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REVIEW

Charles Darwin's *Origin of Species*, directional selection, and the evolutionary sciences today

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Abstract The book *On the Origin of Species*, published in November 1859, is an "abstract" without references, compiled by Charles Darwin from a much longer manuscript entitled "Natural Selection." Here, I summarize the five theories that can be extracted from Darwin's monograph, explain the true meaning of the phrase "struggle for life" (i.e., competition and cooperation), and outline Darwin's original concept of natural selection in populations of animals and plants. Since neither Darwin nor Alfred R. Wallace distinguished between stabilizing and directional natural selection, the popular argument that "selection only eliminates but is not creative" is still alive today. However, I document that August Weismann (*Die Bedeutung der sexuellen Fortpflanzung für die Selektions-Theorie*. Gustav Fischer-Verlag, Jena, 1886) and Ivan Schmalhausen (*Factors of evolution. The theory of stabilizing selection*. The Blackiston Company, Philadelphia, 1949) provided precise definitions for directional (dynamic) selection in nature and illustrate this "Weismann–Schmalhausen principle" with respect to the evolutionary development of novel phenotypes. Then, the modern (synthetic) theory of biological evolution that is based on the work of Theodosius Dobzhansky (*Genetics and the origin of species*. Columbia University Press, New York, 1937) and others, and the expanded version of this system of theories, are outlined. Finally, I document that symbiogenesis (i.e., primary endosymbiosis, a process that gave rise to the first eukaryotic cells), ongoing directional natural selection, and the dynamic Earth (plate tectonics, i.e., geological events that both created and destroyed terrestrial and aquatic habitats) were the key processes responsible for the documented macroevolutionary patterns in all five kingdoms of life. Since the evolutionary development of the earliest archaic bacteria more than 3,500 mya, the biosphere of our dynamic planet has been dominated by prokaryotic microbes. Eubacteria, Archaea, and Cyanobacteria are, together with eukaryotic microorganisms (marine phytoplankton, etc.), the hidden "winners" in the Darwinian struggle for existence in nature.

Keywords Charles Darwin · Evolutionary biology · Natural selection · Symbiogenesis · Synthetic theory

This contribution represents the introduction to the Special Issue "Beyond the Origin: Charles Darwin and modern biology" (Guest editor: U. Kutschera)

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Introduction

During his 5-year-long voyage of the H.M.S. *Beagle* the young theologian and naturalist (geologist, zoologist, and botanist) Charles Darwin (1809–1882) acquired extensive field experiences and had opportunities to study the problem of the nature of species and varieties. In particular, certain fossils of Argentina and the peculiar tortoises, birds, and reptiles of the Galapagos Archipelago had changed Darwin's former Bible-based view concerning the "species question." In July 1837, only 1 year after his return to England, the 28-year-old junior scientist opened his first notebook on the "Transmutation of Species." Fifteen months later, Darwin conceived his concept of natural selection when he studied a book of Robert Malthus (1766–1834) on the principles and consequences of population growth in humans: "In October 1838, … I happened to read for amusement Malthus on *Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species. Here, then, I had at last got a theory by which to work" (Barlow 1958, p. 120). Four years later, Darwin wrote out a sketch of his species theory in 35 pages. This "very brief abstract … was enlarged during the summer of 1844 into one of 230 pages" (Barlow 1958, p. 120). One century ago, these two earliest versions were edited by Darwin's son Francis (1844–1925) and published under the title *The Foundations of the Origin of Species* (Darwin 1909).

The aim of this article, which introduces a series of reviews on various topics related to the general theories of Charles Darwin (see Special Issue "Beyond the Origin: Charles Darwin and modern biology"; Fig. 1), is twofold. First, I will describe the origin and basic contents of Darwin's most influential book *On the Origin of Species* with special reference to the principle of natural selection as originally outlined in this monograph of 1859. In the second part of this essay, I describe the foundation and development of the scientific discipline of *Evolutionary Biology*, which descended, with large modifications and additions, from Darwin's classical "species theories" that were published 150 years ago this month.

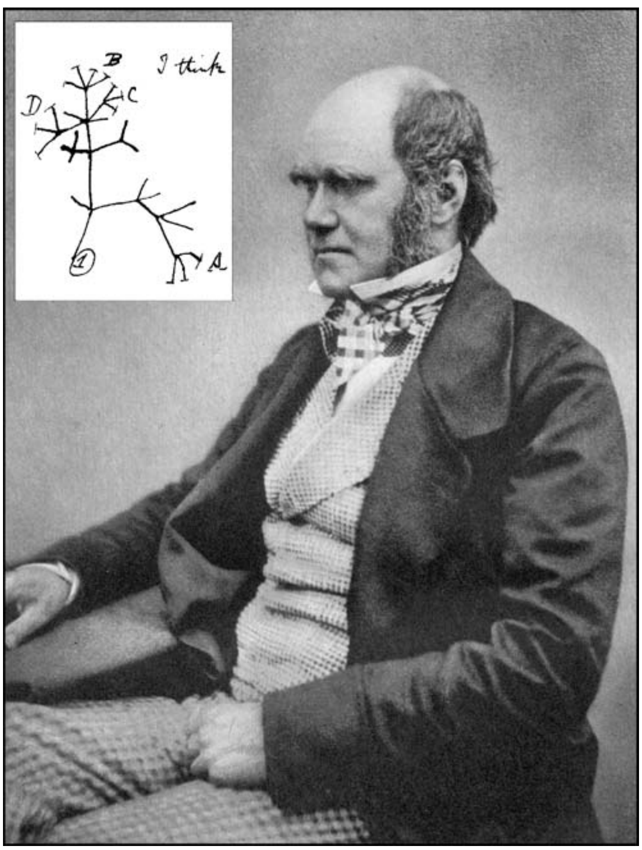

Fig. 1 Photograph of Charles Darwin (1809–1882), at the age of 51, and his first evolutionary tree sketched in 1837, with the added commentary "I think" (adapted from Barlow 1958)

Vestiges of creation, the barnacles, and Alfred Russell Wallace

In 1844, the year when Darwin had completed the second, long version of his "Sketch of the Species Theory," a popular book authored by Robert Chambers (1802–1871) with the provocative title *Vestiges of the Natural History of Creation* was first published. By this time, the 35-year-old Darwin was convinced that his new theory of natural selection was such an important contribution to science that he wrote a special testament: In case of his premature death, the long version should be published, and Darwin dedicated a considerable sum of money for this purpose (page charges for a publisher). The response to the "species book" by R. Chambers, which contained wild speculations that were mixed up with crude errors of scientific facts, elicited many negative responses and devastating reviews by eminent British natural scientists. This hostile criticism of a popular book on the "species question" signaled to Darwin what could happen with his own theory on the transformation of species if he would publish an incomplete version of his manuscript prematurely.

Since Darwin was an independent scientist without pressure to publish (Fig. 2), he gradually enhanced his reputation as a naturalist and taxonomist until his accumulated empirical evidence had reached such a weight that his "species theory" could not be ignored or dismissed as those of R. Chambers, J. -B. de Lamarck, and others. By the middle of the 1850s, shortly after the respected geologist/biologist Charles Darwin had been awarded the "Royal Society Medal" for his outstanding scientific publications, and his classification of the barnacles (crustaceans of the class Cirripedia) was almost completed, the time was ripe. His two-volume monograph on the Cirripedia (Fig. 3; Darwin 1851/1854) proved beyond any doubt that the man of private means was now prepared to resume and finish his work on the species problem. As Newman (1993) pointed out, Darwin's work on cirripedes was remarkable and displayed his genius as a scientist.

