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The modern theory of biological evolution: an expanded synthesis

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Abstract In 1858, two naturalists, Charles Darwin and Alfred Russel Wallace, independently proposed natural selection as the basic mechanism responsible for the origin of new phenotypic variants and, ultimately, new species. A large body of evidence for this hypothesis was published in Darwin's *Origin of Species* one year later, the appearance of which provoked other leading scientists like August Weismann to adopt and amplify Darwin's perspective. Weismann's neo-Darwinian theory of evolution was further elaborated, most notably in a series of books by Theodosius Dobzhansky, Ernst Mayr, Julian Huxley and others. In this article we first summarize the history of life on Earth and provide recent evidence demonstrating that Darwin's dilemma (the apparent missing Precambrian record of life) has been resolved. Next, the historical development and structure of the "modern synthesis" is described within the context of the following topics: paleobiology and rates of evolution, mass extinctions and species selection, macroevolution and punctuated equilibrium, sexual reproduction and recombination, sexual selection and altruism, endosymbiosis and eukaryotic cell evolution, evolutionary developmental biology, phenotypic plasticity, epigenetic inheritance and molecular evolution, experimental bacterial evolution, and computer simulations (in silico evolution of digital organisms). In addition, we discuss the expansion of the modern synthesis, embracing all branches of scientific disciplines. It is concluded that the basic tenets

of the synthetic theory have survived, but in modified form. These sub-theories require continued elaboration, particularly in light of molecular biology, to answer open-ended questions concerning the mechanisms of evolution in all five kingdoms of life.

Introduction

Physicists and chemists investigate the properties and interactions of objects, such as electrons, photons, and atoms, which are physically uniform and invariant in their characteristic traits and behavior. Accordingly, a single experiment adducing the properties of a single entity (e.g., electron or proton) can be used to extrapolate the properties of all comparable entities in the universe. In biology, the "science of the living world," both past and present (Mayr 1997), the situation is very different. The organisms biologists study, which are typically randomly drawn from populations, manifest astonishing variation as a consequence of genetic recombination and random genomic changes. Thus, with the exception of identical twins or cloned individuals, no two members of the same species look exactly alike (even identical twins may differ physically as a result of their individual histories). Because this general rule of "biological variability" applies not only to plants and animals, but also to microorganisms that lack the capacity for sexual reproduction, the concept of "types" is radically different in the context of biology versus that of the physical sciences.

However, there are limits to biological variation and these literally shape evolutionary history. No population is ever capable of generating all possible theoretical genomic variants, in part because sexual genetic recombination is random and because the existence of any particular population is finite. Therefore, biological variation, which provides the "raw material" for evolutionary change, is confined by random events. Nevertheless, non-random processes also shape evolution. The "struggle for existence" among the offspring of each generation eliminates genomic variants that are less adapted to their

Dedicated to Prof. Dr. Dr. hc mult. Ernst Mayr on the occasion of his 100th birthday

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Table 1 List of the principal propositions of Darwin's theory, extracted from the *Origin of Species* (Darwin 1859, 1872)

1. Supernatural acts of the Creator are incompatible with empirical facts of nature
2. All life evolved from one or few simple kinds of organisms
3. Species evolve from pre-existing varieties by means of natural selection
4. The birth of a species is gradual and of long duration
5. Higher taxa (genera, families etc.) evolve by the same mechanisms as those responsible for the origin of species
6. The greater the similarities among taxa, the more closely they are related evolutionarily and the shorter their divergence time from a last common ancestor
7. Extinction is primarily the result of interspecific competition
8. The geological record is incomplete: the absence of transitional forms between species and higher taxa is due to gaps in our current knowledge

environment. Those that survive pass their genetic information on to the next generation. In this way, evolution is the summation of random events (e.g., mutation and sexual recombination) and natural selection, which is largely non-random.

This fundamental process – the “principle of natural selection” (Bell 1997) – was conceived independently by two nineteenth-century British naturalists, Charles Darwin and Alfred Russel Wallace, and has been substantially elaborated upon in the early part of the twentieth century with the rediscovery of Mendelian genetics and subsequent advances in population genetics. Importantly, this “modern synthesis” continues to the present day, as insights are gained from diverse fields of study, particularly molecular biology, which is rapidly detailing the precise mechanisms whereby genomes (and the phenotypes they engender) are altered.

The aim of this article is to review the historical development and the progress made in evolutionary theory from the time of Darwin and Wallace to the present day. Clearly, no such summary can ever be complete, because the literature dealing with evolutionary biology is vast and complex. Here, we only sketch the broad outlines of the basic history of evolutionary theory and enquiry. To do this, we first describe the development of the idea of evolution and its subsequent establishment as a documented fact. We then outline the development and expansion of the modern synthetic theory from 1950 to the present. Although many major questions in evolutionary biology remain unanswered, no credible scientist denies evolution as “a fact.” Yet, many scientists continue to explore and debate precisely how the mechanisms of evolution work.

Charles Darwin and Alfred Russel Wallace

In August 1858, two of the most influential publications in the history of biology were published. These concurrent papers by Darwin and Wallace contained a “very ingenious theory to account for the appearance and perpetuation of varieties and of specific forms on our planet” (foreword by C. Lyell and J. Hooker). Therein, Darwin and Wallace (1858) presented for the first time the hypothesis of descent with modification by means of natural selection. This hypothesis makes five fundamental assertions: (1) all organisms produce more offspring than

their environments can support; (2) intraspecific variability of most characters exists in abundance; (3) competition for limited resources leads to a struggle for life (Darwin) or existence (Wallace); (4) descent with heritable modification occurs; and (5), as a result, new species evolve into being.

Unlike Wallace, Darwin supported his arguments with a large body of facts, drawn mostly from breeding experiments and the fossil record (Table 1). He also provided detailed direct observations of organisms existing in their natural habitats (Darwin 1859, 1872). Thirty years later, natural selection's co-discoverer published a series of lectures under the title *Darwinism* (Wallace 1889), which treated the same subjects as Darwin but in light of facts and data that were unknown to Darwin (who died in 1882). A detailed comparative analysis of the Darwin/Wallace publications reveals that Wallace's contributions were more significant than is usually acknowledged, so much so that the phrase “the Darwin/Wallace mechanism of natural selection” has been proposed to acknowledge the importance of the “second Darwin” (Dawkins 2002; Kutschera 2003a). Although Darwin is usually credited as the “principal author” of evolutionary theory, Ernst Mayr (1988, 1991) points out that it is not correct to refer to “Darwin's theory of descent with modification” (the word “evolution” does not appear in the original 1858 papers of Darwin and Wallace; only in later editions of *The Origin of Species* and in Wallace's *Darwinism*).

If we equate the word Darwinism with the content of the book *On the Origin of Species*, we can distinguish between five separate concepts:

1. Evolution as such
2. Theory of common descent
3. Gradualism
4. Multiplication of species
5. Natural selection (Mayr 1988, 1991).

The first two propositions are discussed in the next section. Thereafter, the development of Darwin's original theory is described (see Fig. 1).

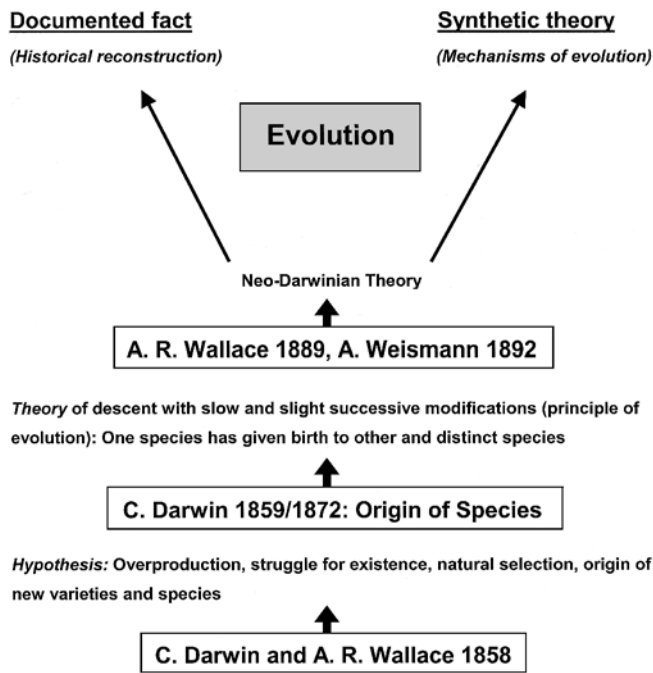


Fig. 1 Scheme illustrating the historical development of the concept of evolution: from the hypothesis of Darwin and Wallace (1858), through Darwin (1859, 1872), Wallace (1889) and Weismann (1892) to the synthetic theory (Dobzhansky 1937; Mayr 1942; Huxley 1942; Simpson 1944; Rensch 1947; Stebbins 1950; and others)

Evolution as a documented fact

The concept that all organisms on Earth have evolved from a common ancestral life form by means of genomic and morphological transformations (evolution as such) was not “invented” by Darwin or Wallace. Mayr (1982) and others have shown that the idea of organismic evolution can be traced back to several Greek philosophers (see also Bowler 1984; Ruse 1996; Junker and Hofffeld 2001; Kutschera 2001; Storch et al. 2001). Likewise, the hypothesis of continuous transformations was proposed by numerous eighteenth- and nineteenth-century authors who are credited by Darwin in the first chapter of his book. However, Darwin (1859) was the first to summarize a coherent body of observations that solidified the concept of organismic evolution into a true scientific theory (i.e., a system of hypotheses, as defined by Mahner and Bunge 1997) (Table 1).

When Darwin (1859, 1872) proposed his theory of descent with slight and successive modifications (gradualistic evolution), the available fossil record was still very fragmentary. Indeed, the early fossil record (periods prior to the Cambrian) was entirely unknown or unexplored. Nevertheless, Darwin (1859, 1872) concluded that if his theory of evolution was valid, aquatic creatures must have existed before the evolutionary appearance of the first hard-shelled organisms (such as trilobites) in the Cambrian period about 550–500 million years ago (mya). Darwin’s dilemma, i.e., the apparent missing Precambrian

fossil record, was used as a major argument against his proposal 1 (evolution as a fact).

This dilemma no longer exists. Scientists have explored the Precambrian in detail (see Schopf 1999; Knoll 2003 for summaries). We now know that life is far more ancient than believed in Darwin’s time. We also know that these ancient forms of life were the ancestors to all subsequent organisms on this planet. Some of the evidence for these new insights is as follows. Geochronologists using techniques such as the uranium–lead (U–Pb)-method for estimating the age of rocks now date the origin of the Solar System at about $4,566 \pm 2$ mya (Halliday 2001). This extensive age is divided into two major “eons,” the Precambrian (4,600–550 mya) and the Phanerozoic (550 mya to the present). The older and much longer of the two (the Precambrian) is composed of two “eras,” the Archaean (from 4,600 to 2,500 mya) and the Proterozoic, which extends from 2,500 mya to the end of the Precambrian. The shorter and younger Phanerozoic encompasses the most recent history of the Earth, which is roughly 15% of Earth’s total history (approximately 550 Ma). In turn, the Phanerozoic is divided into three eras: the Paleozoic, Mesozoic, and Cenozoic (Niklas 1997; Cowen 2000; Kutschera 2001). A general scheme of the geological time scale with representative fossil organisms is shown in Fig. 2.

Based on detailed chemical studies of the oldest of these geological periods, geologists and paleontologists have established that life first emerged on Earth about 3,800 mya (after Earth ceased to be bombarded by extraterrestrial debris; see Halliday 2001). The oldest stromatolites (layered rocks produced by communities of microorganisms) containing fossilized microbes are known from 3,450-Ma-old strata (Western Australia Pilbara sequence), whereas the oldest microscopic thread-like microfossils, which are morphologically similar to extant cyanobacteria, are found in the bedded chert unit of the Archean Apex Basalt of Australia (age $3,465 \pm 5$ Ma). Data drawn from independent lines of evidence demonstrate that these prokaryotic microfossils are not artifacts; they represent remnants of Earth’s earliest microorganisms (Schopf 1993, 1999; Knoll 2003).

