

Evolution: Views

James F Crow, *University of Wisconsin, Madison, WI, USA*

email: jfcrow@wisc.edu

Darwin's original theory of evolution by natural selection is now almost universally accepted by biologists. It has been broadened by the inclusion of Mendelian inheritance and a mathematical formulation, called the new synthesis. Nevertheless, with more detailed study, different views of various aspects of the process have emerged and these are the subject of this article.

Introductory

Article contents

- Pre-Darwinian Views
- Darwinian View
- Neo-Darwinian View
- Anti-Darwinian Views
- Synthetic View
- Shifting Balance View
- Kin Selection View
- Speciation Views
- Neutralist View
- Punctuated Equilibrium View
- Evo-devo View
- Phylogenetic View
- Conclusion

Pre-Darwinian Views

0104.1 Darwin was not the first to suggest that biological species evolve, but most others did not consider possible mechanisms. It was Jean Baptiste de Lamarck who, in the early nineteenth century, was the first to present a coherent view. He is best known for developing the idea, already vaguely held by many, that changes that occur in the body are somehow transferred to the germ cells and thereby affect future generations. It was a very attractive theory of great explanatory power. However, despite numerous attempts, no one has produced convincing evidence of the inheritance of acquired characteristics. Nevertheless, Lamarckian ideas continued to be held, by a minority of biologists, well into the twentieth century. (See A0877.)

Darwinian View

0104.2 Charles Darwin's bombshell, *The Origin of Species*, appeared in 1859. It emphasized two main points. The first was that evolution had actually occurred. The idea was not new, but Darwin's arguments carried more force. The second point was new and revolutionary; this was the idea of natural selection. (See A0883.)

0104.3 Darwin noted that all organisms, even the most slowly reproducing ones, produce more offspring than can survive. Those individuals best able to cope – the fittest – were the most likely to survive and reproduce. To the extent that this capacity was inherited, the next generation would have a larger fraction of the more fit individuals. Thus, average fitness would tend to increase. The idea was so simple and yet so convincing that many nineteenth century biologists must have thought, 'Why didn't I think of it?'

0104.4 In Darwin's time, the argument from design had universal acceptance. It was epitomized by William Paley's watchmaker. According to Paley, if a man

finds a watch and examines it, he discovers a complex set of gears and ratchets, all cooperating to make a functional machine. He concludes that such a complex machine must have had a maker. So, went Paley's argument, living creatures are even more complex and must therefore have required an even greater maker, which could only be God. Darwin showed that no such maker is required, that natural variability coupled with natural selection is sufficient. For many thinkers, this was the demise of the argument from design.

An idea so convincing and so revolutionary was 0104.5 bound to create an intense reaction. The theory was quickly and enthusiastically accepted by many biologists and other interested readers. However, to others it was blasphemy, and the controversy was furious. Darwin was hesitant to include human evolution, and his 1859 book skirts this subject. However, it was the main topic of his later book, *The Descent of Man*, published in 1871.

The gap in the Darwinian theory was the source of 0104.6 variability. Darwin had no idea how to fill the gap. He tried many ideas, none of which worked. He knew only that the variations on which selection acts were small and random as regards needs for survival and reproduction. Heredity at the time was thought to be blending, more of the nature of a fluid than of particles. (The word blood, symbolizing inheritance, is a holdover from that period.) As R. A. Fisher later pointed out, with blending inheritance every mating between different types leads to a decrease of the population variance, just as mixing white and black paints leads to an intermediate gray, and white and black cannot be recovered. In fact, about 50% of the variability is lost each generation. Much of what seems

weak, even nonsensical, in Darwin's later work reflects his continual search for origins of variability. If Darwin had only known of Mendelian inheritance and understood its implications, he might not have engaged in all these speculations. Indeed, Mendel sent a copy of his paper to Darwin, but apparently it was not read. (See A0690; A0694.)

Neo-Darwinian View

0104.7 The gap in Darwin's theory was filled by Gregor Mendel. Mendel published his famous article on inheritance in peas in 1865. This work was not appreciated for 35 years, until, after his death, Mendel's rules were independently rediscovered by three biologists. Mendel's markers, now called genes, were transmitted intact from generation to generation and followed the simple, well-formulated rules that he discovered. (See A0694.)

0104.8 From the standpoint of evolution, the essential point is that the presumed loss of variability that occurs with blending inheritance does not happen. Variability is conserved, and, rather than half the variance being lost every generation, only a tiny amount caused by selection and chance effects in finite populations is lost. This is easily compensated by new mutations. The idea of mutation was introduced in 1901 by Hugo DeVries, one of the co-discoverers of Mendelism. Mutations are inherited genetic changes.