On 9 September 1854, when his comprehensive work on the taxonomy of the barnacles was complete, Darwin began sorting notes for his species theory. To become familiar with variation under domestication, he kept every breed of pigeons he could obtain and joined two of the London pigeon clubs (Roth and Kutschera 2008). After discussions of his concepts with colleagues, his former mentor Charles

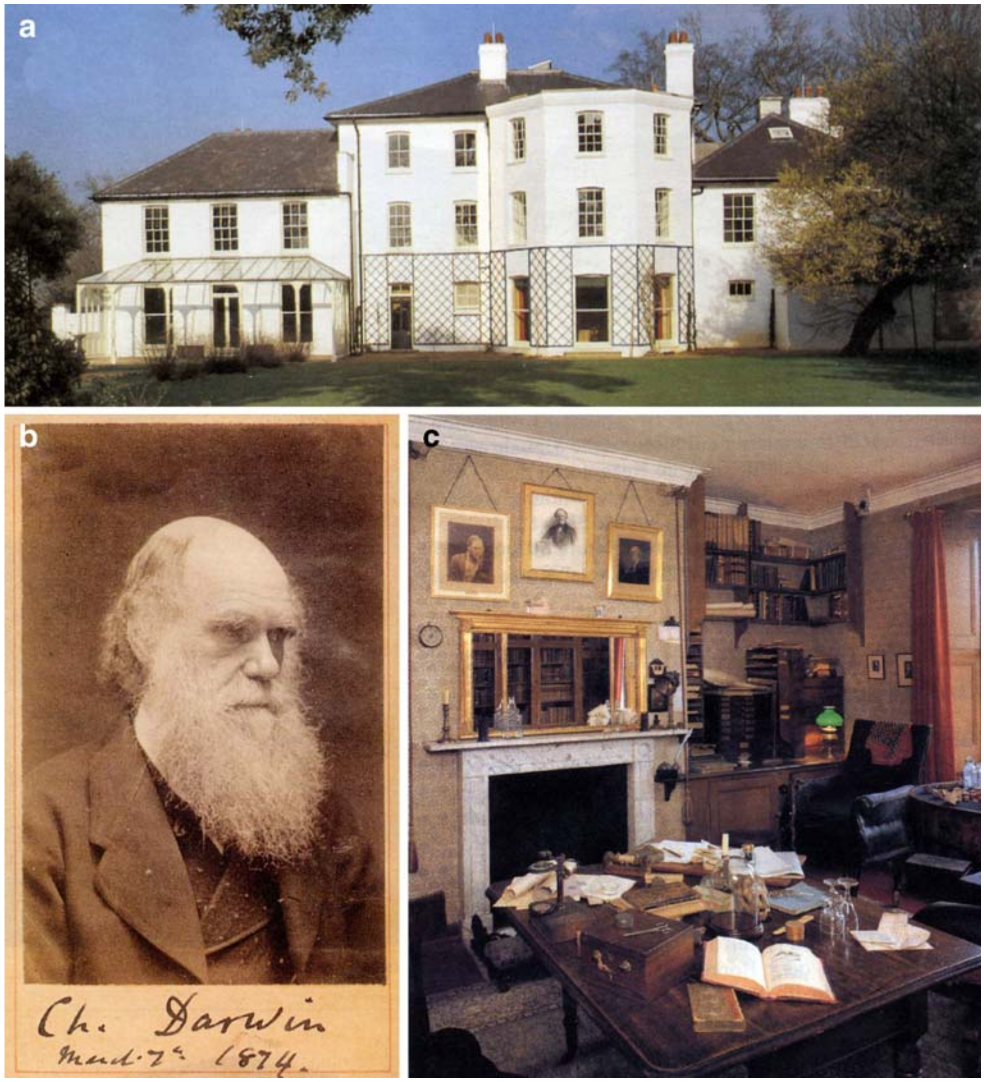

Fig. 2 Charles Darwin's country house at Down/Kent, England (**a**), a signed portrait, ca. 1874 (**b**), and his room where the British naturalist wrote most of his important books on evolution and other topics (**c**) (adapted from different photographs, ca. 1920)

Lyell (1797–1875) urged Darwin to start writing (Desmond and Moore 1991; Ayala 2007).

Under the title *Natural Selection-1854*, Darwin wrote a comprehensive manuscript. This work was already twice the length of the *Origin of Species* and largely completed when, in early 1858, he received a letter from Alfred Russell Wallace (1823–1913) outlining a similar theory on the struggle for existence and the transformation of species in nature. Like Darwin in October 1838, Wallace combined, in February 1858 during a stay in the Malay Archipelago, the principle of Robert Malthus (Fig. 4) with his own observations on variability in natural populations of animals. Based on these findings, Wallace concluded that “The life of wild animals is a struggle for existence.” Under the advice and supervision of the geologist Lyell and the botanist Joseph Hooker (1817–1911), Wallace’s so-called “Ternate Essay” and fragments from Darwin’s species manuscripts were read at the next meeting of the *Linnaean Society of London* and published in volume 3 of the *Proceedings* on August 20 (Darwin and Wallace 1858). By this means, the “Darwin–Wallace principle of natural selection,” a two-author concept, was introduced into the emerging field of evolutionary biology and Darwin’s priority as the first author was documented (Kutschera 2003, 2008a, 2009a). However, after the publication of Darwin’s book *On the Origin of Species* in November 1859—an “abstract” without references, compiled from his large manuscript, that was later supplemented by two other monographs on related topics (Darwin 1868, 1871), the contribution of Wallace as codiscoverer of natural selection was overshadowed. The basic messages of Darwin’s “species book,” from our modern perspective, are summarized in the next section.

Darwin’s system of species theories

Although the tenets of Robert Malthus (Fig. 4) inspired both Darwin (in 1838) and Wallace (two decades later) to propose the principle of natural selection, Darwin (1859)

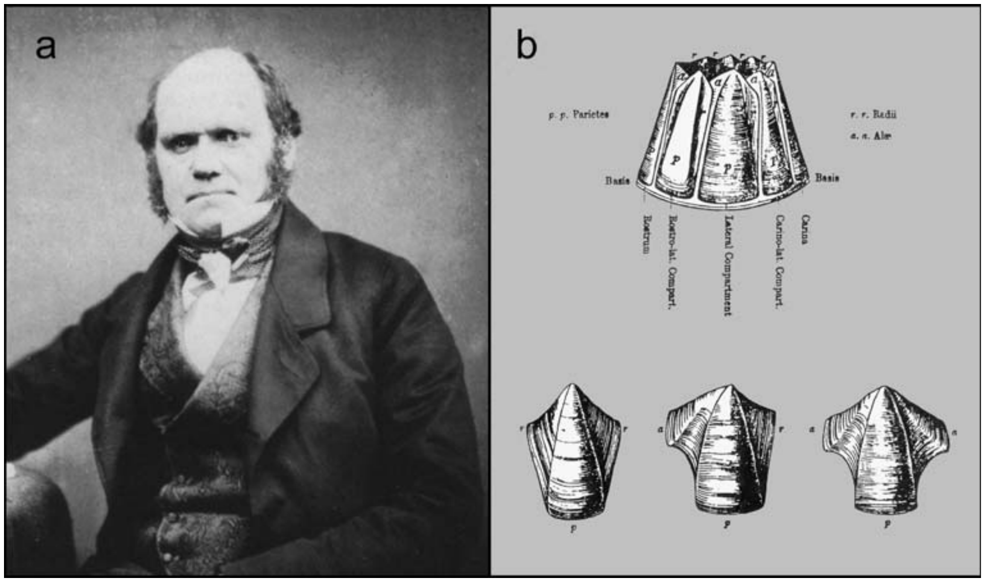

Fig. 3 Charles Darwin, ca. 1854, after he had finished his monograph on the Cirripedia (**a**) and a representative figure reproduced from his famous "barnacle book" (**b**) (adapted from two photographs, ca. 1920)

mentioned the English amateur economist only briefly. In his manuscript with the original title *An Abstract of an Essay on the Origin of Species and Varieties through Natural Selection*, which was published on November 24 under a more precise headline, Darwin (1859) summarized five separate theories pertinent to the "species problem" (Mayr 2004). These Darwinian concepts were drawn here into a reproduction of the only illustration in this monograph, a schematic phylogenetic tree (Fig. 5; see inset of Fig. 1 for Darwin's first sketch of an evolutionary tree drawn in 1837).

In his "species book," Darwin (1859, 1872a) repeatedly argued in a way as if he would describe one homogeneous theory, a view that is incompatible with the fact that organismic evolution consists of two separate processes: Transformations in time, from the Cambrian to the present, and diversifications in geographic and ecological space. Moreover, the word *Origin* in the title of his monograph implies that the author would analyze the emergence of the earliest forms of life on Earth (chemical evolution, see Follmann and Brownson 2009). In contrast to this expectation, in chapter VII (entitled "Instinct"), the reader is informed that the author has "nothing to do with the origin of the primary mental powers, any more than … with that of life itself" (Darwin 1859, p. 159). In other words, the origin of life is not discussed scientifically in Darwin's "species book."

Charles Darwin's five "species theories" can be summarized as follows: (1) Evolution versus independent acts of creations; (2) common descent; (3) gradualism versus saltationism; (4) the multiplication of species; and (5) natural (and sexual) selection (Fig. 5).

On many pages on his book, Darwin argued that no species that has ever lived on this planet is immutable—organic beings descended with modification (i.e., they have evolved). This first Darwinian "theory of descent with slight and successive modifications" (1) was juxtaposed to the Bible-based "theory of independent

Thomas R. Malthus: An Essay on the Principle of Population (1798)

"The power of population is indefinitely greater than the power of the earth to produce subsistence for man. Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio. …

By that law of our nature which makes food necessary for the life of man, the effects of these two unequal powers must be kept equal. This implies a strong and constantly operating check on population from the difficulty of subsistence.

This difficulty must fall somewhere and must necessarily be severely felt by a large portion of mankind".

