Evolution ☆

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Glossary

Common descent Fact that all organisms on Earth are genealogically related, and descended from a Last Universal Common Ancestor (LUCA).

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

Evolution Descent with modification, ie, 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, ie, a group of interbreeding organisms that lives at the same time in a specific environment (habitat).

Species Reproductively isolated group of organisms, breeding among themselves, that have the greatest mutual resemblance, and may consists of one or numerous populations.

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 (Fig. 1(a)). But replication is not perfect, and heritable mutations continuously introduce genetic novelties. Furthermore, sexual reproduction entails the re-shuffling of chromosomes into different combinations, so individuals acquire, via re-combination, variant genomes, thus giving them different traits (or trait values). Populations inhabit ecosystems that afford various opportunities for obtaining

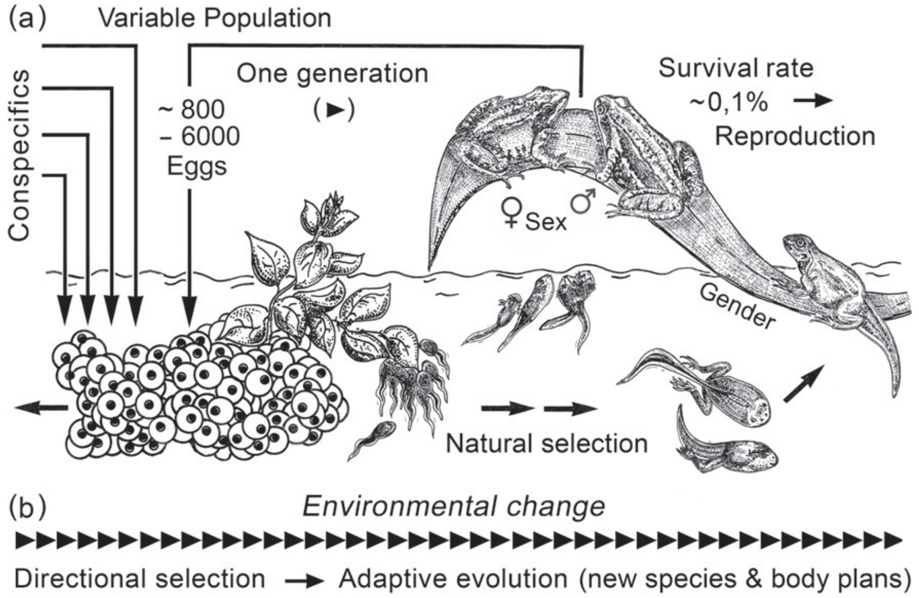

Fig. 1 Populations of organisms and the Darwin–Wallace principle of natural selection. Waterfrogs (*Rana* sp.) produce thousands of fertilized eggs per pair (sexual reproduction, variable offspring) (a). Due to limited resources there is a struggle for life, consisting of competition and cooperation among developing (juvenile) and adult male/female individuals within natural populations (gender-ratio c. 2/3 male). Over hundreds of subsequent generations, gradual changes in environmental conditions can cause adaptive phenotypic evolution by directional natural selection (b). Adapted from Kutschera, U., 2009. Theory Biosci. 128, 191–203.

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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, ie, 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. As Darwin and Alfred Russell Wallace recognized, natural selection is the central process governing biological evolution in groups of animals and plants, although sexual selection, and other processes, may also play an important part.

The Modern Theory: An Expanded Synthesis

While 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 only emerged in the early decades of the 20th 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, B. Rensch). Since that time, some tenets of this model of evolution have been challenged, and an enormous number of new facts and sub-theories 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 (**Fig. 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.). Most 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 re-combination 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, over numerous generations, as a result of changing environmental conditions (**Fig. 1(b)**). Studies on human populations revealed that genetic variability is attributable to re-combination via sexual reproduction and heritable germ-line mutations (c. 50: 50% of variation each).

Biological evolution, which originated with the earliest bacteria, can be divided into several phases (**Fig. 2**). At the cellular level, ancient primary endosymbiotic events (*symbiogenesis*, ie, the fusion of certain prokaryotes) gave rise to eukaryotic cells with the capability to evolve into complex 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 c.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 waterfrogs and other vertebrates (**Fig. 1(a)**), but largely meaningless for those that reproduce a-sexually. Such forms of life (bacteria, etc., see **Fig. 3**) 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, ie, 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 sub-population 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 etc., it acquires differences that result in reproductive isolation once the two sub-populations again become sympatric. Reproductive isolating mechanisms may entail ecological factors, such as occupying slightly different habitats so prospective mates do not come into contact; temporal factors, such as breeding at different times; and physical barriers to reproduction such as chromosomal re-arrangements, 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 sub-populations became isolated from one another on different islands.