0104.9 With the discovery of Mendelian inheritance and mutation, Darwin's theory was complete. New variability arises by mutation. The genes are shuffled every generation by Mendelian segregation and recombination. Those genes that make up the best-adapted combinations are differentially transmitted to the next generation.

0104.10 Mutational changes are not random in an absolute sense. They are constrained by physical and chemical rules. In addition, they are constrained by biological possibilities; a mutation in a mouse is still in a mouse, not an elephant. All mutations are, in a sense, constrained by the evolutionary history of the organism. This 'historical contingency', although an old idea, has recently had more emphasis by numerous writers, conspicuously Stephen Jay Gould. However, mutations are random with respect to their usefulness for future evolution.

0104.11 At last, there was a satisfying theory of evolution. The source of variability was solved. In a broad sense, evolution was now understood. However, of course there were innumerable details to be worked out. Twentieth-century study of evolution has produced a steady fleshing out and deepening of the theory.

Anti-Darwinian Views

The period between 1859 and the turn of the century 0104.12 was not a time of complete acceptance of Darwinism. Several biologists had contrary ideas. Alfred Russel Wallace had simultaneously with Darwin discovered natural selection, yet he never accepted human evolution, especially of the mind. Thomas H. Huxley, who played a large part in popularizing Darwinism, did not think the process was as gradual as Darwin did. Paleontologists believed that evolution occurred by abrupt steps rather than gradually. Many who were interested in reconstructing ancestral trees did not accept natural selection. Lamarckian views were not uncommon. Most of these people accepted evolution as a historical fact, but not the Darwinian mechanism.

The most surprising disagreement, from today's 0104.13 standpoint, was the conflict in England after 1900 between the Mendelists and the biometricians. The Mendelists did not accept statistical analysis and Mendelian gradualism. The biometricians did not accept Mendelism. The argument was exacerbated by the strong personalities of the main rivals, Karl Pearson for the biometricians and William Bateson for the Mendelists. The issue was definitively settled by R. A. Fisher in 1918, when he showed that the correlations that had such a large role in the biometricians' thinking were completely consistent with multiple Mendelian factors. Curiously, on the European mainland and in the United States, there was essentially no conflict; multiple Mendelizing factors were accepted from the beginning. (See A0690; A0700; A0809.)

The most iconoclastic later view came from Richard 0104.14 Goldschmidt in 1940. He emphasized that changes in early embryology, which he said were caused by wholesale reorganization of the chromosomes, could lead to large effects in adults. Such 'hopeful monsters' were the originators of new species. Goldschmidt's views were not taken seriously by most evolutionists, particularly geneticists who regard his monsters as more hopeless than hopeful. Curiously, some of the less extreme of Goldschmidt's ideas are now being resurrected by developmental evolutionists.

Synthetic View

Although the neo-Darwinian theory was satisfying in 0104.15 many ways, it was unsatisfactory in others. Evolution by natural selection was a magnificent explanatory theory. Yet, it was almost completely lacking in predictive power. The neo-Darwinian view was purely qualitative, whereas the most respected scientific theories in the physical sciences are quantitative.

0104.16 The 'modern synthesis' began in the late 1920s. The leaders were three mathematically inclined biologists, R. A. Fisher and J. B. S. Haldane in Britain and Sewall Wright in the United States. These three collectively worked out a theory uniting Mendelian genetics and natural selection. In particular, they showed, for a variety of patterns of inheritance, the rate at which selection of a specified intensity changed allele frequencies. They also brought mutation, random effects and various kinds of selection (e.g. within family selection) into the picture. The result was a satisfying theory, often regarded as the most successful mathematical theory in biology. (See A0467; A0584; A0690.)

0104.17 A high point in these developments was Fisher's Fundamental Theorem of Natural Selection: the rate of change of fitness is equal to the additive genetic variance. The additive genetic variance is the proportion of parental deviation from the average that is transmitted to the progeny. (Variability is measured by the variance, the average of the squared deviations of individual measurements from the average.) This is an elegant statement, comparable to physical theories. The difficulty is that, although the theory is quantitative and can make predictions of a limited sort (for example, the rate of gain in livestock performance), it is not possible to apply this to the uncertain data from evolution in natural populations. The theory, despite its elegance, did not permit many quantitative tests. This had to wait for molecular developments.