Fig. 4 Drawing of the British economist Thomas R. Malthus (1766–1834) and reproduction of the most important passages from his book on the principles of population growth in humans. This "Malthusian rule" inspired both C. Darwin and A. R. Wallace to develop the theory of natural selection

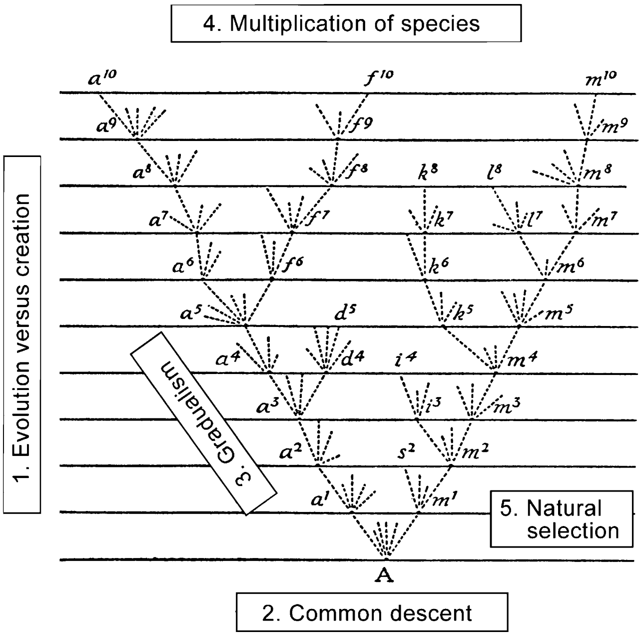

Fig. 5 Reproduction of a section from the original phylogenetic tree in Darwin's *Origin of Species* (1859), combined with the five theories extracted from his "species book" (concepts 1 to 5)

acts of creations." Darwin (1859, 1872a) explained in detail that his concept (theory) of the transformation of species is supported by a large body of facts, whereas the belief in supernatural acts of a Creator (i.e., the constancy of all organic forms) is wrong. Today, descent with modification (i.e., evolution sensu Darwin) is no longer a theory—it is as much a fact as that the Earth is round rather than flat (Kutschera and Niklas 2004). Although five decades earlier, Lamarck (1809) had proposed that organisms may have changed, it was Darwin's accumulated mass of empirical evidence that led to the breakthrough of the concept that all species on Earth have evolved over long periods of time.

In the first edition of the *Origin*, Darwin (1859) speculated that the entire biosphere must be viewed as a continuum: "I believe that animals have descended from at most four or five progenitors, and plants from an equal or lesser number … analogy would led me one step further, namely, to the belief that all animals and plants have descended from some one prototype … probably all the organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed" (Darwin 1859, p. 364). In the sixth edition, Darwin (1872a) had modified and extended his "principle of common descent" (2) considerably. He referred to "lower algae" as primitive intermediate forms between the animal and plant kingdoms and, in the last sentence of the text, had introduced "the Creator" as the cause for the "power of life," breathed into a few forms or one. Today, we know that Darwin's theory of common descent is correct, although his "proto-*Euglena* (i.e., lower algae)" concept was wrong (Kutschera and Niklas 2008). His introduction of "the Creator" (i.e., an unknown process) in later editions of his "species book" caused many controversial discussions among nineteenth century biologists, a topic that is beyond the scope of this article (see for instance, Bronn 1860).

Darwin's third theory (gradualism, 3) was in part based on a philosophical principle (Natura non facit saltum): species transformations should always occur gradually and not in jumps. In more general terms, Darwin (1859, 1872a) argued that species as well as higher taxa arise through gradual, step-by-step transformations. In our modern terminology, according to Darwin (1859, 1872a), microevolution and macroevolution form a continuum. Saltationism—the abrupt, sudden occurrence of new species—was in Darwin's view neither supported by evidence nor possible on theoretical grounds, since species should, during long periods of transformations, always maintain their adaptations. Today it is well established that gradualism is the norm, i.e., Darwin (1859, 1872a) was basically right (Herrada et al. 2008). However, one-step endosymbiotic events have "punctuated" the history of life on Earth, so that novel unicellular body plans emerged in aquatic organisms. The origin of eukaryotic cells with organelles (mitochondria, chloroplasts) was one of the key events in the history of life that finally led to the emergence of animals and plants. Darwin was not aware of this principle of symbiogenesis, which was proposed in 1905, after the discovery of hundreds of new microorganisms (bacteria, cyanobacteria, amoebae, etc.; Kutschera and Niklas 2005, 2008; Kutschera 2009a).

The young Charles Darwin started his career as a "hobby-beetle-collector" (Desmond and Moore 1991) and was, notably as a result of his experience as cirripediologist (Newman 1993) and his 5-year-long occupation as the *Beagle*-"species-specialist," fully aware of the enormous diversity of life on Earth. Today, we know that beetles (Coleoptera, class Insecta) represent the largest single group of animals on this planet—more than 350,000 species have been described (Beutel et al. 2009). In contrast to the "discoverer" of the fact of evolution (Lamarck 1809) who had largely ignored the diversity of life and adopted the now obsolete idea of "spontaneous generations," Darwin (1859) was the first to acknowledge and analyze the horizontal (geographic) dimension of evolution (Mayr 1991, 2004). Although Darwin (1859, 1872a) did not distinguish between varieties and species, he nevertheless proposed a novel concept (theory) for the multiplication of organic forms (4) based on his rather vague "principle of divergence of character and extinction." His phylogenetic tree (Fig. 5) depicts a scheme of increasing biologic diversity in time and space, which is compatible with our modern concept of a single "tree of life" (Herrada et al. 2008; Conway Morris 2009). The exact question as to what species are and how they arise and multiply was addressed decades later by the "architects" of the synthetic theory of biological evolution (see below).

Finally, Darwin's theory of natural selection (5), which formed the core of his *Origin of Species*, dealt with the mechanism of evolutionary change as well as the adaptation of organisms to their local environment. On several pages of his book, Darwin (1859) described natural selection as "the preservation of favourable variations and the rejection of injurious variants," a definition that is largely identical with that given in the full title of his book. In chapter IV, entitled "Natural Selection," he provided a more concise circumscription: "It may be said that Natural Selection is daily and hourly scrutinising … every variation, …; rejecting that which is bad, preserving, and adding up all that is good; … working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life" (Darwin 1859, p. 65). However, as Paterson (2005) has pointed out in a detailed analysis, Darwin (1859) had implicitly adopted the principle of competitive selection in place of the older concept of environmental selection, as envisioned by A. R. Wallace in their two-part essay (Darwin and Wallace 1858). Since both authors failed to distinguish between the stabilizing ("conserving") and directional ("creative") forms of selection, this topic is discussed in detail below.

It should be noted that Darwin (1859, 1872a) also introduced the concept of sexual selection as a subprinciple of the "natural mode" of selection (i.e., the struggle between males and female choice). A discussion of this second Darwinian principle of selection in animal populations is beyond the scope of this essay (for a historic analysis of this topic, see Paterson 2005).

Struggle for life versus Kampf ums Dasein

The paleontologist Heinrich Georg Bronn (1800–1862) translated the second edition of Darwin's "species book" into German. Under the awkward title "Charles Darwin. Über die Entstehung der Arten im Thier- und Pflanzen-Reiche durch natürliche Züchtung, oder Erhaltung der vervollkommneten Rassen im Kampfe um's Daseyn," Bronn (1860) transmutated Darwin's metaphorical term "struggle for life," which applies to animals as well as plants with reference to the production of offspring, into "Kampf ums Dasein" (fight for life). However, Darwin was not pleased with this Malthusian translation of one of his key terms. During the 1860s, he exchanged letters with the German physiologist and psychologist Wilhelm T. Preyer (1841–1897) who became known for the development of a specific assay for the toxic gas carbon monoxide (CO) in the blood (Preyer's test) and as an author of several textbooks. For instance, his monograph on physiological embryology (Preyer 1885) and related publications inaugurated a new area of research in human physiology and development behavior of infants.

In a letter to the "Darwinist" W. T. Preyer dated March 29, 1869, Darwin explained the meaning of this phrase: "About the term 'Struggle for Existence', I have always felt some doubts, but was unable to draw any distinct-line between the two ideas therein included. I suspect that the German term, Kampf etc., does not give quite the same idea. The words 'struggle for existence' express, I think, exactly what—concurrency does. It is correct—to say in English that two men struggle for existence, who may be hunting for the same food during a famine, and likewise when a single man is hunting for food—or again it may be said that a man struggles for existence against—the waves of the sea when shipwrecked" (Engels 2005, p. 48). Darwin's term "concurrency," as a synonym for "struggle for life," had several meanings. In the Oxford New English Dictionary of 1893, we find three different definitions: "1. A running together in place or time; 2. Accordance in operation or opinion, cooperation, consent; 3. Pursuit of the same object with another, competition, rivalry …." Hence, Darwin's term "struggle for existence" (i.e., concurrency) has two different and opposing meanings: competition or cooperation. In our modern English language, "concurrence" means (1) simultaneous occurrence or coincidence and (2) agreement, accordance, cooperation (Kutschera 2009b). These definitions show that Darwin's "two ideas," included in the phrase "struggle for life," refer to the competition for limited resources as well as cooperative (altruistic) acts, as far as they led to an enhancement of the lifetime reproductive success of the individual (Darwinian fitness; Fig. 6). In other words, the "struggle for existence" is neither purely competitive nor exclusively cooperative: it is opportunistic (for case studies on opportunistic reproductive behaviors in leeches and frogs, respectively, see Kutschera and Wirtz 2001; Vieites et al. 2004). This Darwinian definition is compatible with our modern view of evolution at the molecular, cellular, and organismic level, as detailed in the next sections.

