

Evolution

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This article is a revision of the previous edition article by B Guttman, volume 2, pp 663–666, © 2001, Elsevier Inc.

Glossary

Darwinian fitness Relative lifetime reproductive success of an individual within a population, or number of surviving offspring.

Evolution Descent with modification, that is, the cumulative change in the characteristics of populations that occurs in the course of successive generations.

Natural selection Process that determines the composition of a population during the course of time; under changing environmental conditions, directional selection causes adaptive evolution and, hence, the occurrence of new variants and species.

Population Unit of evolution, that is, a group of organisms that live at the same time in a specific environment (habitat).

Species Reproductively isolated group of organisms, breeding among themselves, that have the greatest mutual resemblance.

Symbiogenesis Primary endosymbiotic events that gave rise to organelle-bearing eukaryotic cells during the Proterozoic and subsequent secondary endosymbioses responsible for the origin of unicellular marine phytoplankton.

Introduction: Descent with Modification and Darwinian Fitness

Biological evolution, defined by Charles Darwin in his *Origin of Species* (1859) as “descent with modification,” is attributable to the nature of living beings. Organisms are self-reproducing, open systems that operate on the basis of instructions encoded in their genomes. During the course of reproduction, parental genomes are replicated to produce new copies for the offspring (Figure 1(a)). But replication is not perfect, and heritable mutations continuously introduce genetic novelties. Furthermore, sexual reproduction entails the reshuffling of chromosomes into different combinations, so individuals acquire, via recombination, variant genomes, thus giving them different traits. Populations inhabit ecosystems that afford various opportunities for obtaining the limited resources they need (living and brooding space, food, etc.). Each organism, with its unique combination of traits, has a specific ability to exploit those resources, that is, to maximize reproductive success (‘Darwinian fitness’) in a particular ecological niche. Those that leave the most offspring have, by definition, the highest fitness, and thus are most successful in passing on their genotypes. Thus, populations of organisms in which there is variation, reproduction, and heredity evolve by natural selection. This, as Darwin and Alfred Russell Wallace recognized, is the central process governing biological evolution in groups of animals and plants, although sexual selection, and other factors, may also play an important part.

The Modern Theory: An Expanded Synthesis

Although some major features of biological evolution, and especially the centrality of natural selection, became clear from Darwin's great work, a consensus on the cellular and molecular processes emerged only in the early decades of the twentieth century. By about 1940, it was possible to outline a modern, synthetic theory combining the essential discoveries of

Mendelian genetics with a mathematical analysis of genes in populations as outlined by R. A. Fisher, S. Wright, and J. B. S. Haldane, and with the observations of taxonomists and field naturalists (Ernst Mayr, T. Dobzhansky, G. L. Stebbins, G. G. Simpson, and B. Rensch). Since that time, some tenets of this model of evolution have been challenged, and an enormous number of new facts and subtheories have been added. However, the basic “Darwinian” concept remains intact: our modern theory of biological evolution is an expanded synthesis.

Evolution is a population phenomenon (Figure 1(a)). Individuals grow, reproduce, and die, whereas populations evolve. Studies of morphological, genetic, and biochemical features have shown that expanding natural populations harbor enormous variation, and this variability is the basis for biological evolution. It acts as a kind of ‘genetic insurance’, or a ‘buffer’, that allows the population to maintain itself by adapting to future environmental changes and perils, since the Earth is dynamic so that, over thousands of years, new habitats are generated and destroyed, respectively. In addition, plants and animals have always been under attack by a variety of pathogenic microbes (bacteria, fungi, etc.). All populations are highly polymorphic. The classic observations by T. Dobzhansky of the 1930s on fruit flies demonstrated that populations carry many chromosome types and that the frequencies of these chromosomal variants vary geographically, reflecting subtle adaptations to different environments. The mere recombination of allelic differences already present in a natural population (ignoring further variations created by heritable mutations) is adequate to produce considerable novelty, and thus constitutes the raw material for ‘directional natural selection’, a process that occurs as a result of changing environmental conditions (Figure 1(b)).