0104.22 The mathematical theory of the new synthesis was not accessible to most biologists. However, Theodosius Dobzhansky, a gifted writer, published in 1937 an influential book, *Genetics and the Origin of Species*. Here was a nonmathematical account, with the theory described in accessible terms and with an abundance of data, for by this time there was already a large literature from both field observations and laboratory experiments. Ecologists and classifiers were greatly influenced by Ernst Mayr, and paleontologists by George Gaylord Simpson. These three were responsible for the wide acceptance of the new synthesis. Despite numerous differences over details, there was a wide consensus for the synthetic theory.

Shifting Balance View

0104.18 The theory of change in fitness, developed mainly by Fisher and Haldane, did not consider seriously the effect of chance. Fisher developed the necessary mathematics, but dismissed random effects as unimportant except in the smallest populations. To these two, and many others, evolution was gene-centered. It was viewed as a succession of gene frequency changes

leading to ever-increasing fitness that was limited only by deteriorating environment, mainly the result of competing species.

To Wright, this was not satisfactory. He was 0104.19 interested in combinations of genes, not individual genes, particularly those combinations that produced good adaptation when the component genes were individually deleterious. In such a system, natural selection cannot carry a population from an adapted state to a better one without passing through maladapted intermediates, which selection would reject.

Wright argued that although selection could not 0104.20 produce a better gene combination, this could arise by chance in a small population. He visualized a large population broken up into a number of partially isolated subpopulations. Among these, one might happen by chance to have the better genotype, which would then spread by migration to adjacent colonies and eventually through the whole population. Wright thought of this as a way of evolving genetic complexity and providing for evolutionary creativity. (See A0440; A0467.)

Wright's theory was popular among biologists, but 0104.21 less so among those more mathematically inclined. The process can work only with a proper balance of migration, selection and subpopulation size, and during the time this is happening, the population pays a price in reduced fitness. While Wright thought this an affordable price, others were sceptical. The jury is still out.

Kin Selection View

The Darwinian theory is adequate to explain competi- 0104.23 tion for survival and increased fertility, but how can it account for cooperative and especially altruistic behavior? A clue comes from social insects. A worker bee is sterile, and the only way she can propagate her genes is to care for the queen, who shares a large fraction of the worker's genes. In the same way, an animal can help perpetuate its genes by aiding a relative who shares some of them. The idea was understood by both Fisher and Haldane, but neither carried it further.

Following the Fisher-Haldane lead, William 0104.24 Hamilton developed a much more comprehensive theory and presented a simple rule. A trait will increase if $c < rb$, where c is the cost to the altruist and b the benefit to the recipient, both small quantities and measured in terms of fitness; r is the coefficient of relationship, the fraction of shared genes.

This became the guiding principle for the evolution 0104.25 of social behavior. It is not necessary that individuals be able to identify relatives. For example, there might

be identification with a group. Individuals may behave altruistically toward members of their own group but selfishly toward others. Since individuals in a group are likely to be somewhat related, the kin selection principle applies. It is quite likely that altruistic social behavior in humans was brought about by a tribal structure in our not-too-distant past. Kin selection was aided and strengthened by cultural evolution following similar principles, leading to the new field of evolutionary psychology, now an area of active investigation. (See A1243.)

Speciation Views

0104.26 Although Darwin's great book was entitled *The Origin of Species*, this subject actually received little attention. Yet, it is clear that speciation involves considerations that ordinary evolution of form and function do not.

0104.27 A key ingredient of speciation is the absence of crossing between individuals of different species. The 'biological species' concept was clearly stated by one of evolution's leading figures, Ernst Mayr, who wrote that biological species are

groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.

There are numerous kinds of 'isolating mechanisms', which prevent interbreeding. They have been actively studied for many years, especially in the early days of the modern synthesis. The mechanisms range from hybrid sterility or lethality to sexual isolation, the reluctance to mate with members of another species.

0104.28 The most obvious mechanism for speciation is isolation. If two groups from a population are separated from each other, often by geography, they will pursue separate evolutionary courses. If the environments differ, and even if they do not, the two groups will evolve different sets of genes. Eventually the two will diverge so much that they are no longer compatible, so that even if they are brought together they will no longer hybridize.

0104.29 Speciation by geographical or other isolation is noncontroversial. More questionable is speciation without geographical separation. There are several examples. For instance, the cichlid fishes in some African lakes form separate species despite living in the same lake. The mechanisms are not understood, but it is usually assumed that there is some form of isolation, which might be, for example, local habitat or food preferences. Whether such speciation is common is not clear.