Evidence for the extreme antiquity of life also comes from isotopic studies (Shen et al. 2001). Molecular fossils derived from cellular and membrane lipids (so called “biomarkers”) confirm that cyanobacteria-like organisms inhabited the archaic oceans more than 2,700 mya. These photoautotrophic microbes released oxygen that started to accumulate in the atmosphere at ca. 2,200 mya and subsequently transformed the Earth’s atmosphere (Knoll 1999). Paleontological and biochemical evidence also indicates that the first eukaryotic cells (defined by a membrane-enclosed nucleus) occurred between 2,000 and 1,500 mya (Fig. 2), although key attributes of eukaryotic physiology probably evolved earlier (Knoll 1999, 2003; Martin and Russell 2003). The occurrence of sexually reproducing multicellular eukaryotic Protocista (red algae) has been documented in remarkable detail (Butterfield 2000). Although there are

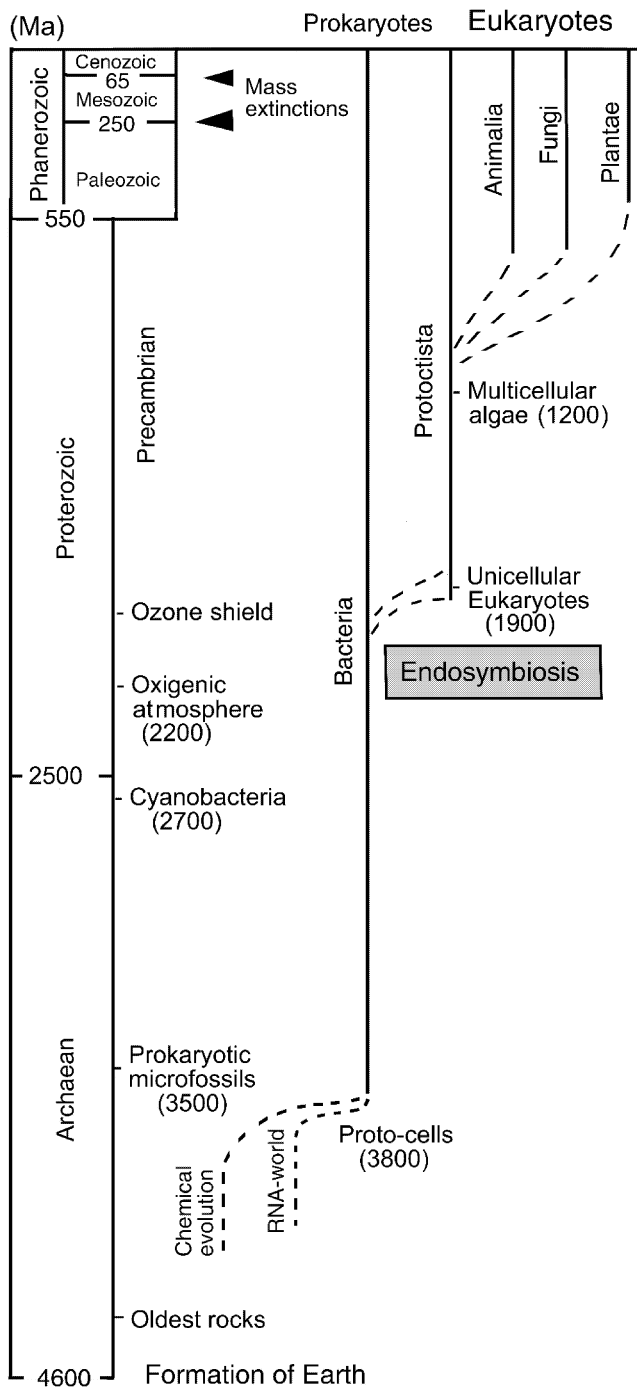


Fig. 2 Geological time scale with key events in the history of life, from the formation of the Earth to the present. All five kingdoms of organisms are included (Bacteria, Protocista, Animalia, Fungi, Plantae). Ma millions of years

some more ancient eukaryotic fossils, *Bangiomorpha* dated at $1,198 \pm 24$ Ma is currently the oldest known multicellular eukaryote (Fig. 3). In the *Bangiomorpha* assemblage, other fossil multicellular eukaryotes were observed, whereas benthic microbial mats (prokaryotes) appear to be absent. These observations indicate that the rise of multicellular algae at ca. 1,200 Ma coexisted with

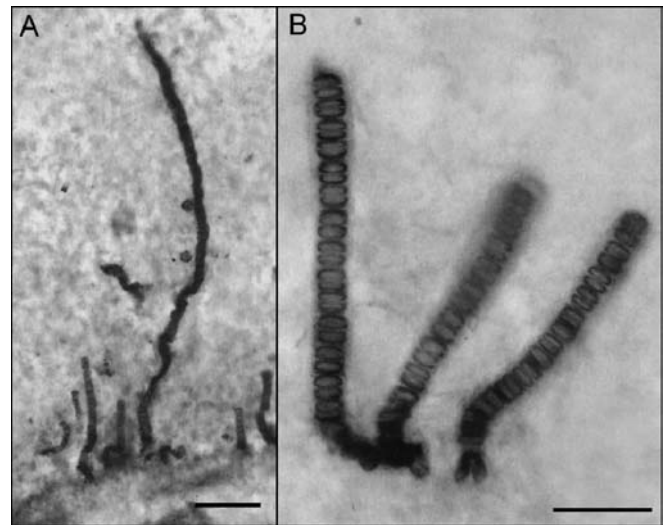


Fig. 3A, B Precambrian eukaryotic fossils (red algae) from the ca. 1,200-my Huntington Formation (Canada). Populations of vertically oriented *Bangiomorpha pubescens* that colonize a firm substrate (A) and three individual filamentous multicellular algae with a bilobed basal hold fast (B). Bars: 100 μm (A), 50 μm (B) (adapted from Butterfield 2000)

and may have caused environmental shifts through the Meso-Neoproterozoic transition (Butterfield 2001).

Historically, Haeckel (1874) was the first evolutionist to propose that the earliest metazoa were microscopic organisms similar in morphology to the embryos (or larvae) of adult animals (gastraea theory). In Precambrian rocks dated at 570 Ma (Doushantuo Formation, China), multicellular organisms are preserved just before the Ediacaran radiation of macroscopic “Vendobionta” (Bengston 1998). Fossil animal embryos preserving different stages of cleavage and multicellular structures with diameters measuring less than 250 μm were discovered in Precambrian strata. In addition, sponges and thalli of multicellular algae have also been found. These discoveries in Precambrian rocks document the existence of not only bacteria, cyanobacteria, and eukaryotic algae, but also the (putative) precursors of the soft (Ediacara) and hard-shelled macroscopic animals of the late Proterozoic and early Phanerozoic (Cambrian).

This brief summary shows that Darwin’s dilemma (the apparent missing Precambrian record of life) has been resolved, although the traces of cellular structures in Precambrian rocks are sparse and more fossils are required to further elucidate the “cradle of life” on our planet (Schopf 1999; Conway Morris 2000; Carroll 2001; Knoll 2003).

In addition to his concerns about the incompleteness of the fossil record, Darwin (1859, 1872) clearly worried about the apparent absence of intermediate forms (connecting links) in the fossil record of life, which challenged his gradualistic view of speciation and evolution. Indeed, with the exception of the famous Urvogel *Archaeopteryx*, which displays a mixture of reptile- and bird-like characteristics (Futuyma 1998; Mayr 2001; Storch et al. 2001), virtually no intermediate forms were known during

Table 2 Representative examples of intermediate forms linking major groups of vertebrates. The specimens were discovered, described or analyzed during the last 20 years and represent connecting links in the fossil record of vertebrates

Evolutionary transition (genus)	Age (Ma)	Description	Reference
1. Fish/amphibian (<i>Panderichthys</i>)	370	Intermediate form fish/amphibian in the series <i>Eusthenopteron</i> (fish ~380 Ma) – <i>Panderichthys</i> – <i>Acanthostega</i> (amphibian ~363 Ma)	Ahlberg et al. (1996)
2. Amphibian/land vertebrate (<i>Pederpes</i>)	350	Intermediate grade between primary aquatic Upper Devonian amphibians and early tetrapods	Clack (2002)
3. Reptile/mammal (<i>Thrinaxodon</i>)	230	Mammal-like reptiles that show a blend of mammalian and reptilian characteristics	Rubidge and Sidor (2001)
4. Terrestrial reptile/ichthyosaur (<i>Utatsusaurus</i>)	240	Extinct marine reptile that shows features that are transitional between ancestral terrestrial amniotes and aquatic ichthyosaurs	Motani et al. (1998)
5. Anapsid reptile/turtle (<i>Nanoparia</i>)	260	Pareiasaur with turtle-like rigid body; all osteoderms are united, forming a rigid covering over the entire dorsum	Lee (1996)
6. Dinosaur/bird (<i>Microraptor</i>)	126	Bird-like four-winged dromaeosaurid that could glide, representing an intermediate stage between the flightless theropods and volant primitive birds such as <i>Archaeopteryx</i>	Xu et al. (2003)
7. Lizard/snake (<i>Pachyrhachis</i>)	95	Primitive snake with limbs, transitional taxon linking snakes to an extinct group of lizard-like reptiles	Tchernov et al. (2000)
8. Land mammal/seacow (<i>Pezosiren</i>)	50	Intermediate form of a primitive seacow with both terrestrial and aquatic adaptations	Domning (2001)
9. Hoofed land mammals/whales (<i>Ambulocetus</i> , <i>Rodhocetus</i>)	48–47	Connecting links between amphibious and terrestrial even-toed ungulates and aquatic whales	Thewissen and Williams (2002)
10. Ancestor of chimpanzees/modern humans (<i>Sahelanthropus</i>)	7–5	The most basal ape-like African hominid. Mosaic of primitive (chimpanzee-like) and derived hominid features	Wood (2002)

Darwin's lifetime. This dilemma has also been resolved by more recent discoveries of intermediate forms in the evolutionary history of many animal and plant lineages (Kemp 1999; Zhou and Zheng 2003; Zimmer 1998). Some examples that cover the past 370 Ma of vertebrate evolution are summarized in Table 2.

Darwin's second postulate (the common ancestor, represented by "a few forms or one") has been verified by a large body of molecular data that has altered our perspectives in many important ways, e.g., the "RNA-world" hypothesis (Joyce 2002). The principle of common descent is documented in the well-supported universal phylogenetic tree of life (Schopf 1999; Pace 2001). The "universal ancestor" of all Earth's organisms appears to have been a diverse community of prokaryotic protocells (Woese 2002) that subsequently evolved into true prokaryotic organisms attended by the emergence of the genetic code and subcellular constituents (Seligmann and Amzallag 2002; Woese 2002; Martin and Russell 2003). When these diverse lines of evidence are taken together (see Fig. 2), there is no question that all life on Earth arose ca. 3,800 mya from a common ancestor, as originally proposed by Darwin (concepts 1 and 2). That Darwin struggled with the genetic mechanism of evolution because he was unaware of Mendel's work is well known. But his failure to know of such a mechanism cannot detract from his many important insights and seminal contributions to the subsequent development of evolutionary thought.

Neo-Darwinism

The five theories that Mayr (1988, 1991) extracted from Darwin's *Origin of Species* concentrate on two separate aspects of organismic (biological) evolution: the evolutionary process as such, and the mechanisms that brought about (and still cause) evolutionary change. Whereas biologists no longer debate the existence of evolution as a fact of life (literally), the mechanisms that account for the transformation and diversification of species are still very much under investigation. Pertinent studies are usually carried out on populations of living organisms (neontology) in contrast to historical reconstructions of evolution based on the fossil record (paleontology) (Mayr 2002). Theories of evolution (i.e., systems of hypotheses that are based on data) continue to be formulated to account in precise detail for the mechanisms of evolutionary change (Mahner and Bunge 1997).

According to Mayr (1982, 1988) and other historians of biology (Reif et al. 2000; Junker and Engels 1999; Junker and Hoßfeld 2001; Junker 2004), the development of the modern theory of evolution can be divided into three stages (Fig. 1).

1. Darwinism

Historically, this stage is represented by the 1859 publication of Darwin's book *On the Origin of Species*. Specifically, it refers to the Darwin/Wallace principle of natural selection as the major driving force in evolution. Since Darwin (1859, 1872) accepted Lamarck's principle of the inheritance of acquired characteristics as a source of biological variability, it is equally fair to call this

the “Lamarck/Darwin/Wallace” period of evolutionary thought.

2. Neo-Darwinism

This stage in the development of evolutionary theory can be traced to the German zoologist/cytologist A. Weismann (1892) who provided experimental evidence against “soft (Lamarckian)” inheritance and who postulated that sexual reproduction (recombination) creates in every generation a new, variable population of individuals. Natural selection then acts on this variation and determines the course of evolutionary change. Hence, neo-Darwinism (i.e., the expanded theory of Darwin) – a term that was coined by Romanes (1895) – enriched Darwin’s original concept by drawing attention to how biological variation is generated and by excluding Lamarckian inheritance as a viable mechanism for evolution. Wallace (1889), who popularized the term “Darwinism”, fully incorporated the novel conclusions of Weismann and was therefore one of the first proponents of neo-Darwinism.

3. Synthetic theory

This novel system of hypotheses for evolutionary processes originated between 1937 and 1950 (Mayr 1982). In contrast to Weismann’s (1892) and Wallace’s (1889) neo-Darwinian concept, the synthetic theory incorporated facts from such fields as genetics, systematics, and paleontology. Hence, the term “neo-Darwinian theory” should not be confused with the “synthetic theory” (or the phrase “neo-Darwinian synthesis”; see Mayr 1991; Reif et al. 2000; Junker 2004).

Although the modern synthesis rested largely on data collected from eukaryotes, modern evolutionists have turned their attention to prokaryotes in an effort to deduce how life began and how sex evolved. When Darwin (1859, 1872), Wallace (1889), and Weismann (1892) proposed their concepts of the mechanisms of evolutionary change, microbiology was in its infancy. Naturalists (Darwin, Wallace) and cytologists (Weismann) studied macroscopic animals and plants. Like humans, these organic beings are diploid, sexually reproducing eukaryotic multicellular organisms in which each cell contains two sets of chromosomes (one set from each parent) other than their haploid gametes (females: eggs, males: sperm cells) that result from meiosis. After fertilization of the egg, the zygote develops into a new diploid ($2n$) individual (the next generation). As Fig. 2 shows, most of these complex multicellular organisms evolved late in the history of life during the Cambrian period (ca. 550–500 mya). Organisms such as these are currently the most visually apparent life forms on our planet, although prokaryotes (bacteria, cyanobacteria) – microbes that have persisted since the Archaean (ca. 3,500 mya) – are still the most abundant (in terms of their collective biomass) and

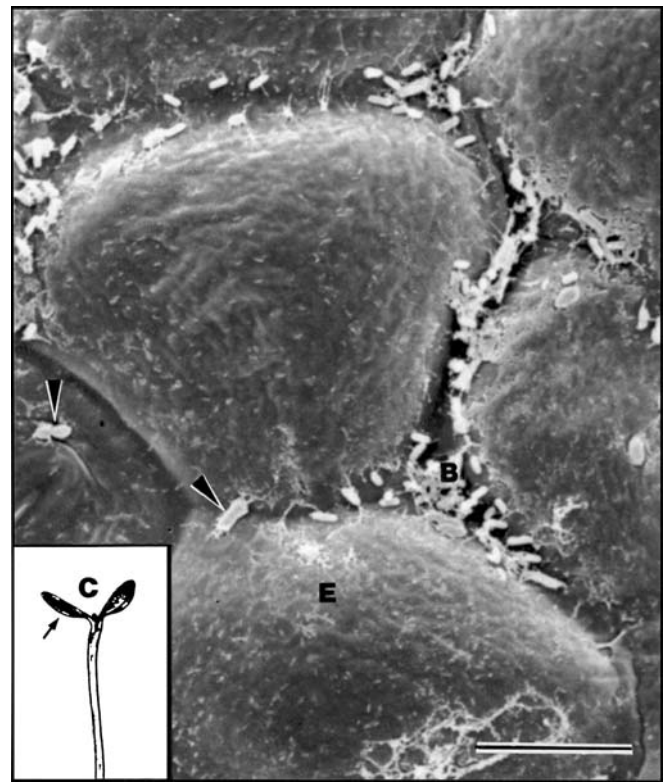


Fig. 4 Epiphytic bacteria associated with the cuticle of the epidermal cells of a sunflower cotyledon (*inset*, *arrow* points to the region depicted). The scanning electron micrograph illustrates that bacteria are ubiquitous microorganisms that inhabit every ecological micro-niche where organic substrates are available. The *arrow-heads* point to bacteria in the process of binary fission. Original micrograph prepared as described by Kutschera (2002). *B* bacteria, *C* cotyledon, *E* epidermal cell. Bar: 10 μ m

ecologically diverse forms of unicellular life (Whitman et al. 1998).