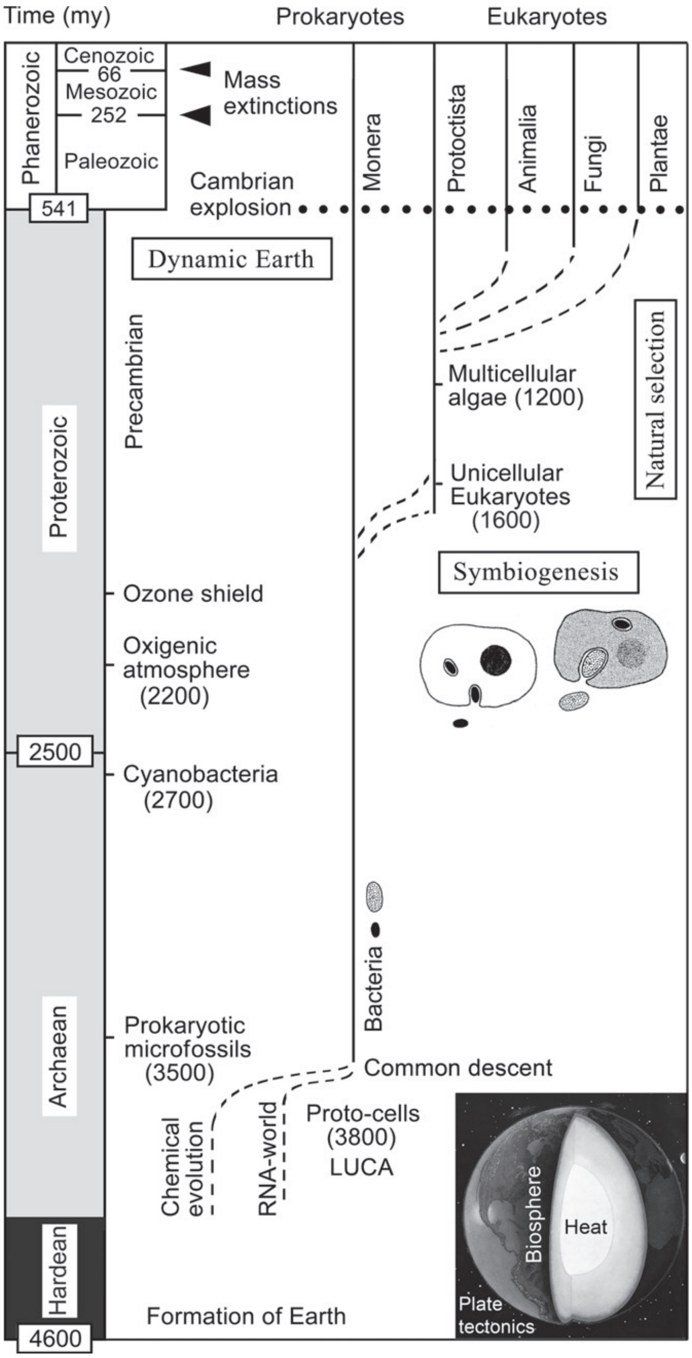

Fig. 2 Evolution of life on Earth. Ancient Proto-cells (LUCA) gave rise to the earliest prokaryotic cells (bacteria-like microfossils) that are about 3500 million years (my) old. Today, the descendants of these archaic microbes represent the dominant group of organisms on Earth (Kingdom 1: Bacteria, syn. Monera). Symbiogenesis (primary endosymbiosis) gave rise to eukaryotic cells, which evolved, via unicellular progenitors, into members of the Kingdoms 2 to 5: Protoctista (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 (Plate tectonics), caused biological evolution, associated with extinctions, in all five Kingdoms of Life (Synade-model). LUCA = Last Universal Common Ancestor. Adapted from Kutschera, U., 2009. Theory Biosci. 128, 191–203.

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, ie, 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 becomes 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 has 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, ie, in small populations genetic changes occur rapidly in a way not determined by directional natural selection.