Biological evolution, which originated with the earliest bacteria, can be divided into several phases (Figure 2). At the cellular level, ancient primary endosymbiotic events (‘symbiogenesis’, i.e., the fusion of certain prokaryotes) gave rise to eukaryotic cells with the capability to evolve into complex

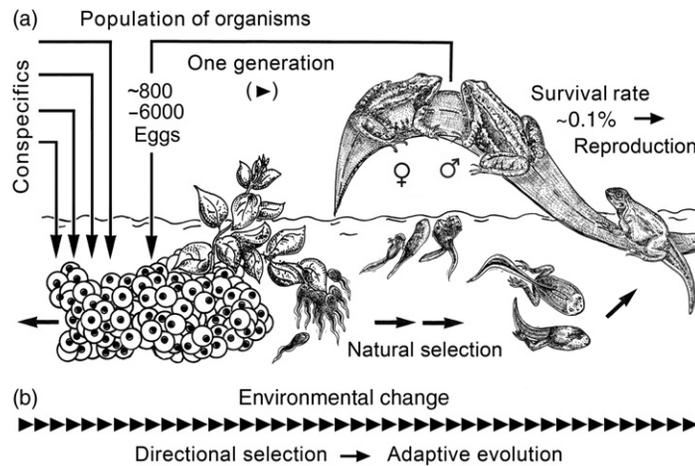


Figure 1 Populations and the Darwin–Wallace principle of natural selection. (a) Water frogs (*Rana* sp.) produce thousands of fertilized eggs per pair. Due to limited resources, there is a struggle for life, consisting of competition and cooperation among individuals within variable populations. (b) Over hundreds of subsequent generations, gradual changes in environmental conditions can cause adaptive phenotypic evolution by directional natural selection. Adapted from Kutschera U (2009) Symbiogenesis, natural selection, and the dynamic Earth. *Theory in Biosciences* 128: 191–203.

multicellular organisms, and later, secondary endosymbioses were responsible for the evolution of the marine phytoplankton. ‘Microevolution’ refers to adaptations, inclusive of ‘speciation’, which denotes the process by which a single species (population) divides into two or more such units. The evolution of humans and chimpanzees from a common ancestor that existed ~6 my ago is a well-documented speciation process. ‘Macroevolution’ refers to the larger changes observed over much longer geologic time intervals as organisms of quite different body plans gradually develop, such as the transition of theropod dinosaurs to birds during the Mesozoic. The ‘biological species concept’ (BSC) of E. Mayr states that a species is a group of populations that are actually or potentially capable of interbreeding with one another. This definition is only relevant to sexually reproducing organisms such as water frogs (Figure 1(a)), but largely meaningless for those that reproduce asexually. Such forms of life (bacteria, etc.) are related only by cell divisions, augmented by occasional lateral gene transfer. The BSC has been applied to most groups of animals as well as plants. However, members of the Kingdom Plantae are able to reproduce in more plastic ways and to hybridize with one another. The BSC has been challenged by the phylogenetic species concept, which says, essentially, that a species shall be considered a distinct branch of a phylogenetic tree that can be distinguished morphologically or genetically. We know that ‘species’ by any conception have diverged from one another in the past and continue to do so; that is, biological evolution is a fact of nature.

Modes of Speciation

As described by E. Mayr and others, speciation probably occurs primarily through geographic isolation. Two populations are said to be ‘sympatric’ if their ranges overlap and ‘allopatric’ if they do not. Speciation in many well-documented instances has evidently occurred when one subpopulation of a species becomes isolated from the rest, often due to geological events (‘dynamic Earth’). During the long time of its isolation

via the rise of new mountain ranges, and so on, it acquires differences that result in reproductive isolation once the two subpopulations again become sympatric. Reproductive isolating mechanisms may entail ecological factors, such as occupying slightly different habitats so that prospective mates do not come into contact; temporal factors, such as breeding at different times; and physical barriers to reproduction such as chromosomal rearrangements, incompatibility between haploid sperm and eggs, or failure of hybrid embryos to develop. Intense speciation events are obvious in archipelagos; the ground finches (Geospizinae) of the Galapagos Islands or the honeycreepers (Drepanididae) of the Hawaiian Islands show how one original population has diverged in the course of several million years into a variety of species, occupying different ecological niches, as subpopulations became isolated from one another on different islands.