0104.30 The biological species concept is fine if there is information about reproductive isolation. Yet, a person studying natural populations often does not

have this information, and the definition of a species becomes more arbitrary. It is a matter of judgment how great the differences must be for the groups to be regarded as separate species. The problem is particularly acute when it comes to assigning species differences over time. It is obviously impossible to test the crossability of two populations that arose millions of years apart. Paleontologists study changes in fossils. They must adopt an arbitrary, and often subjective, definition of how great the differences must be or how long a time is required to produce a new species.

Neutralist View

With the discovery of the structure of DNA and the development of the field of molecular biology, the study of evolution made an abrupt shift. It became possible, for the first time, to compare genetic differences between species that could not be crossed. In our present molecular age, it is hard to imagine that geneticists once had no way to do a genetic analysis other than by matings. Now, DNA comparisons between any two individuals, no matter how different, are not only feasible, but widely practiced.

In 1968, Motoo Kimura started a firestorm when he argued that most molecular changes are selectively neutral and ruled by chance. The same conclusion was reached by King and Jukes and published the next year. At first, this was vehemently opposed by many evolutionists. The prevailing view was that in any moderately large population, a genetic difference could hardly be slight enough not to be influenced by selection. (See A0106; A0307.)

For many reasons, however, the neutralist view has come to be widely influential. Most higher animals and plants have a majority of DNA that is 'junk'. It does not encode a protein nor does it have any other known function. Such regions generally evolve more rapidly than regions containing functional genes. Furthermore, among those DNA regions that encode proteins, the most rapid changes are synonymous (i.e. a DNA change that does not change the encoded amino acid). Finally, there is little correlation between the rates of DNA change over evolutionary time and structural or physiological changes. All of these argue for neutrality. The neutral theory exists in strong and weak form. The strong form asserts that almost all DNA changes are effectively neutral; the weak form asserts that only DNA changes outside protein-coding regions are effectively neutral. (Effectively neutral means that the selective difference is so slight that the fate of mutations is determined by chance.) At present, the weak form is widely accepted; the strong form is not clear. What is needed, and what

is being pursued, is a case-by-case analysis. (See A0109; A0110.)

0104.34 The synthetic theory, satisfying as it was, suffered from having no quantitative tests of its adequacy; its predictive value was only for short-time experiments, often under artificial conditions. The neutral theory permitted long-range predictions. The basic formula for neutral evolution is that the evolution rate is determined by the mutation rate. This is easily understood. Consider a single gene locus. Suppose that new mutations occur at a rate μ (for mutation) per generation, and the number of adults in the population is N . In a diploid population, there are two alleles per individual, so the number of new mutations per generation is $2N\mu$. If we wait a very long time, all the alleles in the population will be descended from one. The chance that this lucky allele was the new mutant is simply $1/2N$. So, the number of successful mutations per generation is $2N\mu/2N=\mu$. The time required for a lucky mutant to spread through the population is about $4N$, so we have to observe the process over a timescale much longer than this, which is fine for study of evolutionary processes over hundreds of millions of years.

0104.35 This simple principle permits prediction of neutral evolution rates from mutation rates. Mutation rates at different loci and at different times differ, of course, but the differences are much smaller than selective differences. So, the observed rough constancy of the molecular evolution rate would be predicted for neutral changes, and this agrees with the observations. Conversely, evolution rates of neutral DNA can be used to estimate mutation rates.

Punctuated Equilibrium View

0104.36 In 1972, Niles Eldredge and Stephen Jay Gould announced what they called a new theory, 'punctuated equilibrium'. They noted that in a fossil sequence there were periods of abrupt change interspersed among long periods of almost no change. The observation was not new; paleontologists had noted this back in the nineteenth century. However Gould and Eldredge gave the subject a new emphasis, as well as a catchy name.

0104.37 The fossil record is necessarily incomplete, and large jumps may simply be the result of not finding the intermediates. Yet, it is clear that, when the fossil record is quite complete, there are periods of very rapid and very slow changes.

0104.38 Some have regarded this as a negation of neo-Darwinism, and a few have even called for a resurrection of Goldschmidt's macromutations. Gould has vacillated in his explanations over the

years. However the consensus now is that no unusual processes need to be invoked. Many species are well adapted to their environments, and if the environment does not change, there is no need to change. The anatomy of sharks has been nearly constant for hundreds of millions of years, presumably because they have a near-optimum shape. On the other hand, when the environment changes, organisms change with it. This is especially true if a new environmental opportunity appears, such as the invasion of the land by previous water-living forms or colonization of a new island. Punctuated equilibrium is a colorful description of an evolutionary observation that is important, but does not violate the established theory.