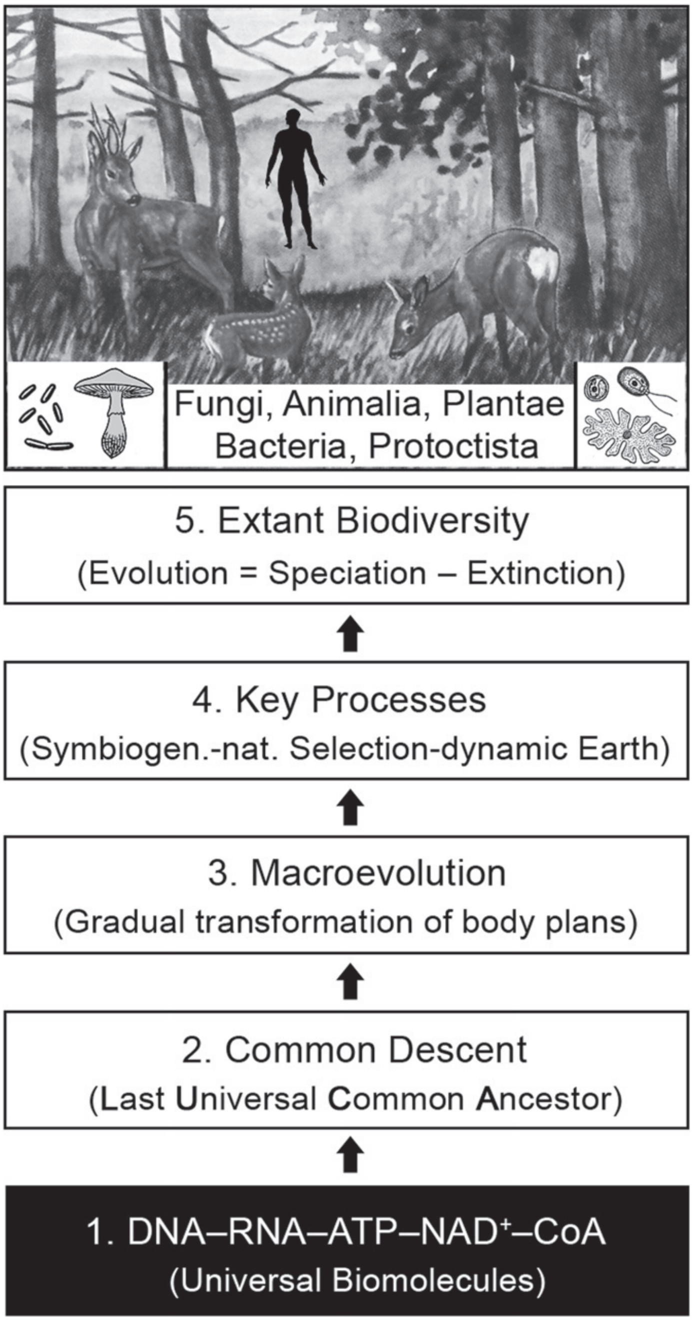

Fig. 3 Common descent, macroevolution and biodiversity on Earth. The unity of cellular biochemistry (1) supports the concept of LUCA (2). As a result, macroevolutionary transitions occurred over millions of years via descent with modifications (3), which was driven by three key processes: symbiogenesis, natural selection, and the dynamic Earth (4). Accordingly, all extant (and extinct) organisms are genealogically related (5). ATP=Adenosine triphosphate, CoA=Coenzyme A, DNA=Deoxyribonucleic acid, NAD^+=Nicotinamide adenine dinucleotide, RNA=Ribonucleic acid. Adapted from Kutschera, U., 2015. Evolutionsbiologie. 4. Auflage. Stuttgart: Verlag Eugen Ulmer.

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 genotype of the much larger parent population (founder effect on islands, etc.).

Common Descent, Mass Extinctions and Evo-Devo

Universal common descent, as postulated by Darwin (1859) and others, is a well-supported concept that accounts for the unity, as well as the diversity of all forms of life on Earth, from prokaryotic microbes (bacteria) to eukaryotic super-organisms (humans and other vertebrates). Animals harbor symbiotic microbes in their gut, and plants are associated with symbiotic fungi (root system), as well as numerous epiphytic bacteria that cover the entire body of the green organism.

The facts that cells originate from mother-cells, heritable material (DNA) from pre-existing genes that are transferred via sexual reproduction to the next generation (Figs. 1 and 2), and the occurrence of five major classes of universal biomolecules are proof for common descent (Fig. 3). As a result, a Last Universal Common Ancestor (LUCA) must have existed c.3800 my ago, from which, via macroevolutionary processes, all extant (and extinct) organisms descended, with major modifications (five Kingdoms, see Figs. 2 and 3).

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 (c. 99%) have appeared in the fossil record, persisted for periods on the order of one to c.20 million years, 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 c.66 my ago and the subsequent rise, and macroevolutionary diversification, of mammals that finally led to the emergence of our species) (Figs. 2 and 3).

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* – ie, 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 time scale 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 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 (ie, 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 (amoebae, algae, marine phytoplankton, etc.) add at least another 30% to this equation. As a result, over a time period of c.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, variable populations of organisms (Figs. 1 and 2). These "units of evolution" are steadily challenged by changes in the environmental conditions – populations either respond with adaptation/diversification, and thus continue to exist in modified forms, or become extinct (Fig. 3).

We have to conclude that there is no longer a single, unifying "Darwinian evolutionary theory": Since c.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" (Figs. 2 and 3).

Further Reading

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