While geographic (allopatric) speciation may be a common process in animals, many plants have evolved through genetic events that may occur sympatrically, via ‘hybridization’ and subsequent polyploidization, that is, the generation of tetra- or hexaploid conditions as a result of the combination of two parental diploid nuclei. A great deal of plant evolution has been explained by introgressive hybridization, in which related species hybridize and one or more chromosomes of one parent species become incorporated into the genome of the other, eventually resulting in a third species with features derived from both parents.

Mathematical analyses of the behavior of genes in populations have shown how the frequencies of alleles change by heritable mutations and/or by various regimes of selection. The rate at which these changes occur depends on the size of the population, that is, in small populations genetic changes occur rapidly in a way not determined by directional natural selection. This phenomenon, called ‘genetic drift’, may be important in speciation. The individuals that become isolated in the first place may themselves have genotypes different from the average genotypes of the much larger parent population (founder effect on islands, etc.).

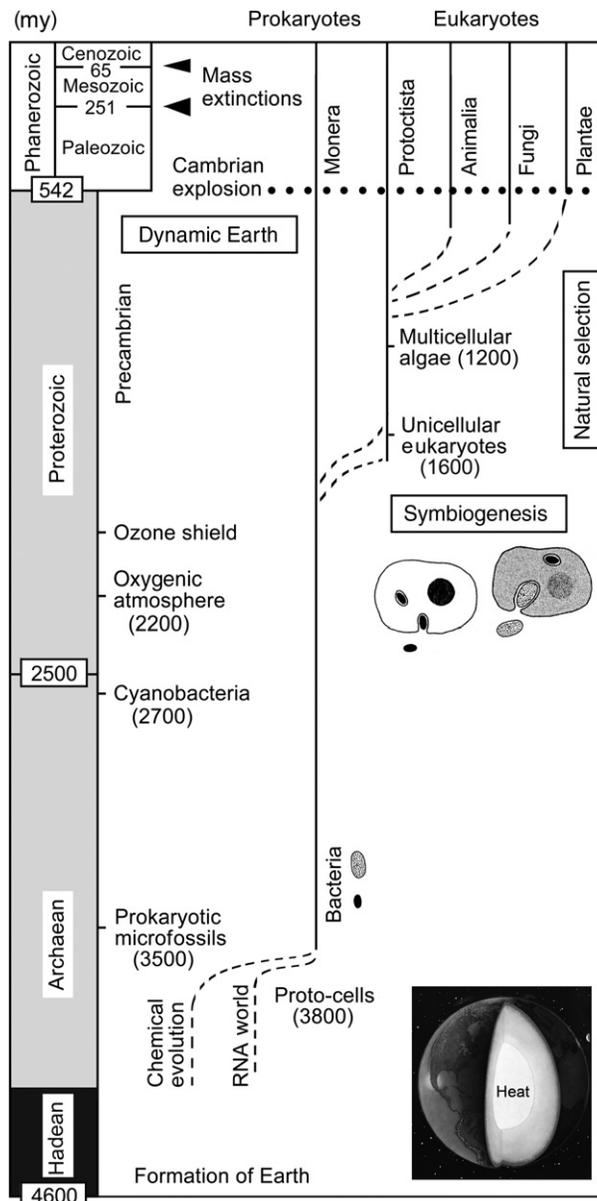


Figure 2 Evolution of life on Earth. The earliest prokaryotic cells (bacteria-like microfossils) are about 3500 my old. Today, the descendants of these ancient microbes represent the dominant group of organisms on Earth (Kingdom Bacteria, syn. Monera). Symbiogenesis (primary endosymbiosis) gave rise to eukaryotic cells, which evolved, via unicellular progenitors, into members of the Kingdoms Protocista (amoebae, algae, phytoplankton, etc.), Animalia (animals), Fungi (mushrooms, etc.), and Plantae (plants). Directional natural selection, driven by changes in environmental conditions via the dynamic Earth, caused biological evolution, associated with extinctions, in all five Kingdoms of Life (synade-model). Adapted from Kutschera U (2009) Symbiogenesis, natural selection, and the dynamic Earth. *Theory in Biosciences* 128: 191–203.