However, the synthetic theory of biological evolution was almost exclusively deduced on observations and quantitative data obtained with eukaryotic, bisexual macroorganisms. This is one of several reasons why we propose that an expansion is necessary in order to incorporate the morphologically primitive (largely uniform) microorganisms (Fig. 4). These microbes reproduce asexually by binary fission, although recombination (horizontal DNA transfer) also occurs.

In the next paragraph the evolutionary synthesis (a historical process) is described. The reader should bear in mind that the data (and hypotheses) that formed the pillars of this period of theoretical development were exclusively obtained using animals and plants as experimental/observational systems.

Post-neo-Darwinian concepts

As pointed out by Mayr (1982, 1988), the most original (and the last to be universally accepted) among Darwin’s five proposals was the theory of natural selection. It took

nearly 80 years until the majority of biologists adopted natural selection as the major shaping force in organismic evolution as opposed to one of four alternative and very popular concepts:

1. Creationism
2. Lamarckism
3. Orthogenesis
4. Transmutationism.

Throughout his book, Darwin (1859, 1872) mentioned that the “theory of creation” is erroneous and incompatible with his observations and data. In the last chapter of his work, entitled “Recapitulation and Conclusions,” Darwin explicitly points out that species are not produced and exterminated by “miraculous acts of creation” (Darwin 1872, p. 504). Yet, creationism is still popular in the guise of “intelligent design,” which persists in the notion that organisms are “designed” by supernatural acts (Kutschera 2003b; Pennock 2003). Such arguments are based on a mixture of selected scientific data and superstition that are refuted by rational thought and data (Futuyma 1995; Kutschera 2001).

Since Darwin (1859, 1872; but not Wallace 1889) believed in an inheritance of acquired characters, it is understandable that the concept of “soft inheritance” (Lamarckism) was popular until ca. 1940. The work of Weismann (1892), who had unequivocally refuted a direct effect of the environment on the parent–offspring germ-line in animals, was not universally accepted, i.e., the neo-Darwinian theory of evolution was in part eclipsed by the old concept proposed by Lamarck.

The third idea, which can be described as “orthogenesis” (there were several competing models), was a misguided analogy between phylogeny and ontogeny. Its proponents believed in an endogenous tendency in evolution toward ever greater perfection and complexity. Evolution was thought of as a programmed event that would ultimately lead to a predetermined end result. Just as in ontogeny, where the zygote develops into an embryo and thereafter into an adult organism, the orthogenesisists postulate a genetic mechanism that ultimately leads to “perfect” evolutionary products. Since a “universal” trend toward ever-increasing complexity is not documented (Carroll 2001; bacteria still exist today, see Figs. 2 and 4) and since no “perfect” organism has ever been found, deterministic concepts such as orthogenesis were no longer taken seriously after 1940 (Mayr 1988).

The fourth alternative anti-selectionist theory of evolution was the idea of saltationist transmutationism. This concept, a brain-child of typological thinking, argues that one organism could convert into another, possibly dramatically different, form of life in one or at most two generations as a result of a “macromutation.” One of the most prominent proponents of this theory, the geneticist Goldschmidt (1940), pointed out that such a macromutation would likely produce unviable “monsters” but that “hopeful monsters” would occasionally occur, i.e., phenotypes well adapted to a novel environment. In this

manner, a completely new kind of organism (or entire lineage) might evolve without benefit of natural selection. This concept was refuted when it became clear that organisms are not types (such as glucose molecules) and that populations consist of numerous genomic variants. As such, a single hopeful monster might survive and be well adapted, but it could never contribute to evolution unless another hopeful monster of the other sex appeared with which it could reproduce and contribute progeny to the next generation. Although “macromutations,” as postulated by transmutationists, have rarely been observed, recent studies indicate that certain mutations with large phenotypic effects may have been of importance in the course of invertebrate evolution (Ronshaugen et al. 2002). However, the original “hopeful monster” theory, as envisioned by Goldschmidt (1940) and others, is not supported by experimental evidence (Mayr 2001). In any event, the real issue is not whether “hopeful monsters” have played some role in organic evolution but whether they represent the most frequent mode whereby radical evolutionary changes occur.

The evolutionary synthesis

Reif et al. (2000) point out that the “evolutionary synthesis” was a historical process that occurred between ca. 1930 and 1950. This intellectual long-term project, carried out by numerous biologists in several countries, finally led to a “product,” a list of consensus statements that form the core of the synthetic (or modern) theory of biological evolution.

According to most historians of biology, the basic tenets of the synthetic theory are essentially based on the contents of six books authored by the Russian/American naturalist/geneticist Theodosius Dobzhansky (1900–1975), the German/American naturalist/systematist Ernst Mayr (born 1904), the British zoologist Julian Huxley (1887–1975), the American paleontologist George G. Simpson (1902–1984), the German zoologist Bernhard Rensch (1900–1990), and the American botanist G. Ledyard Stebbins (1906–2000). These books (Dobzhansky 1937; Mayr 1942; Huxley 1942; Simpson 1944; Rensch 1947; Stebbins 1950) were written by the six most important “architects” of the synthetic theory (see Fig. 8). A detailed historiographical reanalysis reveals that, in addition to Dobzhansky, Mayr, Huxley, Simpson, Rensch, and Stebbins, other biologists made significant contributions (Reif et al. 2000; Junker and Hoßfeld 2001; Junker 2004). However, a detailed discussion of these contributions is well beyond the scope of this article.

Mayr (1982, 1988) described in detail how most of the non-Darwinian theories of evolution were refuted between ca. 1930 and 1950 either by theoretical arguments (populational versus typological thinking) or by observations/experiments. Nevertheless, no consensus as to the mechanisms of evolution emerged among the leading evolutionists of that decade (Fisher 1930). Indeed, two major camps of biologists were established; camps that

persist to the present day: geneticists and mathematical modelers who study evolutionary processes with selected organisms in the laboratory; and naturalists (taxonomists, paleontologists) who draw conclusions based on studies of populations of organisms observed (or preserved) under natural conditions. In this respect, the reductionist approach of geneticists defines evolution as “irreversible changes of the genetic composition of populations” and concentrates on the genotypic level of organismic organization. In contrast, naturalists define evolution as “gradual descent with modification (inclusive of the diversification of species)” and concentrate on the phenotype. In accordance with Mayr (1963, 1988, 2001), we agree that the entire organism is the target of selection and view the reductionist definition of evolution emerging from a strictly genomic perspective as far too narrow. Certainly, irreversible genomic changes are required for evolution to occur, but these changes must be fixed and sustained in populations by means of natural selection, which acts at the level of the phenotypic alterations these genomic changes evoke. Accordingly, in the following sections, we emphasize the process of phenotypic evolution, which is the visible outcome of changes in gene frequencies in large populations.

The first book authored by Dobzhansky (1937), who later coined the famous phrase “nothing in biology makes sense except in the light of evolution,” was the cornerstone of the synthetic theory. While still in Russia, Dobzhansky worked as a naturalist/taxonomist. After emigration to the USA in 1927, he worked for many years in the laboratory of T.H. Morgan, developing the skills and knowledge of an experimental geneticist. Importantly, Dobzhansky was the “catalyst” who brought together the two camps. The results of this consensus among reductionist geneticists and the naturalists/taxonomists are described in detail below.

The synthetic theory: basic tenets

The terms “evolutionary synthesis” and “synthetic theory” were coined with the title of J. Huxley’s (1942) book *Evolution: the Modern Synthesis* wherein the term “evolutionary biology” instead of the phrase “study of evolution” was first introduced. Some years later, Huxley pointed out that one of the major events in the history of science was the emergence and establishment of evolutionary biology as a separate branch of the biological sciences (Smocovitis 1996; Ruse 1996). Indeed, Huxley was the first to stress that “evolution may lay claim to be considered the most central and the most important of the problems of biology. For an attack upon it we need facts and methods from every branch of the science – ecology, genetics, paleontology, geographical distribution, embryology, systematics, comparative anatomy – not to mention reinforcements from other disciplines such as geology, geography and mathematics” (Huxley 1942, p. 13).

In the same vein, G.G. Simpson, another founder of the modern theory, said “The synthetic theory has no Darwin,

being in its nature the work of many different hands. To mention any of these is to be culpable of important omissions [...]. The theory has often been called neo-Darwinian [...]. The term is, however, a misnomer and doubly confusing in this application. The full-blown theory is quite different from Darwin’s and has drawn its materials from a variety of sources largely non-Darwinian and partly anti-Darwinian. Even natural selection in this theory has a sense distinctly different, although largely developed from, the Darwinian concept of natural selection” (Simpson 1949, pp. 277–278).

What were the basic conclusions drawn by the “architects” of the modern theory? Ernst Mayr provides the following summary: “1. Gradual evolution can be explained in terms of small genetic changes (“mutations”) and recombination, and the ordering of this genetic variation by natural selection; 2. the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms” (Mayr and Provine 1980, p. 1). A more detailed list is as follows:

1. The units of evolution are populations of organisms and not types. This mode of thinking led to the biological species concept developed by Mayr (1942) who more recently defined the biospecies as “an interbreeding community of populations that is reproductively isolated from other such communities” (Mayr 1992; Beurton 2002). This species concept can not be applied to microorganisms, which reproduce asexually by binary fission (see Fig. 4).
2. Genetic and phenotypic variability in plant and animal populations is brought about by genetic recombination (reshuffling of chromosome segments) resulting from sexual reproduction and random mutations along the parent–offspring sequence. In contrast to animals, plants lack a germ-line. The amount of genetic variation that a population of sexually reproducing organisms can produce is enormous. Consider a single parent with N number of genes, each with only two alleles. This individual can produce 2^N genetically different sperm or egg cells. Because sexual reproduction involves two parents, each set can therefore produce an offspring with one of 4^N different genotypes. Thus, if each parent genotype has a mere 150 genes with two alleles each (a gross underestimate of the human genome), each parent can give rise to over 10^{45} genetically different sperm or egg cells, and a single set of parents can produce more than 10^{90} genetically different offspring (a number that comes very close to estimates of the total number of particles in the observable universe).
3. Natural selection is the most important force that shapes the course of phenotypic evolution. In changing environments, directional selection is of special importance, because it causes a shift in the population mean towards a novel phenotype that is better adapted to altered environmental conditions. Additionally, in

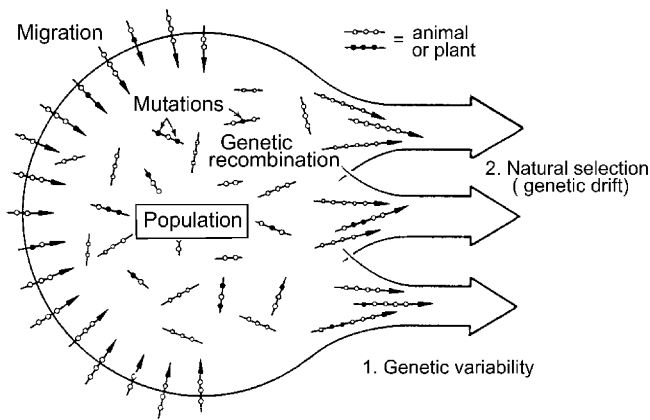


Fig. 5 Scheme to illustrate the interaction of the basic processes that bring about phenotypic evolution in a variable population of organisms (animals or plants) (adapted from Stebbins 1971)

small populations, random genetic drift (loss of genes from the gene pool) may be significant.

4. Speciation can be defined as a “step of the evolutionary process (at which) forms ... become incapable of interbreeding” (Dobzhansky 1937, p. 312). A number of pre- and post-mating isolation mechanisms have been proposed. Geographic isolation of founder populations is believed to be responsible for the origin of new species on islands and other isolated habitats. Allopatric speciation (divergent evolution of populations that are geographically isolated from each other) likely accounts for the origin of many animal species (Mayr 1942, 1963; Mayr and Diamond 2001). However, sympatric speciation (the occurrence of new species without geographic isolation) is also documented in many taxa, notably higher plants, insects, fishes, and birds (Howard and Berlocher 1998).
5. The evolutionary transitions in these populations are usually gradual, i.e., new species evolve from pre-existing varieties by slow processes and maintain at each stage their specific adaptation. There are some exceptions to this general rule that are discussed below. Immigration of individuals from neighboring populations cannot be ignored, but this process is of lesser importance.
6. Macroevolution (i.e., phylogenetic developments above the species level or the occurrence of higher taxa) is a gradual step-by-step-process that is nothing but an extrapolation of microevolution (origin of races, varieties, and species).

It is difficult to depict these six points in order to illustrate the basic processes that bring about phenotypic evolution. Stebbins (1971) was the only “architect” who published a model of the basic tenets of the synthetic theory. A modified version of this classical scheme is shown in Fig. 5.