Charles Darwin, Herbert Spencer, and the principle of evolution

It is well known that, in the first edition of Darwin's book *On the Origin of Species* (1859), the word "evolution" is not used, with the exception of the very

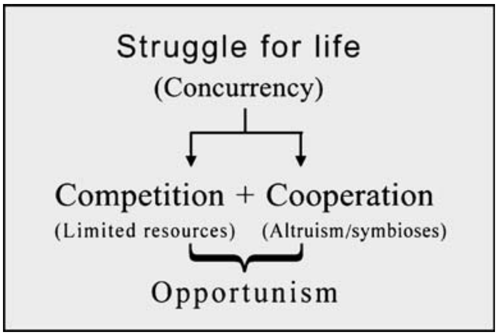

Fig. 6 Scheme depicting the true meaning of Darwin's phrase “struggle for life (or existence).” According to the British naturalist, competition for limited resources and cooperative acts both may contribute to the lifetime reproductive success of organisms, i.e., the “struggle for existence” is neither entirely competitive nor cooperative: under natural conditions, organisms behave opportunistically in order to survive and reproduce

last sentence, which ends with the derivative “… evolved.” In later editions of the *Origin*, Darwin used the “e-word” as a synonym for his phrase “descent with modification” and juxtaposed this naturalistic concept with the “theory of independent acts of creations.” Thirteen years after his most influential book was published, the sixth and last edition appeared in print, wherein Darwin (1872a) occasionally used the term “evolution,” but still preferred to describe his novel concept as the “theory of descent with modification.”

Why did Charles Darwin not used the word “evolution” when he outlined his system of species theories for the first time in 1858/1859? The Latin word *evolutio* means “to unroll,” i.e., the unpacking of a structure that already exists in a more compact or concentrated form. The German zoologist Ernst Haeckel (1832–1919) and other embryologists used the term “evolution” to describe the development of the embryo in animals, a process for which the word “ontogenesis” was coined (Haeckel 1866). Earlier embryologists interpreted their observations via the literal meaning of “evolution”: the development or enlargement of a pre-existing miniature, equipped with all the cellular structures and organs detectable after birth of the animal (Levit et al. 2004). Despite of the fact that Haeckel (1866) introduced the terms “ontogeny” and “phylogeny” (i.e., phylogenetic development), the word “evolution” (sensu phylogeny) was neither used by Haeckel nor by August Weismann (1834–1914). These eminent biologists translated Darwin’s phrase “descent with slight and successive modifications” into “transmutation, transformation, or development” of species (Haeckel 1866; Weismann 1886, 1892, 1904). At least in the German literature, the word evolution (sensu the Darwinian phrase “descent with modification”) was not used until the 1920s (for instance, see, Bueckers 1909).

In his book on *The Expression of the Emotions in Man and Animals*, Darwin (1872b) referred to the philosopher Herbert Spencer (1820–1903) as the “great expounder of the principle of evolution.” As Bowler (2003) has documented in detail, it was Spencer who introduced and popularized the term “evolution” to denote the phylogenetic development of all forms of life on Earth with the intention of progress to higher states. In the last edition, Darwin used Spencer’s “e-word” eight times, notably in the last chapter: “I formerly spoke to very many naturalists on the subject of evolution … It is probable that some did then believe in evolution, … Now things are wholly changed, and almost every naturalist admits the great principle of evolution” (Darwin 1872a, p. 500). In the fourth, fifth, and sixth editions of the *Origin of Species*, Spencer’s term “fitness” is used by Darwin as a synonym for natural selection; it is questionable whether or not this new term was an adequate choice (Mayr 1991, 2004; Gregory 2009). In modern evolutionary biology, the phrase “Darwinian fitness” is a synonym for “lifetime reproductive success” (Dobzhansky 1955; Dobzhansky et al. 1977). Hence, Herbert Spencer’s two terms (evolution and fitness), as adopted by Darwin, are still alive today.

The development and subsequent eclipse of Darwin’s theory of natural selection

The German zoologist and cytologist August Weismann was the most important successor of Darwin with respect to the development of a modern theory of biological evolution (Mayr 1991, 2004; Kutschera and Niklas 2004). He coined the terms “germ plasm,” a potentially immortal substance that is localized in the haploid sex cells (eggs, sperm) of the animal, and the “soma,” i.e., the mortal rest of the body. Moreover, Weismann (1886, 1892, 1904) was one of the first to point out that transmutation (i.e., descent with modification or evolution) is a fact and not “only a (Darwinian) theory,” that acquired characters, modifications restricted to the soma, are not inherited (as Lamarck and Darwin believed), and that sexual reproduction causes variable offspring—the raw material for natural selection in populations of organisms.

Based on these and other insights, Weismann’s improved and extended version of the “Darwin–Wallace principle of natural selection” has been called “Neo-Darwinism” or “Weismannism” (Kutschera and Niklas 2004). In the last edition of *The Origin of Species*, Darwin mentioned “Professor Weismann” and rejected one of his tenets as follows: “Some naturalists have maintained that all variations are connected with the act of sexual reproduction; but this is certainly an error; for I have given in another work a long list of ‘sporting plants’ … that is, of plants which have suddenly produced a single bud with a new … character" (Darwin 1872a, p. 26). Today, we know that sexual reproduction, via genetic recombination, combined with heritable mutations, are the key processes that cause variability in populations of animals and plants—the macroorganisms that Lamarck, Darwin, Weismann, and other nineteenth century pioneers of evolutionary biology investigated. It should be noted that Weismann (1886) was one of the first to point out that natural selection under gradually changing environmental conditions must be viewed as one of the "driving forces" for the transformation of species, whereas Darwin (1859, 1872a) did not explicitly discuss this idea, stating only that, in a slowly changing environment, adaptive evolution may occur. Since these remarks concerning the role of changing environmental conditions were not very precise, the theory of natural selection as originally proposed by Darwin (1859, 1872a) was questioned by many scientist during the first decades of the twentieth century.

The classical arguments against "Darwin's hypothesis of transmutation via natural selection" can be summarized as follows (DeVries 1901; Bueckers 1909; Tower 1906, 1918). All authors accepted Darwin's "Malthusian biopopulation principle" (Fig. 4), i.e., the fact that every species tends to increase at a rapid rate and produces a larger number of individuals than are capable of survival. In addition, there was general consensus that, of these individuals, approximately 98% on average die (or are eaten by predators) before reaching maturity. Hence, only approximately 2% of those born survive in the "struggle for existence" to produce the next generation. However, it was argued that it is not clear whether those individuals which persisted and reached maturity are those which possess variations of a nature such as they are thereby made more efficient than their conspecifics, and hence better able to successfully compete, or whether the survivors are only those individuals whose chance position, when the "accidents of life" happened, save them from extinction and eliminate their less fortunately placed companions. In a monograph published six decades after the "Darwin–Wallace principle" was proposed, Tower (1918) concluded that it has not yet been shown that the surviving individuals are the fortunate possessors of advantageous modifications. At that time, "Darwin's survival dilemma" was summarized as follows. If it proved to be true that the elimination in natural populations is largely a matter of chance position of the individuals when the "accidents of life" occur and that the survivors are on average no better adapted to the local environment than those that are eliminated, it follows that natural selection as a means to drive the transformation of species and to cause biological diversity in natural populations must be abandoned.

Based on this train of thought, DeVries (1901) concluded that "Darwinian natural selection" acts solely as a kind of sieve which allows certain individuals to persist, while others are eliminated. With reference to Darwin's monographs, wherein the plant and animal breeder's observations of occasional sudden hereditary changes or "sports" are summarized (Darwin 1859, 1868, 1872a), as well as own data on the evening primrose (*Oenothera lamarckiana*), the Dutch plant physiologist and geneticist deduced his "mutation theory" (see Kutschera and Niklas 2009). However, it was later shown that the *Oenothera* "mutations" that inspired the new theory (DeVries 1901) were most likely due to extra chromosomes present in his research material, rather than mutations in the modern sense of the word (Birchler and Veitia 2007). Nevertheless, based on these and other data, the geneticist Goldschmidt (1940) later proposed the "hopeful monster theory," which has recently been modified and discussed with respect to primary and secondary endosymbiotic events and the creation of novel unicellular body plans in planktonic organisms (Kingdom Protoctista; Kutschera and Niklas 2008).