Mass Extinctions and Evo-Devo

The fossil record reveals three major patterns in biological evolution: speciation, extinction, and phyletic evolution. Speciation has already been described. ‘Extinction’ is clearly a major feature of evolution. Although a few species have apparently persisted for very long times in relatively stable environments, such as the depths of the ocean, most species of animals and plants (~99%) have appeared in the fossil record, persisted for periods on the order of 1–20 my, and then have gone extinct. Five major ‘mass extinctions’, caused by geological or extraterrestrial events (volcanism, bolide impacts,

etc.), are documented that have given rise to new evolutionary lineages and body plans (for instance, the extinction of the dinosaurs by the end of the Mesozoic ~65 my ago and the subsequent rise of mammals that finally led to the emergence of our species; **Figure 2**).

‘Phyletic evolution’ refers to a gradual change in morphology in a certain direction, for instance, human evolution, which has entailed a gradual increase in height and cranial capacity. However, phyletic evolution may be illusory and phylogenetic development is more properly described as ‘punctuated equilibrium’ – that is, a species generally endures with little or no change until it becomes extinct, but occasional instances of

speciation occur within a few million years, so it may appear that a single species has gradually changed. Instances of apparent phyletic evolution and punctuated equilibrium are both documented in the fossil record.

The synthetic theory of 1950 pictured evolution as being driven largely by natural selection of alleles with small effects, over relatively long times. This viewpoint has been challenged by champions of punctuated equilibrium with rapid speciation and by proposals that more drastic genetic events might be responsible for quite dramatic changes in morphology. It is clear that small genetic effects can account for the large morphological changes observed in fossil series. Furthermore, speciation that appears to be rapid on the geological timescale may actually require tens of thousands of years, a period perfectly consistent with small, slow genetic events. On the other hand, studies of developmental genetics have revealed so-called homeotic genes that govern major morphological changes. The combination of developmental biology with the evolutionary sciences ('Evo-Devo') has revealed modes of rapid evolutionary change that results from modifications in these regulatory genes.

Evolutionary Biology: A System of Theories

The architects of the synthetic theory and the founders of the evolutionary sciences, T. Dobzhansky, E. Mayr, and others, developed their concepts on the basis of Darwin's view of biodiversity, according to which animals and plants (i.e., eukaryotes) are the dominant organisms on a more or less static Earth. However, today it is clear that prokaryotes (bacteria, cyanobacteria) account for more than 50% of the protoplasmic biomass, and eukaryotic microbes (algae, marine phytoplankton, etc.) add at least another 30% to this equation. As a result, over a time period of ~3000 my, biological evolution has been a phenomenon that has predominantly taken place at the level of single cells. Bacteria influence, as symbionts as well as

pathogens, the evolution of animals and plants. Hence, 'symbiogenesis' (endosymbiotic events), directional 'natural selection' (the elimination of less adapted varieties), and the 'dynamic Earth' (plate tectonics) are key processes that have caused and continue to drive the evolutionary development in living populations of organisms (Figure 2). These 'units of evolution' are steadily challenged by changes in the environmental conditions – populations either respond with adaptation/diversification or become extinct.

We have to conclude that there is no longer a single, unifying 'Darwinian evolutionary theory': since ~1990, the synthetic theory of the 1950s developed into modern 'evolutionary biology'. This branch of the natural sciences consists of many theories that describe and explain different aspects of the diversifications (and extinctions) of all forms of life on our ever-changing (dynamic) 'planet of the microbes' (Figure 2).

See also: Darwin, Charles; Dobzhansky, Theodosius; Evolutionarily Rate; Speciation; Wallace, Alfred Russel.

Further Reading

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