Carroll (1997, 2000, 2002), Fleagle (2001), and Gould (2002) point out that the patterns and controlling forces of evolution are much more varied than were postulated by

the pioneers of evolutionary biology (Darwin, Wallace, Weismann) and the “architects” of the synthetic theory (Dobzhansky, Mayr, Huxley and others). The expansion of our modern picture of the mechanisms of evolution is discussed in the following sections, which deal with topics summarized in Fig. 8.

Paleobiology and rates of evolution

The biological species concept – an integral part of the synthetic theory – cannot be applied directly to the fossil record. Nevertheless, a population-based concept does lie behind the systematic study of fossilized organisms. Paleontologists have adopted the morphological species concept, which is also used by the majority of systematists of extant organisms (Benton and Pearson 2001).

In 1944, when Simpson’s book *Tempo and Mode in Evolution* was published, no fossils from the Precambrian period (before 550 mya) and only a few examples of intermediate morphological sequences linking ancestral with derived forms of fossil organisms were described. Today, we know that the earliest prokaryotic microbes inhabited the Earth 3,500 mya (Fig. 2). We also know of numerous “missing links” preserved in the vertebrate fossil record (Table 2). For example, the evolutionary history of several extinct groups of organisms, such as the dinosaurs, has been reconstructed in remarkable detail (Sereno 1999). On the basis of these studies, it is now well established that flying birds evolved from a group of bipedal dinosaurs, four-winged arboreal reptiles that could possibly glide (Wellnhofer 2002; Xu et al. 2003). This conclusion is further supported by the finding that crocodiles are the closest living relatives of birds and that these two taxa represent the only surviving lineages of the Archosauria (Meyer and Zardoya 2003). The origin of the vertebrate class Mammalia has also been reconstructed on the basis of large collections of fossils such as mammal-like reptiles (synapsids). According to Kemp (1999) it is by far the best-represented transition of all in the fossil record at the general taxonomic level (Table 2). The perception that intermediate forms in the fossil record are generally absent had an important effect on the thinking of those credited with constructing the modern synthesis. In his book *Variation and Evolution in Plants* (1950), Stebbins complained about the failure of the fossil record to contribute to our understanding of the phylogenetic development of the early angiosperms. Indeed, Darwin (1859) called the origin of the angiosperms an “abominable mystery.” Nevertheless, this gap in our knowledge is slowly but surely being filled with new information, even for seed plants, e.g., the discovery of the 125-Ma-year-old early angiosperm *Archaeofructus* (Sun et al. 2002). As a result of these and many other advances, paleontology (originally a branch of geology) has developed into the discipline now called paleobiology (Schopf 1999; Briggs and Crowther 1990; Benton 1997; Benton and Harper 1997; Carroll 1997; Niklas 1997; Cowen 2000).

Table 3 Estimates of mean species durations for a variety of fossil groups of organisms. These longevities are based on the application of the morphological species concept

Taxon	Species duration (Ma)
Marine bivalves and gastropods	10–14
Benthic and planktonic foraminifers	20–30
Marine diatoms	25
Trilobites (extinct)	>1
Ammonites (extinct)	~5
Beetles	>2
Freshwater fishes	3
Snakes	>2
Mammals	1–2
Bryophytes	>20
Higher plants: herbs	3–4
Shrubs, hardwoods	27–34
Conifers, cycads	54

Data from Stanley (1985), Niklas (1997), Levin (2000)

Other insights are coming from studies of polyploidy. Stebbins devoted two chapters to the occurrence of more than two genomes per cell and speculated on its role in plant evolution (Stebbins 1950). Today we know that about 50% of all angiosperm species are polyploids and that duplicated genes (genomes) can undergo functional divergence and thus acquire new functions. Indeed, polyploidy may confer ecological benefits that are responsible for the success of many angiosperm species (Soltis and Soltis 2000).

Botanists speculated that sympatric speciation is as important as allopatric speciation (Stebbins 1950), but zoologists tended to ignore this mode of speciation, perhaps because of the emphasis on Mayr's (1942) biological species concept and the role of geographic isolation. Nevertheless, recent studies have shown that genetic divergence can and does occur in sympatric populations. Hence, zoologists, who have been the principal architects of the modern evolutionary theory, have tended to ignore the insights gained from the study of plants until they could see evidence for these phenomena in animals.

In his classic book, Simpson (1944) recognized that the rates of evolution are highly variable in different groups of fossil organisms. More recent quantitative studies have revealed that the (morpho)-species durations in the fossil record are much larger than originally anticipated: from 1–2 Ma in mammals to >20 Ma in bryophytes, conifers, and some marine invertebrates (Table 3). These data show that a species, once evolved and thereafter the occupant of a defined ecological niche, may remain stable over hundreds of thousands of generations. However, examples of more rapid speciation events are well documented. In cichlid fishes (Meyer et al. 1990, Meyer 1993), polyploid angiosperms (Soltis and Soltis 2000), and Southern African ice plants (Klak et al. 2004), reproductive isolation and the resulting (sympatric) origin of novel species can occur within a few hundred (or thousand) generations. Nevertheless, the typical morphospecies undergoes little measurable change in form during more than a million

years (Stanley 1979, 1985; Niklas 1997; Kemp 1999; Levin 2000).

The number of populations of organisms in a particular area is largely determined by the rates of speciation and extinction: the difference represents our extant biodiversity (Niklas 1997). In spite of the fact that the modes of speciation are a key issue in evolutionary biology, there is still debate about the “creative process” that leads to species diversity. Theories of speciation in sexually reproducing organisms are summarized by Howard and Berlocher (1998), Schilthuizen (2001), and Schluter (2001).

Mass extinctions and species selection

Darwin (1859, 1872) discussed not only the origin, but also the decline and demise of species. As a major cause of the extinction of populations and entire species, he proposed interspecific competition due to limited resources (Table 1): over evolutionary time, superior species were envisioned to replace less well-adapted ones (Raup 1994). This perspective has changed in recent years with a greater understanding of the roles of mass extinctions, episodes in Earth's history where the “rules of natural selection and adaptation” appear to have been abandoned.

This perspective was presaged in Mayr's (1963) first major book of the post-synthesis period wherein he points out that extinction must be considered as one of the most conspicuous evolutionary phenomena. Mayr discussed the causes of extinction events and proposed that new (or newly invading) diseases or changes in the biotic environment may be responsible. In addition, he wrote: “The actual causes of the extinction of any fossil species will presumably always remain uncertain... It is certain, however, that any major epidemic of extinction is always correlated with a major environmental upheaval” (Mayr 1963, p. 620).

This hypothesis, largely unsupported by facts when proposed 40 years ago, has since gained considerable support. The term “mass extinction,” mentioned by Mayr (1963, p. 617), but not further defined, is used when many species become extinct within a short time; the events are related to a single cause (or combination of causes); and the extinct species include plants and animals of all body sizes, marine, and non-marine forms (Benton and Harper 1997). Although most species die out during periods of so-called “background extinction,” at least five mass extinctions are generally recognized: Late Ordovician, Late Devonian, Permian-Triassic (P-T), Late Triassic, and Cretaceous-Tertiary (K-T) at ca. 450, 364, 250, 200, and 65 mya (Raup 1994; Benton 1997; Hallam and Wignall 1997). The two most severe mass extinctions (P-T and K-T; see Fig. 2) warrant particular comment.

The biological extinction that occurred at the P-T boundary about 250 mya represents the most severe extinction event in the past 550 million years (Ma). It is estimated that about 70% of vertebrate families on land,

many woody gymnosperms, and more than 90% of species in the oceans were killed. Several causes for this “mother of all extinctions” have been proposed, including volcanism, an asteroid or comet impact, oceanic anoxia, and environmental change (Hallam and Wignall 1997). It is now known that at the end of the Paleozoic (Permian), the supercontinent of Pangea formed; this geological event was associated with the eruption of the Siberian flood basalts, 250 mya. These giant volcanic eruptions, confined to a time interval of only a few hundred thousand years, were probably the major cause for the catastrophe in the late Permian biosphere (Jin et al. 2000; Benton and Twitchett 2003), since evidence in support of a large extraterrestrial impact during the P-T extinction is problematic (Benton and Twitchett 2003; see also Jin et al. 2000).

The K-T boundary records the second largest mass-extinction event: this global catastrophe wiped out 70% of all species, among which the dinosaurs are the best known (Serenio 1999). Small mammals survived to inherit vacated ecological niches, enabling the rise and adaptive radiation of the lineages that ultimately evolved into *Homo sapiens* (Benton 1997). Paleontologists have proposed numerous hypotheses to account for the “dinosaur murder mystery.” Two theories have survived – volcanic upheaval and asteroid collision.

The Deccan traps in India are layered flows of basaltic lava laid down at the K-T boundary (68–64 mya). These rock layers suggest that a global volcanic catastrophe may have occurred and been the driving force behind the K-T (and the earlier P-T) extinction event (Benton 1997). According to the more popular second scenario, a giant 10-km asteroid (or comet) struck Earth at a velocity of at least 10 km/s. The incredible energy liberated by this collision would have caused a global environmental disaster resulting from fire, acid rain, tsunamis, storm, and cold and darkness followed by greenhouse warming (Alvarez 1997). Evidence supporting this “Alvarez extinction event” (Mayr 2001) is compelling and includes the K-T-iridium anomaly, impact tracers such as shocked quartz, and the discovery of the 65-Ma-old 180 km subsurface Chicxulub crater in Yucatan, Mexico (Alvarez 1997). Regardless of the cause, many different animals suffered during the K-T extinction event (Benton 1997). The effect on land plants is more controversial (for contrasting ideas, see Niklas 1997; Wilf et al. 2003).

In summary, the “environmental upheaval hypothesis” of Mayr (1963) has been confirmed. Although much of evolutionary history may be gradual, occasional catastrophic events have punctuated its steady (background) pace. It is obvious that the few “lucky survivors” determined subsequent historical patterns in the history of life.

Macroevolution and punctuated equilibrium

Darwin (1859, 1872) introduced the concept of gradualism: higher taxa (and hence novel body plans) are the

products of accumulated small differences over extended evolutionary time (Table 1). Mayr (1942, p. 298) concluded that “all available evidence indicates that the origin of the higher categories is a process which is nothing but an extrapolation of speciation. All the processes of macroevolution and the origin of higher categories can be traced back to intraspecific variation even though the first steps of such processes are usually very minute.”

Two decades later, the same author reinforced this viewpoint: “The proponents of the synthetic theory maintain that all evolution is due to the accumulation of small genetic changes, guided by natural selection, and that transspecific evolution is nothing but an extrapolation and magnification of the events that take place within populations and species ... essentially the same genetic and selective factors are responsible for evolutionary changes on the specific and on the transspecific levels ... it is misleading to make a distinction between the causes of micro- and macroevolution” (Mayr 1963, pp. 586–587). Stebbins (1971, p. 161) came to the same conclusion: “...the evolution of higher categories has been by means of the same processes which have brought about the evolution of races and species.”

In spite of the consensus among the “architects” of the synthetic theory, the extent to which macroevolution is the product of microevolutionary modifications is still debated (Stanley 1979; Erwin 2000; Simons 2002). In general, a continuity between micro- and macroevolution is documented in many fossil lineages available today. The results summarized in Table 2 show that the fossil record of vertebrates includes forms intermediate between fishes and amphibians, between amphibians and land vertebrates (reptiles), between reptiles and mammals, and between reptiles (theropod dinosaurs) and birds. It is obvious that millions of years ago the characteristics that currently distinguish these five classes of vertebrates were not yet established.

Another striking example of “macroevolution in progress” is seen among the grasses (Poaceae), which display C₃ and C₄ pathways of photosynthesis (Kellogg 2000). The C₄ mode of CO₂-assimilation evolved from the basal C₃-mechanism, which is retained in 90% of all extant flowering plants. Numerous C₃–C₄ intermediate forms have been described in a variety of taxa. The evolutionary intermediacy of C₃–C₄ plants has been documented by several lines of evidence, including gas exchange measurements (Sage and Monson 1999). The pattern of macrofossils shows that the earliest grasses (C₃) appear in the Eocene (about 55 mya), whereas the earliest C₄ macrofossils are dated at 12.5 mya (Kellogg 2000). These data demonstrate that C₄ plants evolved from C₃ forms. This macroevolutionary process can be reconstructed and experimentally analyzed in terms of the many C₃–C₄ intermediates (Sage and Monson 1999; Kellogg 2000; Schütze et al. 2003).

Taken together, these examples accord well with the basic tenet of the synthetic theory that continua exist between small-scale allele frequency changes in popula-

tions and large-scale phylogenetic changes leading to novel body plans (Simons 2002).

However, evolutionists acknowledge that exceptions exist. One example is the origin of eukaryotic cells from prokaryotic ancestors by means of endosymbiosis (see Fig. 2). Another is proposed by Ronshaugen et al. (2002) who provide experimental evidence suggesting that the divergence of six-legged insects from crustacean-like arthropod ancestors with multiple limbs (about 400 mya) may have occurred within a relatively short time period. These two examples are not easily reducible to the gradualistic mechanisms treated by the architects of the modern synthesis, although macroevolutionary alterations in body plans by means of many small evolutionary steps can occur rapidly when viewed in the perspective of geological time scales (Mayr 1942, 1963; Niklas 1997).

The “punctuated equilibrium” theory of Gould and Eldredge (1993) was originally proposed as an alternative to Darwin’s concept of gradualism. According to this theory, evolution tends to be characterized by long periods of morphological stasis (“equilibrium”), “punctuated” by episodes of rapid phenotypic change. The evidence in support of this model, which is the opposite of a continuous anagenetic transformation of populations or “phylogenetic gradualism,” was recently summarized by Gould (2002). Over the past decades, numerous studies have shown that evolutionary transitions are gradual, although the rates of phylogenetic developments may vary. It follows that evolution is both gradual and occasionally more or less “punctuated” (Kellogg 2000; Mayr 2001; Bokma 2002). At any rate, the conflict between the gradualist and punctualist interpretation of the fossil record is no longer an issue, i.e., evolutionary rates can and do vary, often appreciably (Table 3). The real issue is whether “rapid” evolution as gauged by geological time scales is evidence for the absence of microevolutionary modifications of genomes as gauged by reproductive time scales. Although the debate lingers on, the evidence that the mechanisms underlying macroevolution differ from those of microevolution is weak at best.