The theoretical arguments against Darwinian "natural selection" as a major "driving force" for the transformation of species summarized above, in tandem with the mutation theory of DeVries (1901), motivated the entomologist Tower (1906, 1918) to reinvestigate these topics. With the support of the *Carnegie Institution of Washington*, he studied large populations of chrysomelid beetles of the genus *Leptinotarsa* and analyzed the variability, ecology, habits, as well as the development of these insects of economic importance ("potato beetles"; Fig. 7a, b). Tower (1906, 1918) discovered occasional extreme heritable variants in natural populations of these beetles, but concluded that these "mutants" are not a special kind of variability, different from that of "ordinary fluctuating variation," but part of the normal variation in populations. He concluded that there is no evidence that "mutants have taken any great part in evolution of these beetles, all

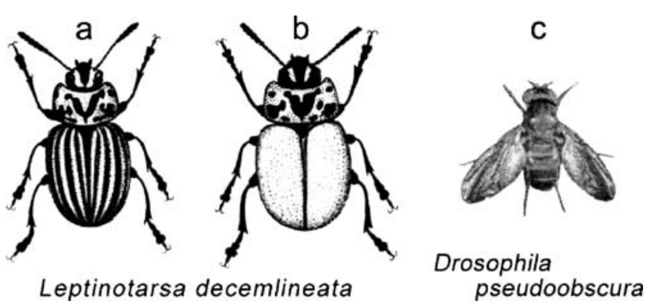

Fig. 7 Insects as model organisms for the study of evolutionary processes in wild populations. Potato beetles (*Leptinotarsa decemlineata*), dark-pigmented individual that represents the norm (**a**), and mutant phenotype, with drastically reduced pigmentation (**b**). The fruit fly (*Drosophila pseudoobscura*) was used by T. Dobzhansky to study speciation in nature (**c**) (adapted from Tower 1906)

evidence showing them to be most rigorously exterminated by natural selection … the evolution of the genus *Leptinotarsa* and of animals in general, has been continuous and direct, developing new species in migrating races by direct response to the conditions of existence … natural selection acts as the conservator of the race by limiting the variations to a narrow range of possibilities … The breeding 'mutants' in our gardens and laboratories cannot tell us how they would succeed in nature … they fare badly … and they play a minor role in the evolution of species" (Tower 1906, p. 314).

These comprehensive experimental studies did not support the "classical" Darwinian theory of natural selection, a concept that does not explicitly refer to the directional role of gradual changes in the environmental conditions. Moreover, Tower (1906, 1918) refuted the "mutation theory" for the abrupt origination of new species as proposed by DeVries (1901), at least with respect to beetles and other insects.

Stabilizing versus directional natural selection

The arguments against the "creative" role of natural selection in populations of organisms summarized above are still alive today. For instance, during the discussion at the end of a public lecture on "Charles Darwin and modern evolutionary biology" that I delivered in March 2009 at a German University, a physicist challenged the role of natural selection in the following words: "Selection produces nothing new; it only removes from the population degenerate, less adapted or malformed variants; therefore, Darwinism is wrong and has to be replaced by other concepts." I answered that "the first part of your commentary is true. In constant environments, stabilizing selection tends to eliminate all deviations from the average—the well-adapted individuals that represent the 'norm' of the population. However, when the environmental conditions change, extreme phenotypes may have a better chance of survival than there 'normal' conspecifics and hence will, over many subsequent generations, dominate the population. Today it is well established that directional natural selection is a creative process that permits the survival and proliferation of novel phenotypes in new environments, whereas stabilizing selection preserves the average individuals." It is likely that Darwin and Wallace (1858) and Darwin (1859, 1872a) had directional (and not stabilizing) selection in mind, but, unfortunately, they did not distinguish between these two types of selection.

According to Dobzhansky (1955), the Russian biologist Ivan I. Schmalhausen (1884–1963) was the first to distinguish between the dynamic (directional) and stabilizing modes of natural selection in populations of organisms. However, in a little-known monograph on the role of sexual reproduction with respect to organismic evolution that was published 4 years after Darwin's death, the German zoologist Weismann introduced the principle of directional natural selection in the following words: "Die Selektionstheorie lässt neue Arten daraus hervorgehen, dass von Zeit zu Zeit veränderte Lebensbedingungen eintreten, welche neue Ansprüche an den Organismus stellen, … und dass in Folge dessen Selektionsprozesse einsetzen, welche bewirken, dass unter den vorhandenen Variationen allein diejenigen erhalten bleiben, welche den veränderten Lebensbedingungen am meisten entsprechen. Durch stete Auswahl in der gleichen Richtung häufen sich die anfangs noch unbedeutenden Abweichungen und steigern sich zu Art-Unterschieden." ("The theory of natural selection causes the production of new species, because from time to time the environment changes in such a way that new conditions for the organisms are created … and that, as a result, natural selection permits the survival and reproduction of those variants that best fit to these changed environmental conditions. Via the gradual accumulation of small changes in the same direction, different species arise"; Weismann 1886, p. 16).

It should be noted that Weismann (1886) did not cite an example for his novel, post-Darwinian concept of directional selection. Moreover, he failed to mention the stabilizing form of selection, so that Schmalhausen (1949) must be credited with the explicit elucidation and documentation of the two types of processes hidden behind the "Darwin–Wallace principle of natural selection" (Levit et al. 2005). Schmalhausen (1949) pointed out that, despite of the occurrence of the "Darwinian struggle for existence," no phenotypic changes may take place when the population is adapted to a constant environment. Then, natural selection acts as a stabilizing factor by eliminating all deviation from the norm, i.e., the average phenotype. As Paterson (2005) remarked, this process, which preserved the perfect "work of the Creator (i.e., Nature's broom)" must have been known to Charles Darwin via the books of Lyell and others, but he failed to describe stabilizing selection explicitly in his "species books" (Darwin 1859, 1868, 1871, 1872a).

In contrast to Weismann (1886), the Russian biologist provided direct proof for the directional (dynamic) role of natural selection when the environmental conditions gradually change. Schmalhausen (1949) cited three examples from the scientific literature. One of his classic case studies for directional selection in nature, the investigations of the entomologist Harrison (1920), are schematically depicted in Fig. 8, combined with a modified version of the original diagram of Schmalhausen (1949). In the time period between 1886 and 1909, Harrison (1920) investigated free-living populations of the autumnal moth (*Epirrita*

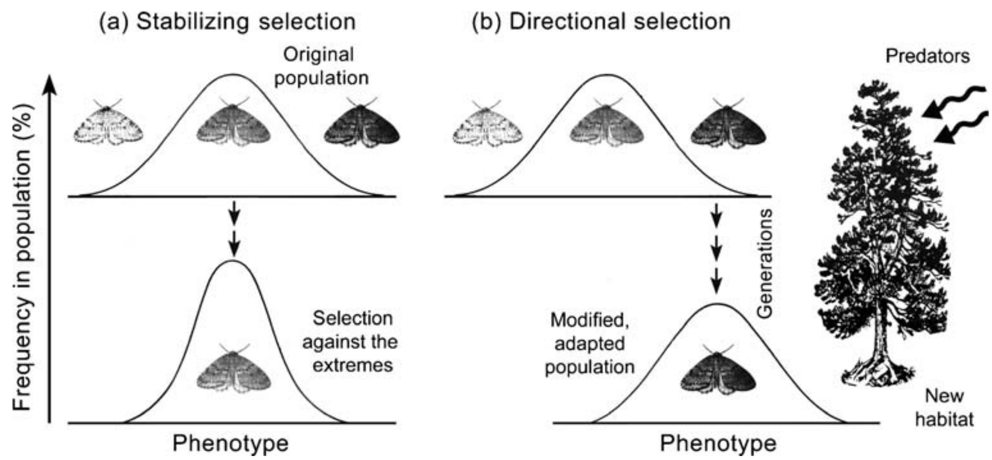

Fig. 8 Scheme illustrating the principles of stabilizing (**a**) and directional natural selection (**b**), as originally defined by Schmalhausen (1949), supplemented by a case study on autumnal moths (*Epirrita autumnata*) of Harrison (1920). The entomologist observed that, after the environment had changed in a coniferous wood, dark-pigmented moths had a good chance of survival, whereas nonadapted (lightly pigmented) conspecifics were frequently eaten by predators and hence eliminated. As a result, dark-pigmented (invisible) moths dominated the new population after approximately 23 years (generations) (adapted from Schmalhausen 1949)

syn. *Oporabia autumnata*). In the year 1800, a continuous colony of *E. autumnata* was broken into two distinct subpopulations where the environmental conditions later drastically changed. After 1885, one division had to live in a dark coniferous wood and the other in an open birch wood (with some alder), where conifers (pines) were disappearing. Harrison (1920) discovered that, on average, the pinewood insects had a darker pigmentation, whereas the birch moths were pale silvery. In the pine wood where the dark-pigmented (adapted) moths outnumbered the pale varieties by more than 25:1, Harrison (1920) observed that the number of isolated lepidopterous wings belonging to the species *E. autumnale* lying on the ground were mostly pale (i.e., not dark-pigmented). Since in the pine wood, owls, nightjars, and possibly bats heavily prey on moths, he concluded that natural selection, carried out by nocturnal birds in company with baths, occurred during dawn, causing the preferential elimination of the nonadapted (visible) individuals within the variable insect populations. Hence, the relatively rapid change in color towards dark-pigmented (invisible) individuals in the pine wood insect populations was largely caused by directional natural selection (differential predation by birds after the environment had changed; Fig. 8). In addition, Harrison (1920) addressed the "question of melanism," a topic that will be discussed in the next section.