Evo-devo View

From the beginning of evolutionary studies, developmental biologists have emphasized that evolutionary changes observed in adult forms have their origins in embryonic changes. For many years, the techniques of embryology were not able to yield deep evolutionary insights. However all of that has changed in recent years. Molecular studies of development have taken center stage, and this is now one of the most active fields of research. This is evolutionary developmental biology, or 'evo-devo' for short.

Some of the most striking findings have been the great conservation of genes over wide evolutionary distances. The genes that affect the insect eye also affect the vertebrate eye, despite the enormous difference in structure. In addition, genes affecting the nerve cord in invertebrates, where it is on the bottom, are the same as those in vertebrates, where it is on top. (See A0112.)

The study of comparative function of genes in greatly different species has been a central theme of evo-devo. Structural differences in widely different species can now be analyzed in molecular terms. One of the features of the new methodology is the investigation of many species that were previously intractable. Evo-devo is not yet a mature subject, but a rapidly growing youngster.

Phylogenetic View

From its very beginnings, the study of evolution has involved the reconstruction of the evolutionary past. This depended mainly on the fossil record, but comparative anatomy and embryology played major roles. Constructing evolutionary sequences has long been a popular activity. The historical record was viewed as a tree, starting with a single form which by successive branching gave rise to the present plethora of species. To a large extent, the inferences about

closeness of relationships depended on individual judgments. Naturally, there were disagreements.

0104.43 The situation has been greatly clarified, and the subject enriched by molecular methods. By comparison of DNA sequences it is possible, with sufficient data, to infer the sequence of events by which the current types were produced. Furthermore, a timescale can be introduced by the assumption of a constant 'molecular clock'. The basis for such a clock is the rough constancy of the mutation rate relative to other factors that change more rapidly. Thus, a tree constructed from DNA sequence comparisons is best made from noncoding DNA regions. When the data are abundant, trees based on DNA comparisons agree with those based on anatomy and the fossil record.

0104.44 The construction of trees has been greatly aided by the development of high-speed computers. The methods for determining the tree structure that best fits the data are computer-intensive, and there is now a cottage industry devoted to developing methods with their associated computer programs. This is a rapidly advancing field at present, and we can look forward to an increasingly complete record of the history of life. (See A0111.)

0104.45 A complication arises in the study of single-celled organisms, such as bacteria. There are mechanisms for transferring DNA from one organism to another by means of viruses or virus-like entities (transposons). Such 'horizontal' transfer of genes within a generation means that the evolutionary structure is no longer tree-like, but is more like a network. This makes a simple phylogenetic tree impossible. Fortunately, although such horizontal transfer also occurs in multicellular species, its frequency is small relative to direct parent-to-offspring (vertical) transmission.

Keywords

Darwin, Lamarck, neo-Darwinian view, modern synthesis, shifting balance theory, neutral evolution, molecular evolution, altruism, punctuated equilibrium, evo-devo

Also, transposon-mediated changes in the DNA usually leave characteristic footprints that enable them to be identified. (See A0064.)

Conclusion

The understanding of evolution has been greatly 0104.46 enriched by the many new techniques and views that have occurred since the modern synthesis in the 1930s, especially the abundant information from molecular studies. Yet, this synthesis still remains the fundamental stem to which all the branches have been grafted.

Further Reading

- Carroll SB, Grenier JK and Weatherbee SD (2001) *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design*. Oxford, UK: Oxford University Press. [A highly readable textbook of evo-devo.]
- Gould SJ (2002) *The Structure of Evolutionary Theory* Cambridge, MA: Belknap Press. [A massive, wide-ranging tome, with much history and Gould's own views.]
- Graur D and Li W-H (2000) *Fundamentals of Molecular Evolution*, 2nd edn. Sunderland, MA: Sinauer Associates. [A discussion of the techniques and results of molecular evolution.]
- Kimura M (1983) *The Neutral Theory of Molecular Evolution*. Cambridge, UK: Cambridge University Press. [An accessible account of the neutralist view, by its principal protagonist.]
- Maynard-Smith J and Szathmary E (1995) *The Major Transitions in Evolution*. Oxford, UK: Oxford University Press. [The big picture, from the origins of life to the evolution of language.]
- Page M (ed.) (2002) *Encyclopedia of Evolution*, vols 1 and 2. Oxford, UK: Oxford University Press. [An enormous, up-to-date compendium: everything you want to know about evolution, and more.]