Weismann’s hypothesis

The theory for the inheritance of acquired characteristics advanced by Jean-Baptiste de Lamarck (1744–1829) and accepted by Darwin (1859, 1872) was strenuously opposed by August Weismann (1834–1914). This eminent zoologist/cytologist was an ardent proponent of natural selection, so much so that he has been recognized as second only to Darwin in his profound affect on evolutionary theory (Mayr 1988) (see Fig. 1). In a classic experiment, Weismann cut off the tails of successive generations of mice and showed that the tail length of the progeny of each generation was the same as that of the preceding generations. Additionally, Weismann absolutely rejected any brand of Lamarckian “soft inheritance” based on his detailed cytological studies that indicated

that the reproductive cells giving rise to the gametes (sperm and egg cells) in animals segregate early in development from non-reproductive cells such that they cannot be influenced by alterations of non-reproductive tissues or organs (the concept of the germ-line). Weismann (1892) proposed the word “germplasm” for reproductive cells (specifically their chromosomes) and the term “soma” for non-reproductive cells (and their chromosomes) and, as early as 1889, he argued that sexual reproduction provided the variability in populations required for adaptive evolution.

By the 1930s and 1940s, many other scientists performed experiments similar to Weismann’s mouse-tail studies and the notion of “soft inheritance” was discarded forever. Mendelian genetics had developed by that time to provide a firm basis to explain the variation among individuals in a population required by Darwin’s theory. Since 1960 molecular genetics has demonstrated that changes in the base-pair composition of DNA are translated into changes in protein structure or developmental regulations and that no change in a protein or other cellular constituents other than nucleic acids can alter the information encoded in DNA. Thus, the “hard inheritance” postulated by Weismann has been demonstrated as a fact.

The term “Weismann’s hypothesis” now stands for the explicit proposal that sexual reproduction functions to provide variation for natural selection to act upon (Mayr 1982; Burt 2000). Nevertheless, the adaptive significance of sex (and why sexual reproduction evolved) has remained a matter of considerable debate because of the 50% “fitness cost” of meiosis which, in theory, should favor asexual reproduction (Niklas 1997). Note that during sexual reproduction, each parent contributes only 50% of its genome to its offspring. The resulting genomic variation thus introduced into a population can lead to maladapted individuals. In contrast, asexual reproduction ensures that new individuals are as adapted to their environment as their parents, since every individual in the population leaves progeny that are clones of itself. So why does bisexual reproduction abound?

According to Mayr (1982) the 50% “fitness cost” of sexual reproduction can be resolved if we consider the fact that environments are constantly changing, whereas Niklas (1997) has pointed out that sexual and asexual reproduction are not mutually exclusive, especially for plants. The variable offspring produced by sexual reproduction may include some individuals better suited to new environmental conditions, whereas asexually propagated individuals remain adapted to past environmental conditions. Likewise, Hamilton et al. (1990) proposed that the genetic variability that sexual reproduction provides allows plants and animals to cope with parasites and diseases. In an evolutionary “arms race,” pathogenic organisms can grow and adapt so rapidly that they can circumvent the host’s defenses. More recently, Rice and Chippindale (2001) have provided evidence that sexual reproduction is advantageous because it accelerates phenotypic evolution by allowing beneficial mutations

to spread without being held back by the baggage of deleterious mutations at other loci in the genome. All these ideas and experiments support Weismann's original concept (1892) that sexual reproduction produces variable progeny and thereby promotes adaptive evolution.

Sexual selection and altruism

Darwin (1859) introduced the concept of sexual selection. In his book *The Descent of Man* (1871) he described numerous examples, e.g., the peacock's tail and the lion's mane. Darwin argued that competition among males resulted in the selection for traits that increased the mating success of competing males, traits that could nevertheless decrease the chances of survival of the individual. Darwin argued that "competition" could take one of two forms, either physical combat among males or competition for the attention of females. Large body size and musculature provide advantages in male combat, whereas traits such as colorful male plumage and complex display behavior increase the attention of females ("female choice"). Darwin's (1871) ideas were not widely accepted (Andersson 1994) and the proponents of the synthetic theory (Dobzhansky 1937; Mayr 1942; Huxley 1942) largely ignored the concept of female choice. The study of sexual selection only gained momentum in the post-synthesis era.

Dawkins (2002) argued that A.R. Wallace (and not Darwin) first proposed that males with bright plumage demonstrate their health and high-quality as a sexual partner. According to this "good-genes sexual selection hypothesis," female mate choice affords an evolutionary advantage. This perspective has received empirical support. Møller and Alatalo (1999) report a correlation, albeit small, between offspring survival and male secondary sexual characters across a large number of taxa (birds, amphibians, fish, insects). Additionally, experiments with blackbirds indicate that males with the brightest bills have a strong immune system (Pennisi 2003). Thus female choice may foster the general health of blackbird populations. These and other data are consistent with the concept that female choice influences the traits of males and may even be beneficial to males in ways that have nothing to do directly with mating success.

Models of both sympatric and allopatric animal populations also indicate that sexual selection has the potential to drive rapid divergence and hence may generate reproductive isolation (Panhuis et al. 2001). Studies of the explosive diversification of cichlid fishes in the three Great Lakes of East Africa indicate that sympatric speciation may have been a major driving force during this adaptive radiation (Meyer 1993; Schluter 2001). Clearly, however, more information on the role of sexual selection during speciation is required (Panhuis et al. 2001).

Since the publication of the *Origin of Species* (Darwin 1859), generations of anti-evolutionists have argued that altruistic behavior (self-denying acts performed for the

benefit of others) is incompatible with the principle of natural selection. Nonetheless, altruistic behavior, such as parental care and mutualism, has been observed and documented throughout the animal kingdom, from lower invertebrates to mammals (Krebs and Davies 1993; Kutschera and Wirtz 2001; Trillmich and Diesel 2002; Clutton-Brock 2002). One of the more conspicuous forms of altruism occurs in certain social insects, such as ants, bees and wasps, that have a sterile worker class.

In a classic paper, Hamilton (1972) asked "in what sense can a self-sacrificing sterile ant be considered to struggle for existence or to endeavor to maximize the numbers of its descendants?" This question – the evolution of eusociality in insects and the occurrence of worker altruism (Hölldobler and Wilson 1990) – has been answered by the theory of inclusive fitness or kin selection (Hamilton 1972). According to the Darwin/Wallace principle, natural selection refers to individual differences in reproductive success (RS), where RS is the number of surviving offspring produced during an individual's lifetime. Hamilton (1972) enlarged on this idea and included RS effects on the relatives of the individual: the term *inclusive fitness* refers to RS plus the RS of relatives, each devalued by the corresponding degree of relatedness (Hölldobler and Wilson 1990). Numerous studies of a variety of animal species have shown that altruism is not in conflict with evolutionary theory. However, a modification and expansion of our view of a single organism in a population was necessary: the individual no longer seems to have a unitary self-interest, but is part of a complex parent–relative network. For a critical discussion of this subject the reader is referred to Hölldobler and Wilson (1990), Krebs and Davies (1993), Griffin and West (2002), Clutton-Brock (2002), and Jost (2003).

Endosymbiosis and eukaryotic cell evolution

The evolution of the first eukaryotic cells from their prokaryotic antecedent condition has received considerable attention (Martin et al. 2001; Martin and Borst 2003). This key event in the history of life occurred about 2,000–1,500 mya during the early Proterozoic (Fig. 2). Two non-mutually exclusive hypotheses have been advanced to explain the origin of eukaryotes: endosymbiosis and autogenesis. The endosymbiotic hypothesis (also called a theory) envisions the evolution of the first eukaryotic cells to have resulted from the permanent incorporation of once autonomous, physiologically different prokaryotic cells within a host prokaryotic cell-type. According to this concept, mitochondria evolved from some form of ancient aerobic bacteria, whereas chloroplasts evolved from some form of cyanobacteria-like prokaryote. Once these residents gained permanent residency in their host cell, they continued to function and replicated such that derivative confederations were produced when the host cell underwent binary fission (Margulis 1993). In contrast, the autogenous hypothesis argues that the mitochondria and

chloroplasts (as well as other eukaryotic organelles and structures such as the endoplasmic reticulum) evolved as a consequence of selection pressures for physiological specialization within an ancient prokaryotic cell-type. According to this hypothesis, the host cell membrane invaginated to encapsulate internal physiologically different portions of the ancestral cell-type. Over evolutionary time, these membrane-bound regions became increasingly specialized and evolved into the various organelles that currently define the stereotypical eukaryotic cell.

The endosymbiotic hypothesis is supported by the fact that mitochondria and chloroplasts are double membrane-bound, reproduce like prokaryotes by binary fission (Fig. 4), have circular DNA, and are sensitive to bacteriocidal substances (Martin et al. 2001). Additionally, the oligonucleotide sequences of living cyanobacteria closely align with those of modern-day cyanobacteria, whereas those of mitochondria align well with the oligonucleotide sequences of the proteobacteria (a group of purple non-sulfur bacteria) (Schopf 1999; Pace 2001). The evidence for the autogenous hypothesis is less convincing (Niklas 1997). However, the endosymbiotic hypothesis does not easily account for single membrane-bound organelles, the evolution of the endoplasmic reticulum, or the appearance of single membrane-bound organelle-like structures in prokaryotic cells. Nor does the endosymbiotic hypothesis directly address the origin of the nucleus, which is itself a double membrane-bound structure. In this regard, it is notable that both models speculate that the host cell-type, which was presumably either some form of an anaerobic-aerotolerant prokaryote or an inefficient aerobic prokaryote, had the capacity for some form of endocytosis, i.e., the ability to invaginate its outer cell membrane, either for engulfing prokaryotic cells (according to the endosymbiotic theory) or encapsulating internally physiological regions of the host cell (according to the autogenous hypothesis). Curiously, the outer cell membrane of modern-day bacteria is remarkably inflexible and generally lacks the ability to form closed vesicles. Whether this feature characterized the most ancient forms of bacterial life, however, is unknown.

The evolution of the first eukaryotic cells cannot be divorced from the phylogenetic development of mitotic and meiotic cell division (and thus the evolution of sexual reproduction). Limited space precludes a detailed discussion of these features of eukaryotic evolution. Cogent discussions of this topic can be found in a number of books and papers (e.g., Margulis 1993; Margulis and Schwarz 1998; Martin et al. 2001; Martin and Borst 2003; Martin and Russell 2003).

Evo-devo and Hox genes

Historians of science have long noted that one major discipline, developmental biology (formerly called embryology), was not part of the evolutionary synthesis, although this branch of biology was discussed in detail by Darwin (1859, 1872). In his essay, Mayr (1993) describes

the anti-evolution sentiments of several embryologists of the synthesis-period and noted that “The representatives of some biological disciplines, for instance, developmental biology, bitterly resisted the synthesis. They were not left out of the synthesis, as some of them now claim, but they simply did not want to join”. Over the past two decades, however, developmental biology and evolutionary theory have united to form a new branch of biological enquiry called evolutionary-developmental biology or “evo-devo” (Hall 1999), which explores how developmental processes evolve and how they ultimately obtained the various body plans of past and present-day organisms.

According to Arthur (2002), the single most important factor responsible for the synthesis of developmental biology and evolutionary theory was the discovery of a group of regulatory genes called the homeotic (Hox) gene family. These genes encode DNA-binding proteins (transcription factors) that profoundly influence embryonic development. For example, the suppression of abdominal limbs in insects is determined by functional changes in a protein called Ultrabithorax, which is encoded by a Hox gene (Ronshaugen et al. 2002). Importantly, the Hox family of genes has been identified in arthropods (insects, crustaceans, chelicerates, myriapods), chordates (fishes, amphibians, reptiles, birds, mammals), and has analogs among plant and yeast species. On the basis of comparative gene analyses in several taxa, the evolution of the Hox-gene clusters in vertebrates has been reconstructed. Although the common ancestor of mouse and human lived around 75 mya, the architectures of their Hox-gene clusters are identical (Meyer 1998). Therefore, the Hox gene family is extremely ancient and apparently highly conserved, which has profound implications for the evolution of developmental processes and patterns. For a detailed discussion of some recent evo-devo studies, see Meyer (1998), Hall (1999), Schierwater and DeSalle (2001), Arthur (2002), and Gilbert (2003).

Phenotypic plasticity

Natural selection does not act directly on the genotype. It acts on the phenotype, which if well adapted to its environment survives, reproduces, and passes some of its genomic components on to the next generation. In this sense, the phenotype can be viewed as a *tactical* expression of the *strategy* of its genotype. One such strategy is for the genotype to produce a range of phenotypic expressions, each of which is suited to a particular environmental circumstance. Indeed, for many organisms, the same genotype can give rise to many different phenotypic variants whose appearance or behavior depends on (or is at least correlated with) its environmental setting. This phenotypic variation or “plasticity” (which is a measure of an organism’s norm of reaction) dictates the range of habitats that a particular genotype can occupy. In theory, a genotype that engenders a high degree of phenotypic plasticity has an improved chance of being passed on to the next generation, provided that the

“plasticity” enhances the functional performance of the phenotype (Niklas 1997; Pigliucci 2001).

Arguably, plant development is more “plastic” than that of most animals. Well known examples of plant plasticity are the differences in the size, shape, thickness, and anatomy of sun and shade leaves produced by the same tree as well as the differences in the form and anatomy of submerged versus aerial leaves on many aquatic plants (Bradshaw 1965; Sultan 2000). An explanation for the contrast in the degree to which plants and animals exhibit phenotypic plasticity may lie in the fact that plant development is typically indeterminate (i.e., the individual continues to grow indefinitely in size), metameric (e.g., the same organ types are continuously produced), and intimately tied to external physical cues (e.g., light quality and intensity). Likewise, most plants are sedentary organisms which begin and end their lives in very much the same location. Thus, the individual plant cannot leave its location when its environment becomes unfavorable and, regardless of its environmental circumstances, the development of new organs is dictated in part by their immediate environmental conditions (Niklas 1997, 2000a). Taken together, these features of plant life would appear to require a higher degree of phenotypic plasticity than might be expected from animals that can migrate as individuals to find suitable or favorable habitats. This perspective is supported by the observation that many forms of sedentary animals (e.g., sponges, corals, bryozoans) exhibit a higher degree of phenotypic plasticity than do animals capable of locomotion and migration.