In an essay published five decades ago, Haldane (1959) concluded that natural selection is generally centripetal, i.e., it favors individuals near the norm of the population, at the expense of those which deviate from it. The main effect of this process of rejection (i.e., stabilizing selection under constant environmental conditions) is to prevent species from changing. He also pointed out that natural selection with evolutionary consequences has only been observed under drastically modified environmental conditions, which impose a heavy selection pressure on the corresponding population. Haldane (1959) mentioned the moth *Biston betularia* when he outlined the principles of directional (dynamic) versus stabilizing (centripetal) selection, but did not cite the work of Weismann (1886) and Schmalhausen (1949) who where the spiritual fathers of this elaboration of the "Darwin–Wallace principle" described in 1858 (Kutschera 2003, 2008a; Levit et al. 2005).

Today, it is well established that directional natural selection is a key process that accounts for the adaptive evolution in many lineages of extant and extinct organisms (Niklas 1997; Endler 1986; Brodie et al. 1999; Paterson 2005; Carroll 2006; Klingsolver and Pfennig 2007; Birney 2007; Bell 2008; Kutschera 2003, 2009a, b; Gregory 2009; Majerus 2009). Nevertheless, more work is required to further elucidate the role of the environment with respect to the survival and reproduction of individual variants in free-living populations of prokaryotic and eukaryotic organisms (Rieseberg et al. 2002).

Theodosius Dobzhansky and the biological theory of evolution

The Russian/American naturalist–geneticist Theodosius Dobzhansky (1900–1975) contributed a *Foreword* to the English translation of Schmalhausen's book of 1949 (the original version was published 1947 in Russian). In this short essay, Dobzhansky wrote that "An upsurge of activity … has taken place in the last … years in the field of evolutionary biology, (which is) caused by convergence and unification of the contributions to evolutionary thought coming from various biologic disciplines. For evolution does not constitute the subject matter of any one biologic science. Genetics, systematics, comparative morphology and embryology, paleontology, and ecology have all been profoundly influence by and have made important contributions to evolutionary thought." With reference to the books of Dobzhansky (1937), Mayr (1942), Huxley (1942), Simpson (1944), and Rensch (1947), he wrote that "… we have arrived at a biologic synthesis. The book of I. I. Schmalhausen advances the synthetic treatment of evolution" (Dobzhansky, p. ix, in Schmalhausen 1949). Hence, the monograph of Schmalhausen (1949) should be added to the list of the six "architects" of the synthetic theory of biological evolution (Dobzhansky 1937; Mayr 1942; Huxley 1942; Simpson 1944; Rensch 1947; Stebbins 1950), which was summarized from a modern perspective by Reif et al. (2000), Gould (2002), Kutschera and Niklas (2004), Haffer (2007), and others. In this section, I summarize some largely unknown facts and conclusions published by Dobzhansky that document how Darwin's classical idea of "natural selection in the field" gradually evolved into our current view of this process.

During the 1940s, the Russian/American biologist was a research associate in the Department of Genetics at the *Carnegie Institution of Washington*, Cold Spring Harbor, New York. Dobzhansky used small flies of the genus *Drosophila* as material of his field and laboratory studies (Fig. 7c). The general purpose of his research was to investigate the hereditary variability present in natural populations and its role in the evolutionary process. During his tenure, Dobzhansky published several interesting articles in the *Annual Report* of this institution. In the Carnegie Year Book No. 45, he pointed out that "Darwin's theory of evolution by natural selection is accepted by most biologists despite the fact that it is based mainly on inference from indirect evidence and on analogies with artificial selection as practiced in domesticated animals and cultivated plants. Direct observation of and experimentation with natural selection are seldom possible. Evolutionary changes in nature are, as a rule, too slow to be perceptible within a human lifetime" (Dobzhansky 1946, p. 162). Three years later, Schmalhausen's monograph (1949), describing for the first time examples for directional selection, appeared in print (Fig. 8), and in 1955, H.B.D. Kettlewell published his first article on selection experiments concerning industrial melanism in lepidopterans. Recently, the geneticist and naturalist Michael E. N. Majerus (1954–2009) summarized the pertinent literature on industrial melanism in the peppered moth (*B. betularia*), one of the most significant and clearest examples of directional natural selection, and hence "Darwinian evolution," in action (Kettlewell 1955; Majerus 2009).

Sixty years ago, Dobzhansky pointed out that the majority of naturalists agree that adaptation to the environment is the principal driving force of organismic evolution. With reference to the pseudoscientific views of the Russian agronomist Trofim Lysenko (1898–1976), he wrote that "Living beings are not passively molded by physical agencies, as mechano-Lamarckists believed. Nor can a species change by exertion of its will, as supposed by psycho-Lamarckists and finalists. Moreover, organisms are not altered by a kind of sympathetic magic which makes them able to 'select' useful and to reject useless materials from changed environments, as imagined by Lysenko. It is the view of a majority of evolutionists that mutation and Mendelian recombination continually produce innumerable genetic materials, some of which are more and others less suitable for perpetuation in various environments. … To say that evolution is brought about because organisms are changed by environment is inexact. Organisms change in the process of becoming better able to survive and reproduce in the environments in which they live" (Dobzhansky 1949, p. 201–202). After these general remarks, the author summarized the process of biological evolution in the following words: "Evolution is a response of the organism to the challenge of the environment. And this challenge does not arise from physical conditions alone, but also from interactions with other organisms that share the same environment" (Dobzhansky 1949, p. 202). If we replace "the organism" by "populations of organisms" and "the challenge" by "challenges," Dobzhansky's characterization of evolution is still valid.

The origin of our modern species concept

In contrast to Alfred R. Wallace, Charles Darwin did not provide a precise species definition in his books on the "species question"(see Kutschera 2003). In his monograph *Genetics and the Origin of Species* (1937), Dobzhansky proposed a novel "reproductive isolation principle," which formed the core of Ernst Mayr's biological species concept published in 1942 (Haffer 2007). The more general question whether or not species represent reproductively independent lineages or "units of evolution" (see Rieseberg et al. 2006) was answered by Dobzhansky with respect to his fruit fly studies (Fig. 7c) as follows: "One can easily show that species of *Drosophila* are biologically real, not arbitrary, entities." If they live in the same natural habitat (i.e., in sympatry), the populations are reproductively isolated. …"This isolation usually persists in laboratory environments as well." With respect to the isolation mechanisms, Dobzhansky concluded that "because species have distinct food and microhabitat preferences, conspecific individuals meet more often than individuals of different species. More widespread …

than this ecological isolation is ethological (behavioural, sexual) isolation" (Dobzhansky 1972, p. 664).

Moreover, in this article, the author pointed out that it does not make sense to use one universal species definition applicable to both sexual and asexual organisms (i.e., animals and plants versus bacteria). Today, we know that Dobzhansky was right: microbiologists have not yet reached a consensus for defining their fundamental unit of biodiversity, the bacterial species or "ecotype" (Kutschera 2004).

In a recent article commemorating the comparative analysis of 12 fruit fly species, it was stated that *Drosophila* research revolutionized cell biology and developmental genetics (Birney 2007). If we take into account that Dobzhansky's fruit fly studies were the basis of most of his theoretical deductions, we must conclude that the entire field of evolutionary biology, with all of its subdisciplines, benefited considerably from classical work on the *Drosophila* species complex that goes back to the seminal investigation of this naturalist–geneticist. For recent discussions on the modes and mechanisms of speciation in nature, the reader is referred to Coyne and Orr (2004), Hendry (2009), and Willis (2009).

