics in the darkest chapter in the history of evolutionary biology. By the 1920s, this movement was at its peak in the United States. At this time, 24 states had passed laws permitting eugenic sterilization [11]. Further, this movement was led by prominent scientists of the day. For instance, in 1921 Henry Fairfield Osborn was both the president of the American Museum of Natural History and the host of the second International Congress of Eugenics, and his signature was prominent on advertisements for the Congress.

In response to the pernicious effects of eugenics, some states passed laws limiting the teaching of evolution. One such state was Tennessee, and this law led to the Scopes trial. Osborn and other prominent scientists may have refused to testify on behalf of the defense at the Scopes trial in part perhaps because of Clarence Darrow's opposition to eugenics. William Jennings Bryan led the opposition to teaching the theory of evolution. Despite this, Bryan was not personally a fundamentalist. Rather, he opposed the political and social aspects of the evolutionary agenda and viewed creationism as a tool to suppress these unsavory offshoots of evolutionary theory.

Yet it was not the opposition of creationists that halted the eugenics movement. Rather, it was the horrible excesses of World War II that made it clear to all that eugenics was no longer politically tenable. Modern evolutionary theory has largely failed to acknowledge this dark chapter. Instead, criticisms of eugenics focus on the problems of classifying the unfit and the difficulty of selecting against deleterious recessive alleles. Because recessive alleles are masked in heterozygotes, selection has little impact when the allele frequency is low. Eugenics seems to be viewed as too difficult to properly implement, rather than as scientifically and morally flawed. Indeed, a number of well-meaning evolutionary biologists continue to sound the alarm concerning mutation unchecked by selection. For instance, in this context Herron and Freeman [12] write: "The implications for the future are ominous, and the obvious solutions unappealing."

Yet Darwin was not a eugenicist. In the *Descent of Man*, Darwin [8] elaborated a subtle and powerful argument against the nascent political movement that later would be called eugenics. In the first step of this argument, he extends his theory of evolution

to multiple levels of selection by pointing out that groups of individuals could be selected under some circumstances:

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase.

In this passage, Darwin focuses on a trait – morality – that is assumed to be inherited at least in part and that “...gives but a slight or no advantage...” at the level of the human individual. In other words, at this level of the biological hierarchy, morality is selectively neutral. When individual-level selection alone operates, moral individuals will on average have no more offspring than immoral ones. Thus, the frequency of moral individuals will neither increase nor decrease. Darwin then points out that at a higher biological level – the tribe – the results of selection are quite different: “A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy... would be victorious over most other tribes....” In other words, when between-tribe conflict occurs, tribes that contain many moral individuals will prevail over tribes with fewer such individuals. Tribes that in aggregate have a high moral standard will increase in frequency relative to tribes that in aggregate have a low moral standard. The effects of tribe-level selection thus differ from the effects of individual-level selection. The latter will not affect the frequency of individuals that vary in moral standard, while the former very clearly

does affect the frequency of tribes that in aggregate vary in moral standard. If between-tribe selection was a potent force in human evolution, the existence of human morality can be explained by this sort of natural selection.

It was this levels-of-selection thinking that caused Darwin to differ profoundly from some of his contemporaries. He continues: “We civilized men... do our utmost to check the process of elimination; we build asylums for the imbecile, the maimed, and the sick; we institute poor-laws; and our medical men exert their utmost skill to save the life of every one to the last moment.” He then points out that human sympathy is the basis for both morality and for our caring for the helpless. He concludes: “Nor could we check our sympathy, even at the urging of hard reason, without deterioration in the noblest part of our nature” [8].

In modern terms, Darwin is recognizing a conflict between levels of selection. At the individual level of selection, letting the unfit perish or actively preventing such individuals from reproducing (which is what eugenicists advocate) may well be adaptive. On the other hand, the tribe or group that institutes such policies loses “the noblest part” of its nature – recall “the spirit of patriotism, fidelity, obedience, courage, and sympathy...” All of that is lost. Such a society will fail in competition with other societies that maintain this part of human nature, even against “the urging of hard reason.” Thus, eugenics is selected for at the level of the individual, but selected against at the level of the group [13]. Our moral revulsion of eugenics evolved.

While Darwin’s wisdom regarding eugenics has been largely forgotten, his view of the evolution of groups in general [14] and of morality in particular is now widely accepted, as we see here [15]:

Natural selection underpins the evolution of good and evil in human beings. This claim may sound far-fetched, but increasingly archaeological and anthropological evidence and the work of a small coterie of theoreticians indicate that Paleolithic people clustered together using common languages and culture to develop norms that protected equality, liberty, and fraternity, and thus forged cooperative groups that behaved altruistically. Such bonds allowed the group to present a united front to

less-fortunate neighbors, thereby providing backup for dispatching rivals in combat with little risk to self and probably with considerable benefit in terms of resources grabbed.

As an aside, one can of course see the contradiction of human cooperation: cooperation within a group often facilitates more efficient conquest of other groups.

In any event, there is also no doubt group-level thinking is common in human society, as personified by the motto of the three musketeers: “All for one, and one for all,” the immortal words of Winston Churchill describing the Battle of Britain, “Never... was so much owed by so many to so few,” and the lyrics to one of the most famous rock-and-roll songs of all time, “When all are one, and one is all” (Led Zeppelin, *Stairway to Heaven*). And yes, often a common enemy serves as a unifier for a group, as for instance in the unlikely case described by Alexander Solzhenitsyn [16]: “Whatever they’d been talking or thinking about was forgotten. The whole column had one thing and one thing only on its mind. ‘Get ahead of ten! Beat them to it!’ Things were all mixed up. No more sweet or sour. No more guard or zek. Guards and zeks were friends. The other column was the enemy.”

In some cases, we may see even today in modern society the kind of group-level selection that Darwin envisioned. During the Fukushima Daiichi nuclear accident, successful shut down of the doomed power plants depended on the willingness of a number of workers to sacrifice themselves for the “good of the group” as described in some news reports, for instance this one from 5 days after the earthquake titled “50 workers bravely stay at troubled Japan reactors”: “Adding to this natural bonding, jobs in Japan confer identity, command loyalty and inspire a particularly fervent kind of dedication. Economic straits have chipped away at the hallowed idea of lifetime employment for many Japanese, but the workplace remains a potent source of community... Japanese are raised to believe that individuals sacrifice for the good of the group” [17]. And without these workers’ sacrifice, the release of radioactivity would likely have been much greater and caused greater peril to Japanese society.

Conclusions

In modern biology, some great scientists spend their entire careers without citing articles older than a few years [18]. Yet it is undeniable that the central principles of evolutionary biology can be traced back to Darwin's work over 150 years ago. The modern synthesis of Darwin's theory and Mendelian genetics provided a mechanistic basis for understanding variation and heredity but also ushered in the era of eugenics. Darwin's view of eugenics, however, illustrates the value of a multilevel theory and counters the thinking that led to evolution's darkest chapter.

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