Epigenetic inheritance and molecular evolution

One major achievement of the evolutionary synthesis was the refutation of the Lamarckian concept of acquired inheritance (Mayr and Provine 1980). Recently, however, the Lamarckian perspective has re-emerged in the context of the study of epigenetics, that is, developmental processes that are promoted indirectly by a series of events that are not directly dictated by gene products. One example is the expansion of the vertebrate embryonic eye and brain, which is hydrostatically driven. The mechanics of eye and brain expansion is ultimately related to gene function, but the proximate causality is not. Another example is the methylation of certain regions of the genome, one form of gene “silencing” that is important in both plant and animal embryogenesis. Importantly, a variety of environmental factors, such as temperature, can influence the intensity of DNA methylation. These and other examples of epigenetic phenomena indicate that the nucleotide sequences *sensu stricto* are not the only heritable information (Kakutani 2002). However, these studies do not support Lamarck’s idea that morphological changes acquired during the lifetime of an animal can be transferred via the germ-line to the next generation. Epigenetic phenomena are the emergent properties of the

genome and the response of the genome to its environment, both of which are heritable and mutable.

During the first years of the post-synthesis period, the discovery of the molecular structure of DNA and the publication of comparisons of amino acid sequences has given rise to the study of molecular evolutionary biology (Page and Holmes 1998). In its broadest sense, this branch of biology examines the “archaeology” and structure of the genome of extant organisms in an effort to reconstruct phylogenetic relationships (molecular systematics) (Meyer and Zardoya 2003; Schütze et al. 2003) and to elucidate the molecular basis of adaptation and speciation (Golding and Dean 1998). Among the various insights that have emerged from molecular evolutionary biology is the recognition that many evolutionary novelties come from modifications (mutations) of regulatory as well as structural genes (Doebley and Lukens 1998). Likewise, gene duplication and divergence in function has been emphasized in treatments of the evolutionary appearance and divergence of the Bacteria, Archaea, and Eukarya (Page and Holmes 1998) and the origin of novel functions (neo-functionalization, see Zhang 2003). The concept that gene duplication can provide the raw material for evolution, which goes back to the 1930s, has received substantial support from numerous molecular studies (Zhang 2003). The molecular basis of phenotypic evolution has become one of the most important areas of study in the post-synthesis era. Although much has been learned over the past two decades, many basic questions nevertheless remain unanswered (Page and Holmes 1998; Zhang 2003).

For example, are the majority of phenotypic variants the result of selection or neutral genetic changes? According to the neutral theory of molecular evolution the majority of DNA (and protein) divergence between species is driven by random genetic drift and mutation, and not by positive natural selection (Futuyma 1998). The neutralist–selectionist debate is summarized by Page and Holmes (1998), where a detailed treatment of this subject can be found. A recent analysis of genomic data indicates that positive selection is responsible for protein evolution in fruit flies and other species (Fay et al. 2002). These and other results are largely incompatible with the neutral theory and provide evidence for the occurrence of natural selection at the molecular level (Bell 1997; Kutschera 2003a).

Experimental bacterial evolution

Despite their numerical abundance and their important roles in biogeochemical cycles, bacteria (Fig. 4) were largely ignored by the architects of the synthetic theory, which dealt with the evolutionary processes of bisexual eukaryotic macroorganisms (animals, plants). Today, the study of bacterial evolution is a burgeoning field that is contributing many insights into evolution as a whole.

The new field of experimental evolution with cultivated bacteria was exemplified by a classic paper by

Lenski and Travisano (1994) who described the propagation of 12 populations of *E. coli* B over 10,000 generations (1,500 days) in an identical test-tube environment. Each population was founded by a single cell from a strain that was unable to exchange DNA. It follows that spontaneous mutations were the only source of genetic variability in these populations. To mimic natural selection, a glucose-limited minimal medium was used. Both cell size and relative fitness (measured in a competition experiment with the frozen-thawed ancestor) changed in this artificial system as a result of the successive fixation of several beneficial mutations (Elena et al. 1996). This experimental system revealed that punctuated evolution occurs in bacterial populations as a result of beneficial mutations followed by natural selection (survival and propagation of those varieties that best cope with the low-sugar environment). Wahl and Gerrish (2001) subsequently developed an integrated theoretical framework for the analysis of similar in vitro evolution experiments. This approach has now been used to study experimentally the evolution of strains of budding yeast, viruses, and self-replicating RNA-molecules (ribozymes) (Schuster 2001; Joyce 2002).

In a recent review article, Elena and Lenski (2003) described the advantages of microorganisms for evolution experiments, methods for measurement of relative fitness of ancestral and evolved bacterial populations, and the genetic basis of evolutionary adaptations. In this excellent summary, the state of the art of experimental bacterial evolution is described and the relevance of in silico studies with “digital organisms” is stressed. This topic is discussed in the next section.

Computer simulations of phenotypic evolution

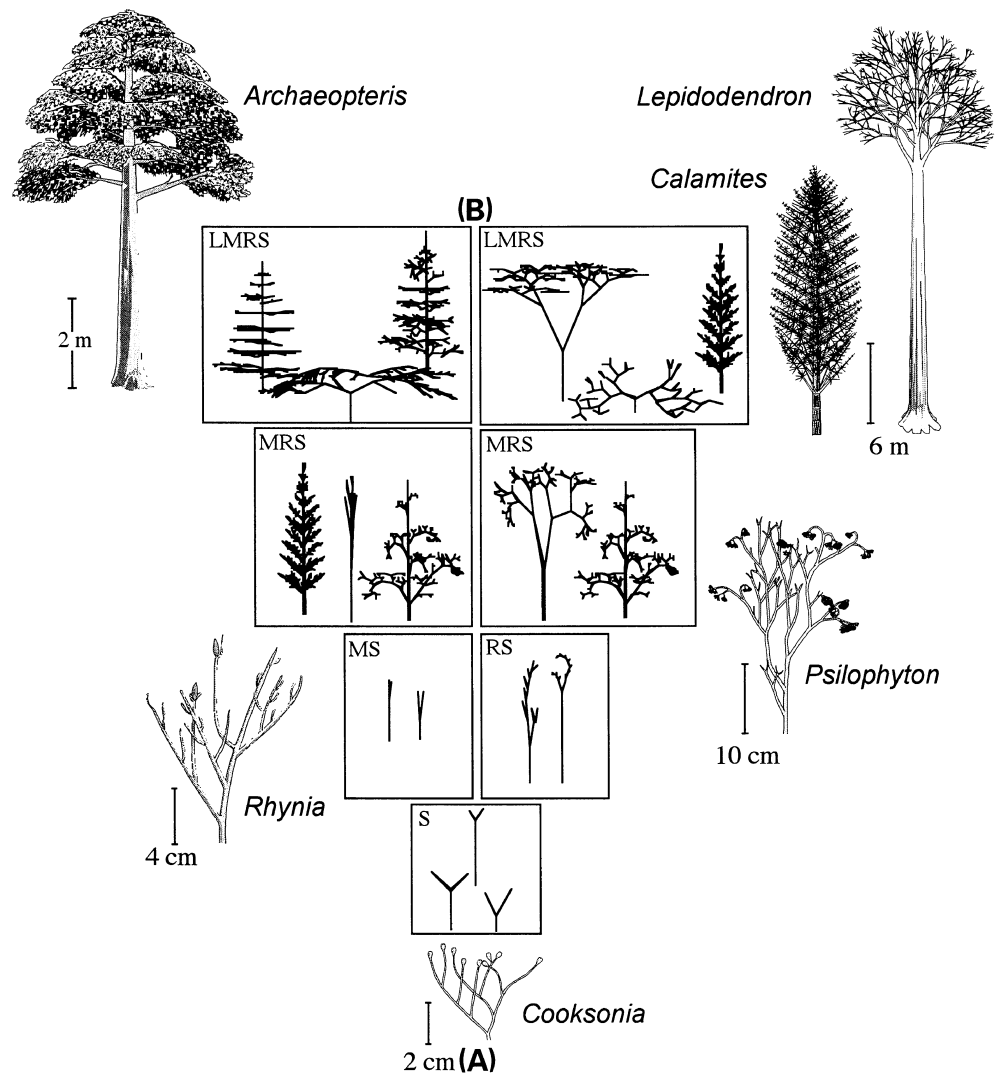
Recent developments in computer technology and mathematical principles have provided the tools with which to model organismic evolution. The approach has been to simulate all conceivable phenotypic variants for a particular lineage or grade of organic organization (i.e., to construct a “morphospace”) and to quantify the performance of each of these variants in terms of one or more biological functions believed to influence relative fitness, such as visual acuity in animals or photosynthesis in plants (i.e., to generate a “fitness landscape” *sensu* Sewall Wright’s metaphor for adaptive evolution). This approach has been used in one of two ways: to quantify the number of species occupying different regions of the morphospace and thereby identify phenotypic regions that are well-adapted or maladaptive; or to simulate “adaptive walks” in which the performance of the one or more biological tasks is increasingly maximized or optimized as morphological transformations are simulated by a computer. Clearly, this approach is purely heuristic in the sense that the results of computer simulations reflect the various assumptions used by a particular worker. Nevertheless, attempts to simulate the evolution of “digital organisms” can shed light on a number of historical trends

seen in the fossil record that would otherwise resist a quantitative description (Lenski et al. 2003).

For example, computer models have been used to mimic the early evolution of ancient vascular plants (tracheophytes) (Niklas 1992, 1997, 1999, 2000a, 2000b). These models have three components: (1) an *N*-dimensional domain of all mathematically conceivable ancient morphologies (the morphospace for ancient tracheophytes); (2) a numerical assessment of the ability (fitness) of each morphology to intercept light, maintain mechanical stability, conserve water, and produce and disperse spores; and (3) an algorithm that searches the morphospace for successively more fit variants (an adaptive walk). Beginning with one of the most ancient plant forms (*Cooksonia*, Early Devonian; see Fig. 6A), tracheophyte evolution is simulated by locating neighboring morphologies that progressively perform one or more tasks more efficiently. The resulting “adaptive walks” indicate that early tracheophyte evolution likely involved optimizing the performance of many tasks simultaneously rather than maximizing the performance of one or only a few tasks individually, and that the requirement for optimization accelerated the tempo of morphological evolution in the Mesozoic (from the Early Devonian to the late Carboniferous; see Fig. 6A). A comparison of the fossil plants depicted in Fig. 6A that evolved over a period of 100 Ma and the “digital organisms” (Fig. 6B) reveals a striking similarity in form and design.

These simulations draw attention to the distinction between maximization and optimization and to the fact that natural selection acts on the phenotype as a whole and not on its individual parts (Mayr 2001). Every organism must perform a wide range of biological functions to grow, survive, and reproduce. No single function is more important than any other, because the phenotype is an integrated functional whole and because environmental factors influencing one or more parts of the phenotype indirectly or directly affect the whole organism. Importantly, different biological tasks have different phenotypic requirements and some tasks have antagonistic design requirements. Therefore, although it is possible to maximize the performance of one task, this maximization comes at some expense in terms of performing other tasks. In this respect, computer simulations of early vascular plants (Fig. 6B) indicate that the survival of an organism depends on resolving the performance of all biological tasks, which requires optimization rather than maximization. An additional insight from these simulations is that natural selection cannot create a “perfect” organism, because optimization results in organisms that perform all of their functional obligations reasonably well simultaneously but not perfectly in terms of each individual task. One result of optimization is that the number of phenotypes capable of optimizing the performance of their tasks is larger than the number of phenotypes capable of maximizing the performance of all other tasks. The result of optimization, therefore, is a richer spectrum of phenotypic possibilities.