Bacteria and plate tectonics

In a key paper published 9 years ago, Carroll (2000) proposed that the synthetic theory of biological evolution as established in the 1950s is insufficient and should be supplemented by novel insights from geology, molecular, cell, and developmental biology unknown to the "architects" of the modern synthesis (T. Dobzhansky, E. Mayr, and others). A more complete version of this "expanded evolutionary synthesis" was published 5 years ago (Kutschera and Niklas 2004). The authors summarized ten "post-synthesis disciplines," from geology/paleobiology (i.e., causes of mass extinctions, rates of organismic evolution) to experimental evolution/computer simulations (i.e., cultivated bacteria, digital organisms). In a subsequent elaboration of this analysis, it was concluded that the term "Darwinism" should be abandoned and that evolutionary biology today must be viewed as a system of theories from the geological and life sciences (Kutschera 2008b; Scott and Branch 2009). With respect to Darwin's *Origin of Species*, two additional facts should be stressed that have largely been overlooked in previous accounts of this topic. First, in none of Darwin's books, bacteria are mentioned and, second, the British naturalist ignored the principle of the dynamic Earth.

In 1828, when Darwin was a student at Cambridge University, the contamination of the Thames River by industrial waste and sewage was acknowledged by a London commission and soon became a subject of public interest. In a drawing by William Heath (1795–1840), the "monster soup commonly called the Thames" was illustrated satirically (Fig. 9). Unfortunately, a cholera outbreak occurred in 1854 before the Clean Water Act of 1852 exerted any positive effect on the quality of water in London. The so-called contagion theory of epidemic disease, pointing to certain microbes (bacteria) as causative agents, was—like microbiology as a scientific discipline—still in its infancy when Darwin started his career as a biologist (see Kutschera and Niklas 2009). This may be the reason why Darwin (1859, 1872a), who used the light microscope during his "barnacle years" (Newman 1993), did not take microbes into account when he published his monograph on the evolution of life on Earth: bacteria, photoautotrophic cyanobacteria, in Darwin's time called "blue–green algae," are not mentioned in the *Origin of Species* and the two other "species monographs" (Darwin 1868, 1871).

Fig. 9 The discovery of microbes and other organisms in the polluted water of the Thames River. This cartoon was published several years before the "germ theory of disease" was postulated (adapted from a drawing of W. Heath, ca. 1828)

On February 20, 1835, the 26-year-old Darwin felt a heavy earthquake in Valdivia, Chile, now estimated to have been of magnitude 8.5 on the Richter scale. In his book *The Voyage of the Beagle*, which was praised in 1839 by Alexander von Humboldt (1769–1859) as an outstanding work (Barrett and Corcos 1972; Jackson 2009), the junior scientist remarked that "A bad earthquake at once destroys the oldest associations; the earth, the very emblem of solidity, has moved beneath our feet like a thin crust over a fluid—one second of time has created to the mind a strange idea of insecurity, which hours of reflection would not have produced" (Darwin 1839, p. 287). However, despite of this clever interpretation of the Earth as a mobile system consisting of a crust floating on a viscous solution, Darwin (1859, 1872a) implicitly assumed that the continents and oceans are immobile.

Eight decades ago, the German scientist Alfred Wegener (1880–1930) proposed that the present-day continents may be viewed as the fragmented pieces of former, much larger landmasses. He proposed that a hypothetical supercontinent, Pangaea, existed about 300 mya and thereafter broke up (Wegener 1929). This seminal idea of continental drift later evolved into the much more sophisticated theory of plate tectonics (i.e. large, solid rock construction; Werner 2000; Kutschera 2009a). This key concept from the geological sciences states that the Earth's outermost layer (the lithosphere) is fragmented into more than ten larger and smaller plates that are moving relative to one another as they ride atop the hotter, more mobile asthenosphere (Fig. 10). Although the exact physical forces responsible for plate movements at rates of up to 6 cm/year are not yet known in detail, there is consensus that these geological processes are caused by heat from radioactive decay within the Earth (heavy, unstable chemical elements such as uranium, thorium, and potassium). Over millions of years (my), the "internal heat-driven" dynamic Earth created mountains, deep oceans, earthquakes, and volcanic eruptions. These geological processes had large effects on the evolution of life on Earth via the creation and destruction of terrestrial and aquatic habitats (Kutschera 2009a).

Volcanic islands: Darwin's living laboratory

In September 1835, Charles Darwin visited the Galapagos Archipelago and was deeply impressed by the unique fauna and flora on these volcanic islands. As mentioned in the *Origin of Species*, Darwin's observations and collections during these 5 weeks contributed to the inception of his theory of descent with modification. Decades of ongoing research has shown that the Galapagos Archipelago consists of 13 main and more than 130 smaller volcanic islands and rocks located in the eastern Pacific Ocean 973 km off the west coast of South America (Ecuador). The islands are localized atop the Galapagos hotspot, an area where the crust of the Earth is being melted from below by a mantle plume, creating volcanoes (Fig. 10). The oldest islands have formed approx. 10 my ago (mya) (Werner 2000; Helsen et al. 2009), whereas the youngest islands (Isabela and Fernandina) are still being created: the most recent volcanic eruption occurred in April 2009 on Fernandina. Since the Galapagos Archipelago contains a high level of endemic plant and animal species (approximately 30%), which are descendants of imported organisms that reached the islands millions of years ago, "Darwin's living laboratory" is still explored today by evolutionary biologists. Three examples for the ongoing "Galapagos research program" are briefly discussed below.

More than 30 years of research has shown that "Darwin's finches," small birds that inhabit different islands, evolved from one founder population that arrived

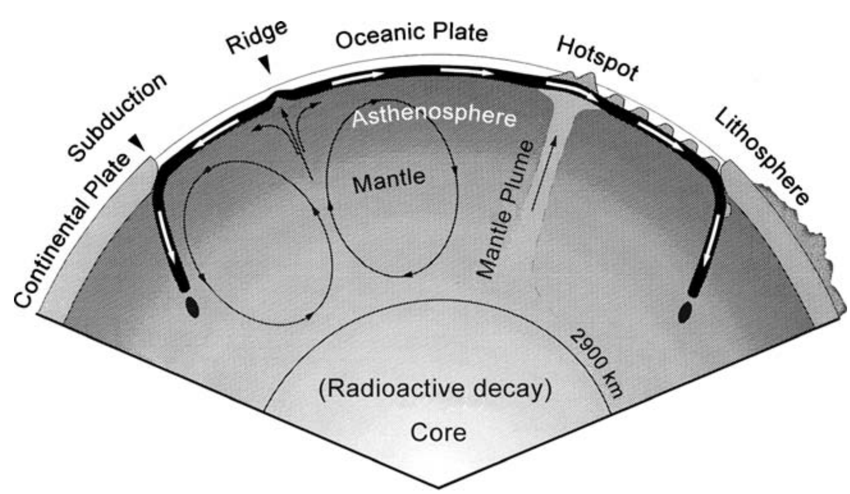

Fig. 10 Schematic view of a section of the Earth, depicting the processes of plate tectonics and the dynamics of the lithosphere (crust plus uppermost mantle, *arrows*). The Galapagos Archipelago is a marine "hotspot," created and maintained by volcanic activity. Radioactive decay of uranium, etc. provides the energy (heat) for the movements of the continental and oceanic plates (adapted from Werner 2000)

on the Archipelago about 2 to 3 mya (Grant and Grant 2002, 2008; Losos and Ricklefs 2009). Moreover, these investigators provided convincing evidence for directional natural selection in certain bird populations. Much less famous than these small birds are the Galapagos *Opuntia* cacti shown in Fig. 11a and the marine iguanas (Fig. 11b). A recent molecular phylogeny of all the six *Opuntia* species (as well as 14 varieties) described on the basis of morphological data revealed that these plants descended from one founder population (Helsen et al. 2009). However, no clear relationship was discovered between the morphological and genetic differences so that more work is required to further elucidate the "species question" in these giant endemic cacti.

The marine iguanas on the Galapagos island were described by Darwin in 1835 as follows: "The black lava rocks on the beach are frequented by large (2–3 ft), most disgusting, clumsy Lizards. They are as black as the porous rocks over which they crawl and seek their prey from the sea" (Darwin 1839, p. 380). Since this brief description, numerous studies on the ecology, behavior, and evolution of the Galapagos marine iguanas (*Amblyrhynchus cristatus*), the only extant marine lizard on Earth, have been published (Wikelski 2005). One study that is related to the concept of directional natural selection is of special significance. As Darwin and other pioneers of Galapagos research have noted, the marine iguanas are tame animals that display virtually no flight response when approached by humans or other mammals. Since these animals lived over millions of years without natural predators, the algae-feeding reptiles have adapted to such a unique, "paradise-like" island habitat. Rödl et al. (2007) have shown that these predator-naive lizards, which are now confronted with imported cats and dogs that attack and sometimes kill them, are characterized by a deficient predator recognition system. Although it was shown that a corticosterone stress response to experimental chasing, which is absent in naive reptiles, is rapidly restored with experience, it remains much too low to permit successful escape from introduced predators. Hence, due to this "poorly designed," insufficient predator-induced stress response, introduced cats and dogs have drastically reduced the populations of marine iguanas on some islands—on San Cristobal these unique lizards (Fig. 11b) are virtually extinct (Rödl et al. 2007). With respect to the "Weismann–Schmalhausen principle of directional selection," we have to conclude that, in the absence of predators, animals that did not engage in such a costly flight behavior may have had a higher "Darwinian fitness" and, hence, after thousands of subsequent generations, dominated the island populations. Under the current strong selection pressure caused by imported carnivores, only those few individuals may survive that possess an above-average corticosterone-mediated stress response and, hence, are capable to escape, survive, and reproduce.