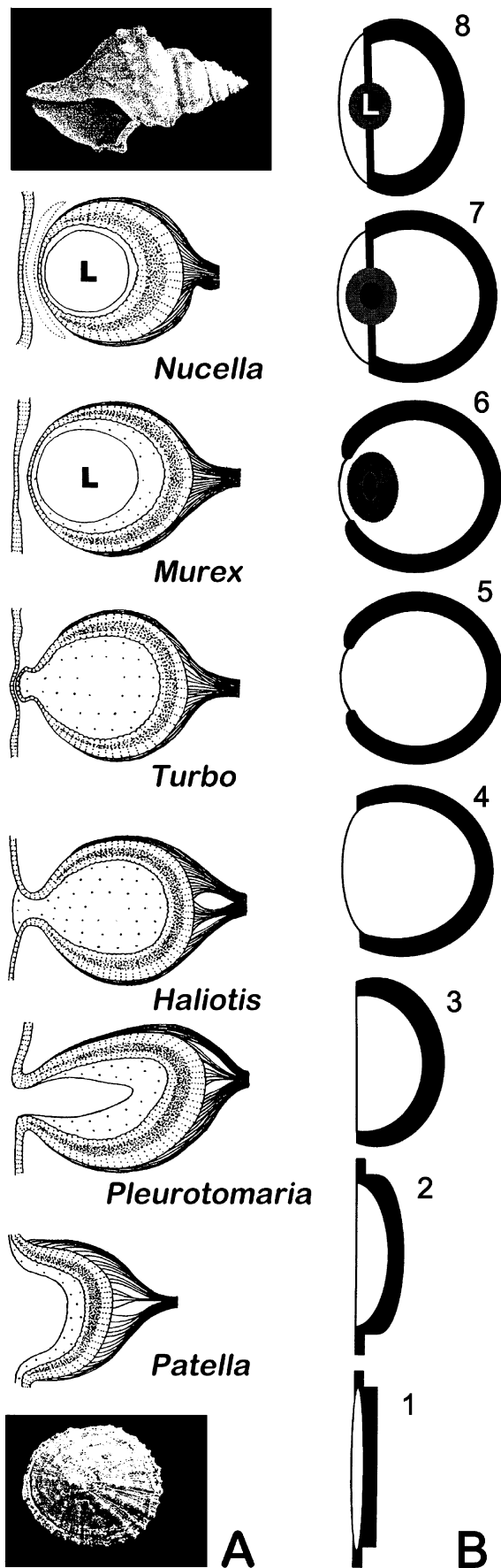
Fig. 6A, B Reconstruction of the evolution of land plants (tracheophytes) based on the fossil record (**A**): *Cooksonia*, *Rhynia* and *Psilophyton* from the Early Devonian (~400 Ma ago), *Archaeopteris* from the Late Devonian (~350 Ma), *Calamites* and *Lepidodendron* from the Late Carboniferous (~300 Ma ago). Computer simulation of early vascular land plant evolution (**B**). The virtual organisms were maximised for water conservation (S), mechanical stability (M), reproductive efficiency (R), and light interception (L) (stages 1–4). The fossils (**A**) and the digital plants (**B**) are very similar. (Adapted from Niklas 1992, 2000b)



In his *Origin of Species*, Darwin wrote: “If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down” (Darwin 1859, p. 189). In this context, it was perfectly obvious that Darwin was thinking of the evolution of the eye, since he also wrote “that the eye, with all of its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection seems, I freely confess, absurd in the highest possible degree” (1859, p. 189). Darwin was well aware of the many difficulties revolving around a precise and detailed explanation for the evolution of the eye. Indeed, it is even argued by creationists today that no such explanation is possible, because the eye could not possibly be the result of natural selection. This misconception stems from two failures on the part of its advocates: first, the assumption that the evolution of the eye has to be explained by defining “the eye” purely typologically, and,

second, by ascribing the actual process of the evolution of the eye as an “accident.” Once these two misconceptions are removed, the evolution of “the eye” is easily explained as the result of a complex but completely understandable interaction between natural variation and selection.

That “the eye” cannot be defined typologically is immediately obvious once we consider the multiple evolutionary origins of this organ broadly defined, e.g., the compound insect eye, the protozoan photoreceptor, the vertebrate lens eye (Oakley 2003). The failure of typological definitions in this case stems from the fact that “the eye” is an outstanding example of convergent evolution and thus is most profitably defined in terms of its function. When broadly defined functionally, “the eye” has evolved in many different animal lineages (e.g., Protista, Porifera, Ctenophora, Cnidaria, Platyhelminthes, Annelida, Mollusca, Onychophora, Arthropoda, Echinodermata, Tunicata, and Vertebrata) (Salvini-Plawen and Mayr 1977; Futuyma 1998; Oakley 2003).



Turning to its natural variation within each clade and the “accidental” (nonpredictable) nature of natural selection (Endler 1986; Grant and Grant 2002), detailed anatomical and morphological comparisons among individuals drawn from the same population indicate that this variation can be substantial, even among vertebrate species. Such natural variation, which is heritable, permits the operation of natural selection for each of the three major functions of “the eye” within individual lineages: (1) light/shadow detection, (2) the detection of the direction of incident light (orientation), and (3) image formation. Likewise, partially or entirely complete sequences in the evolution of “the perfect eye” (e.g., from simple light-sensitive epithelial cells to such highly differentiated lenticular eyes as are found in the Gastropoda, Cephalopoda, Insecta, or Vertebrata lineages) can be reconstructed because all of the various evolutionary stages are readily observed among extant members of these lineages and because some are preserved in the fossil record (Salvini-Plawen and Mayr 1977). An example, the evolution of complex lens eyes in aquatic snails, is depicted in Fig. 7A.

Likewise, computer simulations demonstrate that even with a pessimistic estimate of the amount of time required for heritable variation to obtain efficient eyes by means of the operation of natural selection is on the order of about 300,000 generations (Nilsson and Pelger 1994). These simulations (Fig. 7B) illustrate that the geologically rapid evolution of a lens with a mathematically ideal distribution of refractive index is possible in part because the proteins used to construct the lens are already present in ancestral forms. Since natural selection can operate on small random phenotypic variations, no distribution of refractive index is inaccessible mathematically. In summary, these studies (Fig. 7A, B) corroborate the fact that evolutionary novelties can arise as a result of “intensification in function” of a pre-existing structure. It should be noted that a second process, called “change in function” (Mayr 1963), is documented in the fossil record (Table 2) and gave rise to new organs such as the wings of birds (Wellnhofer 2002; Xu et al. 2003).

Conclusions

The major achievement of the modern synthesis (i.e., the unification of biology during the 1930–1950 period) was

Fig. 7 Reconstruction of the evolution of complex lens eyes in gastropods (snails) by comparison of eye anatomy in extant species (A): eye cup (*Patella*), deeper cup (*Pleurotomaria*), pinhole eye (*Haliotis*), closed eye (*Turbo*), lens eye (*Murex*, *Nucella*). The shells of two species are shown (*Patella*, a sedentary algae feeder; *Nucella*, an agile predator). Computer-generated model sequence of the evolution of a simple pit eye (B). Initial stage (1): flat patch of light-sensitive cells sandwiched between a transparent protective layer and a second layer of dark pigment. Final stage (8): camera-type lens (L) eye with a geometry similar to that found in aquatic animals (snails, cephalopods, fish) (A: adapted from Salvini-Plawen and Mayr 1977; B: adapted from Nilsson and Pelger 1994)

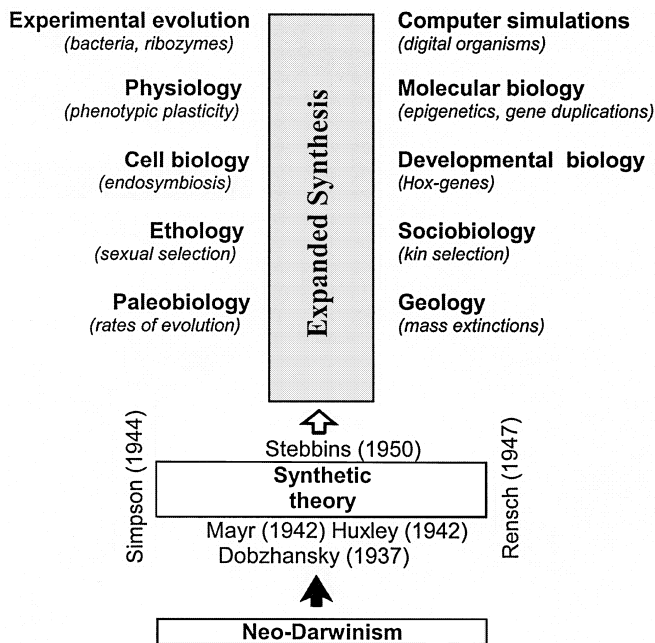


Fig. 8 Scheme illustrating the expansion of the synthetic theory of biological evolution by integration of ten additional scientific disciplines. The list is not complete, i.e., the expanded synthesis is an open system composed of many sub-theories dealing with various aspects of the evolutionary process

the attainment of a broad consensus about the mechanisms that bring about evolutionary change. This general theory, which emerged from a neo-Darwinian perspective, was a major advance in the life sciences (Fig. 1). And it continues to cast a bright light on what may be called the post-modern synthesis, one that continues to expand and elaborate our understanding of evolution as the result of the continuous and tireless exploration of virtually every branch of science, from paleobiology/geology to natural history and cell/molecular biology (Fig. 8). Indeed, the “evolution” of evolutionary theory remains as vibrant and robust today as it ever was.

It should be noted that evolutionary biology is no longer a purely academic discipline. It is now an essential part of the applied sciences. Bull and Wichman (2001) have summarized many socially relevant examples in which evolutionary principles and methods have been used to solve practical problems such as the creation of new drugs, industrial enzymes, the development of computer programs, or the management of bacterial resistance to prescribed antibiotics.

Sadly, the efforts and insights of those exploring the rich fabric of evolutionary biology continue to be challenged by those advocating “intelligent design” or some other version of creationism (Kutschera 2003b; Pennock 2003). This challenge to rational and scientific thought – one that remains insensitive to the huge body of evidence supporting evolutionary biology – is as persistent and pernicious today as it was during the time of Darwin. We have no wish to explore the delicate and sometimes

fragile relationship between religious belief and scientific enquiry. We do however draw attention to the fact that the challenge posed by creationism is serious because it jeopardizes our future as a species by virtue of rejecting science and its philosophical basis (methodological naturalism) at every level and across all disciplines. By so doing, it intrinsically rejects the benefits that science offers humanity. Scientists tend not to enter into public debates about creationism versus science, many of which are now taking place in local communities rather than in more general public forums (Pennock 2003; Gilbert 2003; Scott and Branch 2003). This reticence can have grave consequences. In our view, evolutionary biologists – indeed, all scientists – must step forward and educate the public about science in general and evolution in particular. We cannot afford to be shy or modest about what we have learned. It is our responsibility to advocate scientific thinking and to educate non-scientists.

References

- Ahlberg PE, Clack JA, Luksevics E (1996) Rapid braincase evolution between *Panderichthys* and the earliest tetrapods. *Nature* 381:61–64
- Alvarez W (1997) *T. rex* and the crater of doom. Princeton University Press, Princeton, N.J.
- Andersson M (1994) Sexual selection. Princeton University Press, Princeton, N.J.
- Arthur W (2002) The emerging conceptual framework of evolutionary developmental biology. *Nature* 415:757–764
- Bell G (1997) Selection: the mechanism of evolution. Chapman and Hall, New York
- Bengston S (1998) Animal embryos in deep time. *Nature* 391:529–530
- Benton MJ (1997) Vertebrate palaeontology (2nd edn). Chapman and Hall, London
- Benton MJ, Harper DAT (1997) Basic palaeontology. Addison Wesley Longman, Essex
- Benton MJ, Pearson PN (2001) Speciation in the fossil record. *Trends Ecol Evol* 16:405–411
- Benton MJ, Twitchett RJ (2003) How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol Evol* 18:358–365
- Beurton PJ (2002) Ernst Mayr through time on the biological species concept: a conceptual analysis. *Theory Biosci* 121:81–98
- Bokma F (2002) Detection of punctuated equilibrium from molecular phylogenies. *J Evol Biol* 15:1048–1055
- Bowler PJ (1984) Evolution: the history of an idea. University of California Press, Berkeley, Calif.
- Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* 13:115–155
- Briggs DEG, Crowther PR (eds) (1990) Palaeobiology: a synthesis. Blackwell Science, Oxford
- Bull JJ, Wichman HA (2001) Applied evolution. *Annu Rev Ecol Syst* 32:183–217
- Burt A (2000) Perspective: sex, recombination and the efficacy of selection: was Weismann right? *Evolution* 54:337–351
- Butterfield NJ (2000) *Bangiomorpha pubescens* n. gen., n. sp: implications for the evolution of sex, multicellularity and the Mesoproterozoic/Neoproterozoic radiation of eukaryotes. *Paleobiology* 26:386–404
- Butterfield NJ (2001) Paleobiology of the late Mesoproterozoic (ca. 1200 Ma) Huntingdon Formation, Somerset Island, arctic Canada. *Precambrian Res* 111:235–256
- Carroll RL (1997) Patterns and processes of vertebrate evolution. Cambridge University Press, Cambridge