Conclusions

The eminent astronomer and philosopher John Herschel (1792–1871) once labeled the question as to the origin, diversification, and adaptation of species on Earth as the "mystery of mysteries," a phrase that Darwin (1859, 1872a) quoted in his most influential book. Although Charles Darwin was not the first to deduce the concept of descent with modification (evolution) by means of natural selection, he clearly was the doyen of a research agenda that decades later led to the emergence of the scientific discipline of evolutionary biology (a term coined by Huxley in 1942). In his *Foreword* to Ivan Schmalhausen's seminal book, wherein the concepts of stabilizing versus directional natural selection are introduced, Theodosius Dobzhansky pointed out that many disciplines, from genetics to ecology, have contributed to the field of evolutionary biology. Moreover, he complained that "Among the major subdivisions of modern biology only physiology and biochemistry still remain largely unaffected by evolutionary ideas, doubtless to mutual detriment" (Dobzhansky, p. ix, in Schmalhausen 1949). Fortunately,

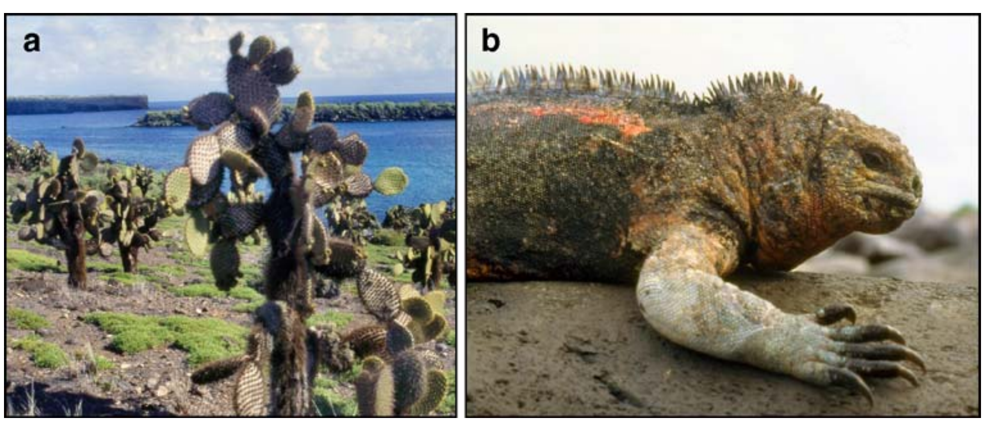

Fig. 11 The unique flora and fauna on the Galapagos island Espanola. Giant *Opuntia* sp. (**a**) and an adult individual of a marine iguana (*A. cristatus*; **b**). These large lizards are vegetarians (algae feeders) that live and forage in the sea (original photographs)

this is no longer the case. The modern evolutionary sciences today, which are comprised of a system of theories that explain a variety of aspects concerning the phylogenetic development of populations of organisms in all five kingdoms of life (Fig. 12), have integrated such diverse fields as cell, developmental, and molecular biology as well as physiology/biochemistry (Love 2009; Kutschera and Niklas 2004, 2005, 2008; Niklas and Kutschera 2009). Moreover, the Earth sciences (i.e., geology), inclusive of paleontology, are today a key area in evolutionary research (Conway Morris 2009). The succession of geochronologically dated fossils known today clearly document that life has slowly evolved from a few simple, unicellular bacterial ancestors to the many different types of organisms that inhabit our planet today. It should be noted that the age of the (dynamic) Earth was an enigma when Darwin (1859, 1868, 1871, 1872a) published his classical system of "species theories." Moreover, no Precambrian fossils were known at that time, bacteria were ignored by most of the nineteenth century "transmutationists," and the principle of symbiogenesis (endosymbiosis) was not yet discovered. Hence, our modern view of the evolution of life differs considerably from Darwin's "young, static, bacteria-free Earth concept" that was essentially based on observations on animals and higher plants as well as a few of their fossilized remains.

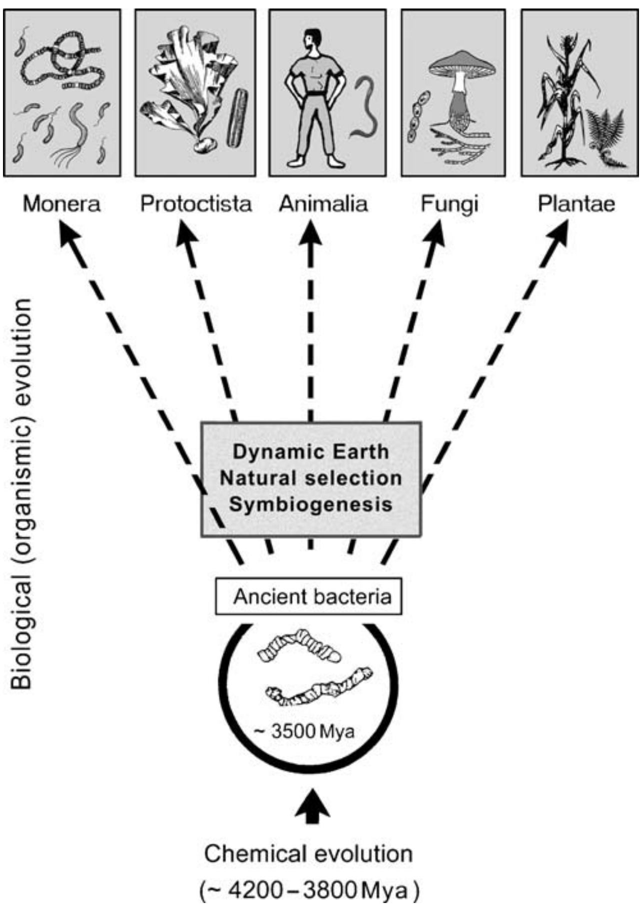

Fig. 12 Summary of the processes that led to the first prokaryotic cells on Earth (chemical evolution) and subsequently caused the extant biodiversity with respect to the five kingdoms of life (biological evolution). The first kingdom (Monera, syn. Bacteria) comprises prokaryotic microorganisms that did not evolve via endosymbiosis, whereas all members of kingdoms 2 to 5 (Protoctista, Animalia, Fungi, and Plantae) are composed of eukaryotic cells that are the product of primary endosymbiosis (symbiogenesis). Hence, symbiogenesis, (directional) natural selection, and the dynamic Earth were the key processes responsible for the development of life on this ever-changing planet (Synade model of macroevolution; Kutschera 2009a)

Decades of "post-Darwinian" geological and biological research revealed that the Earth is about 4,560 my old, the first cells (ancient bacteria) evolved about 3,500 mya, symbiogenesis (i.e., primary endosymbiosis, leading to the first eukaryotic cells) occurred about 2,000 to 1,500 mya, directional natural selection has always been a key factor of organismic evolution, and the dynamic Earth (plate tectonics) was responsible for the repeated creation and destruction of habitats on our ever-changing planet (volcanism, tsunamis, etc., processes that lead to mass extinctions; Niklas 1997; Dalrymple 2004; Tice and Lowe 2004; Schopf 2006; Kutschera and Niklas 2004, 2005, 2008; Crane 2009; Kutschera 2009a). In addition, we know that prokaryotes are the true "winners" of the approximately 3,500 my long evolutionary "struggle for life" on Earth: Microbes (bacteria, archaea, and cyanobacteria, i.e., the kingdom Monera, inclusive of viruses) represent more than 50% of the protoplasmic biomass on Earth, followed by the Protoctista (marine phytoplankton, algae, amoebae, slime molds, etc.; approximately 30%), so that "Darwin's animal and plant world" comprises less than 20% (possibly only 10%) of the living substance on this dynamic "green planet of the bacteria" (Armbrust 2009; Mascarelli 2009). Moreover, recent studies have shown that minerals of the lithosphere coevolved with cellular life that reaches up to 2.8 km beneath the surface of the Earth where radioactive decay of Uranium, a source of heat that drives plate tectonics (Fig. 10), provides the energy for populations of unique underground bacteria (Hazen et al. 2008; Mascarelli 2009). Hence, the terrestrial biosphere is much larger and more complex than Charles Darwin, August Weismann, Theodosius Dobzhansky, Ernst Mayr, and most of the other evolutionary biologists of the twentieth century have imagined and our model depicted in Fig. 12 represents only a crude approximation to the "reality of life" on our dynamic Earth.

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