- Carroll RL (2000) Towards a new evolutionary synthesis. *Trends Ecol Evol* 15:27–32
- Carroll RL (2002) Evolution of the capacity to evolve. *J Evol Biol* 15:911–921
- Carroll SB (2001) Chance and necessity: the evolution of morphological complexity and diversity. *Nature* 409:1102–1109
- Clack JA (2002) An early tetrapod from Romers gap. *Nature* 418:72–76
- Clutton-Brock T (2002) Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72
- Conway Morris S (2000) The Cambrian “explosion”: slow-fuse or megatonnage? *Proc Natl Acad Sci USA* 97:4426–4429
- Cowen R (2000) History of life. (3rd edn). Blackwell Science, Oxford
- Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London
- Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London
- Darwin C (1872) On the origin of species (6th edn). John Murray, London
- Darwin C, Wallace A (1858) On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. *J Proc Linn Soc Lond* 3:45–63
- Dawkins R (2002) The reading of the Darwin-Wallace papers commemorated – in the Royal Academy of Arts. *Linnean* 18:17–24
- Dobzhansky T (1937) Genetics and the origin of species. Columbia University Press, New York
- Doebley J, Lukens L (1998) Transcriptional regulators and the evolution of plant form. *Plant Cell* 10:1075–1082
- Domning DP (2001) The earliest known fully quadrupedal sirenia. *Nature* 413:625–627
- Elena SF, Lenski RE (2003) Evolution experiments with microorganisms: the dynamics and genetic bases of adaptation. *Nat Rev Genet* 4:457–469
- Elena SF, Cooper VS, Lenski RE (1996) Punctuated evolution caused by selection of rare beneficial mutations. *Science* 272:1802–1804
- Ender JA (1986) Natural selection in the wild. Princeton University Press, Princeton, N.J.
- Erwin DH (2000) Macroevolution is more than repeated rounds of microevolution. *Evol Dev* 2:78–84
- Fay JC, Wyckoff GJ, Wu C-I (2002) Testing the neutral theory of molecular evolution with genomic data from *Drosophila*. *Nature* 415:1024–1026
- Fisher RA (1930) The genetical theory of natural selection. Clarendon Press, Oxford
- Fleagle JG (2001) The unfused synthesis. *Evol Anthropol* 10:191
- Futuyma DJ (1995) Science on trial: the case for evolution. Sinauer, Sunderland, Mass.
- Futuyma DJ (1998) Evolutionary biology (3rd edn). Sinauer, Sunderland, Mass.
- Gilbert SF (2003) Opening Darwin’s black box: teaching evolution through developmental genetics. *Nat Rev Genet* 4:735–741
- Golding GB, Dean AM (1998) The structural basis of molecular adaptation. *Mol Biol Evol* 15:355–369
- Goldschmidt R (1940) The material basis of evolution. Yale University Press, New Haven, Conn.
- Gould SJ (2002) The structure of evolutionary theory. Harvard University Press, Cambridge, Mass.
- Gould SJ, Eldredge N (1993) Punctuated equilibrium comes of age. *Nature* 366:223–227
- Grant PR, Grant BR (2002) Unpredictable evolution in a 30-year study of Darwin’s finches. *Science* 296:707–711
- Griffin AS, West SA (2002) Kin selection: fact and fiction. *Trends Ecol Evol* 17:15–21
- Haeckel E (1874) The gastraea theory, the phylogenetic classification of the animal kingdom and the homology of the germ-lamellae. *Q J Microsc Soc* 14:142–165
- Hall BK (1999) Evolutionary developmental biology. Kluwer Academic, Dordrecht
- Hallam A, Wignall PB (1997) Mass extinctions and their aftermath. Oxford University Press, Oxford
- Halliday AN (2001) In the beginning. *Nature* 409:144–145
- Hamilton WD (1972) Altruism and related phenomena, mainly in social insects. *Annu Rev Ecol Syst* 3:193–232
- Hamilton WD, Axelrod R, Tanese R (1990) Sexual reproduction as an adaptation to resist parasites: a review. *Proc Natl Acad Sci USA* 87:3566–3573
- Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, Mass.
- Howard DJ, Berlocher SH (eds) (1998) Endless forms: species and speciation. Oxford University Press, New York
- Huxley JS (1942) Evolution: the modern synthesis. Allen and Unwin, London
- Jin YG, Wang Y, Wang W, Shang QH, Cao CQ, Erwin DH (2000) Pattern of marine mass extinction near the Permian–Triassic boundary in South China. *Science* 289:432–436
- Jost J (2003) On the notion of fitness, or: the selfish ancestor. *Theory Biosci* 121:331–350
- Joyce GF (2002) The antiquity of RNA-based evolution. *Nature* 418:214–221
- Junker T (2004) Die zweite Darwinsche Revolution. Geschichte des Synthetischen Darwinismus in Deutschland 1924 bis 1950. Basiliken, Marburg, Germany
- Junker T, Engels E-M (eds) (1999) Die Entstehung der Synthetischen Theorie. Beiträge zur Geschichte der Evolutionsbiologie in Deutschland 1930–1950. Verlag für Wissenschaft und Bildung, Berlin
- Junker T, Höbfeld U (2001) Die Entdeckung der Evolution. Eine revolutionäre Theorie und ihre Geschichte. Wissenschaftliche Buchgesellschaft, Darmstadt, Germany
- Kakutani T (2002) Epi-alleles in plants: inheritance of epigenetic information over generations. *Plant Cell Physiol* 43:1106–1111
- Kellogg EA (2000) The grasses: a case study in macroevolution. *Annu Rev Ecol Syst* 31:217–238
- Kemp TS (1999) Fossils and evolution. Oxford University Press, Oxford
- Klak C, Reeves G, Hedderson T (2004) Unmatched tempo of evolution in Southern African semi-desert ice plants. *Nature* 427:63–65
- Knoll AH (1999) A new molecular window on early life. *Science* 285:1025–1026
- Knoll AH (2003) Life on a young planet: the first three billion years of evolution on earth. Princeton University Press, Princeton, N.J.
- Krebs JR, Davies NB (1993) An introduction to behavioural ecology (3rd edn). Blackwell Science, Oxford
- Kutschera U (2001) Evolutionsbiologie. Eine allgemeine Einführung. Parey, Berlin
- Kutschera U (2002) Bacterial colonization of sunflower cotyledons during seed germination. *J Appl Bot* 76:96–98
- Kutschera U (2003a) A comparative analysis of the Darwin–Wallace papers and the development of the concept of natural selection. *Theory Biosci* 122:343–359
- Kutschera U (2003b) Designer scientific literature. *Nature* 423:116
- Kutschera U, Wirtz P (2001) The evolution of parental care in freshwater leeches. *Theory Biosci* 120:115–137
- Lee MSY (1996) Correlated progression and the origin of turtles. *Nature* 379:812–815
- Lenski RE, Travisano M (1994) Dynamics of adaptation and diversification: a 10000-generation experiment with bacterial populations. *Proc Natl Acad Sci USA* 91:6808–6814
- Lenski RE, Ofria C, Pennock RT, Adami C (2003) The evolutionary origin of complex features. *Nature* 423:139–144
- Levin DA (2000) The origin, expansion, and demise of plant species. Oxford University Press, Oxford
- Mahner M, Bunge M (1997) Foundations of biophilosophy. Springer, Berlin Heidelberg New York
- Margulis L (1993) Symbiosis in cell evolution: microbial communities in the Archean and Proterozoic eons (2nd edn). WH Freeman, New York

- Margulis L, Schwartz KV (1998) Five kingdoms: an illustrated guide to the phyla of life on Earth (3rd edn). WH Freeman, New York
- Martin W, Borst P (2003) Secondary loss of chloroplasts in trypanosomes. *Proc Natl Acad Sci USA* 100:765–767
- Martin W, Russell MJ (2003) On the origins of cells: a hypothesis for the evolutionary transitions from abiotic geochemistry to chemoautotrophic prokaryotes, and from prokaryotes to nucleated cells. *Philos Trans R Soc Lond B* 358:59–85
- Martin W, Hoffmeister M, Rotte C, Henze K (2001) An overview of endosymbiotic models for the origins of eukaryotes, their ATP-producing organelles (mitochondria and hydrogenosomes), and their heterotrophic lifestyle. *Biol Chem* 382:1521–1539
- Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York
- Mayr E (1963) Animal species and evolution. Harvard University Press, Cambridge, Mass.
- Mayr E (1982) The growth of biological thought: diversity, evolution and inheritance. Harvard University Press, Cambridge, Mass.
- Mayr E (1988) Toward a new philosophy of biology: observations of an evolutionist. Harvard University Press, Cambridge, Mass.
- Mayr E (1991) One long argument: Charles Darwin and the genesis of modern evolutionary thought. Harvard University Press, Cambridge, Mass.
- Mayr E (1992) A local flora and the biological species concept. *Am J Bot* 79:222–238
- Mayr E (1993) What was the evolutionary synthesis? *Trends Ecol Evol* 8:31–34
- Mayr E (1997) This is biology: the science of the living world. Harvard University Press, Cambridge, Mass.
- Mayr E (2001) What evolution is. Basic Books, New York
- Mayr E (2002) Die Autonomie der Biologie. *Naturwiss Rundschau* 55:23–29
- Mayr E, Diamond J (2001) The birds of northern Melanesia. Oxford University Press, New York
- Mayr E, Provine W (eds) (1980) The evolutionary synthesis: perspectives on the unification of biology. Harvard University Press, Cambridge, Mass.
- Meyer A (1993) Phylogenetic relationships and evolutionary processes in East African cichlid fishes. *Trends Ecol Evol* 8:279–284
- Meyer A (1998) Hox gene variation and evolution. *Nature* 391:225–228
- Meyer A, Zardoya R (2003) Recent advances in the (molecular) phylogeny of vertebrates. *Annu Rev Ecol Syst* 34:311–338
- Meyer A, Kocher TD, Basasibwaki P, Wilson AC (1990) Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. *Nature* 347:550–553
- Møller AP, Alatalo RV (1999) Good-genes effects in sexual selection. *Proc R Soc Lond B* 266:85–91
- Motani R, Minoura N, Ando T (1998) Ichthyosaur relationships illuminated by new primitive skeletons from Japan. *Nature* 393:255–257
- Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago
- Niklas KJ (1997) The evolutionary biology of plants. University of Chicago Press, Chicago
- Niklas KJ (1999) Evolutionary walks through a land plant morphospace. *J Exp Bot* 50:39–52
- Niklas KJ (2000a) The evolution of plant body plants: a biomechanical perspective. *Ann Bot* 85:411–438
- Niklas KJ (2000b) Modeling fossil plant form–function relationships: a critique. In: Erwin DH, Wing SL (eds) Deep time: paleobiology's perspective. Paleontological Society, Kans., pp 289–304
- Nilsson D-E, Pelger S (1994) A pessimistic estimate of the time required for an eye to evolve. *Proc R Soc Lond B* 256:53–58
- Oakley TH (2003) The eye as a replicating and diverging, modular developmental unit. *Trends Ecol Evol* 18:623–627
- Pace NR (2001) The universal nature of biochemistry. *Proc Natl Acad Sci USA* 98:805–808
- Page RDM, Holmes EC (1998) Molecular evolution: a phylogenetic approach. Blackwell Science, Oxford
- Panhuis T, Butlin R, Zuk M, Tregenza T (2001) Sexual selection and speciation. *Trends Ecol Evol* 16:364–371
- Pennisi E (2003) Colourful males flaunt their health. *Science* 300:29–30
- Pennock RT (2003) Creationism and intelligent design. *Annu Rev Genom Hum Genet* 4:143–163
- Pigliucci M (2001) Phenotypic plasticity: beyond nature and nurture. Johns Hopkins University Press, Baltimore, Md.
- Raup DM (1994) The role of extinction in evolution. *Proc Natl Acad Sci USA* 91:6758–6763
- Reif W-E, Junker T, Hoßfeld U (2000) The synthetic theory of evolution: general problems and the German contribution to the synthesis. *Theory Biosci* 119:41–91
- Rensch B (1947) Neuere Probleme der Abstammungslehre. Die transspezifische Evolution. Enke, Stuttgart, Germany
- Rice WR, Chippindale AK (2001) Sexual recombination and the power of natural selection. *Science* 294:555–559
- Romanes GJ (1895) Darwin and after Darwin, vol 2. Open Court, Chicago
- Ronshaugen M, McGinnis N, McGinnis W (2002) Hox protein mutation and macroevolution of the insect body plan. *Nature* 415:914–917
- Rubidge BS, Sidor CA (2001) Evolutionary patterns among Permian–Triassic therapsids. *Annu Rev Ecol Syst* 32:449–480
- Ruse M (1996) Monad to man: the concept of progress in evolutionary biology. Harvard University Press, Cambridge, Mass.
- Sage RF, Monson RK (eds) (1999) C4 plant biology. Academic Press, London
- Salvini-Plawen LV, Mayr E (1977) On the evolution of photoreceptors and eyes. *Evol Biol* 10:207–263
- Schierwater B, DeSalle R (2001) Current problems with the zootype and the early evolution of Hox genes. *J Exp Zool* 291:169–174
- Schilthuizen M (2001) Frogs, flies and dandelions: the making of species. Oxford University Press, Oxford
- Schluter D (2001) The ecology of adaptive radiation. Oxford University Press, Oxford
- Schopf JW (1993) Microfossils of the Early Archean Apex chert: new evidence of the antiquity of life. *Science* 260:640–646
- Schopf JW (1999) Cradle of life: the discovery of Earth's earliest fossils. Princeton University Press, Princeton, N.J.
- Schuster P (2001) Evolution *in silico* and *in vitro*: the RNA model. *Biol Chem* 382:1301–1314
- Schütze P, Freitag H, Weising K (2003) An integrated molecular and morphological study of the subfamily Suaedoideae Ulbr (Chenopodiaceae). *Plant Syst Evol* 239:257–286
- Scott EC, Branch G (2003) Evolution: what's wrong with 'teaching the controversy'. *Trends Ecol Evol* 18:499–502
- Seligmann H, Amzallag GN (2002) Chemical interactions between amino acid and RNA: multiplicity of levels of specificity explains origin of the genetic code. *Naturwissenschaften* 89:542–551
- Sereno PC (1999) The evolution of dinosaurs. *Science* 284:2137–2147
- Shen Y, Buick R, Canfield DE (2001) Isotopic evidence for microbial sulphate reduction in the early Archean era. *Nature* 410:77–81
- Simons AM (2002) The continuity of microevolution and macroevolution. *J Evol Biol* 15:688–701
- Simpson GG (1944) Tempo and mode in evolution. Columbia University Press, New York
- Simpson GG (1949) The meaning of evolution: a study of the history of life and of its significance for man. Yale University Press, New Haven, Conn.
- Smocovitis VB (1996) Unifying biology: the evolutionary synthesis and evolutionary biology. Princeton University Press, Princeton, N.J.

- Soltis PS, Soltis DE (2000) The role of genetic and genomic attributes in the success of polyploids. *Proc Natl Acad Sci USA* 97:7051–1057
- Stanley SM (1979) *Macroevolution: pattern and process*. WH Freeman, San Francisco
- Stanley SM (1985) Rates of evolution. *Paleobiology* 11:13–26
- Stebbins GL (1950) *Variation and evolution in plants*. Columbia University Press, New York
- Stebbins GL (1971) *Process of organic evolution* (2nd edn). Prentice-Hall, N.J.
- Storch V, Welsch U, Wink M (2001) *Evolutionsbiologie*. Springer, Berlin Heidelberg New York
- Sultan SE (2000) Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci* 5:537–542
- Sun G, Ji Q, Dilcher DL, Zheng S, Nixon KC, Wang X (2002) *Archaeofractaceae*, a new basal angiosperm family. *Science* 296:899–904
- Tchernov E, Rieppel O, Zaher H, Polcyn MJ, Jacobs LL (2000) A fossil snake with limbs. *Science* 287:2010–2012
- Thewissen JGM, Williams EM (2002) The early radiation of cetacea (mammalia): evolutionary pattern and developmental correlations. *Annu Rev Ecol Syst* 33:73–90
- Trillmich F, Diesel R (2002) Parental care. In: Bateson PPG, Alleva E (eds) *Encyclopedia of biology*. Academic Press, New York, pp 313–325
- Wahl LM, Gerrish PJ (2001) The probability that beneficial mutations are lost in populations with periodic bottlenecks. *Evolution* 55:2606–2610
- Wallace AR (1889) *Darwinism. An exposition of the theory of natural selection with some of its applications*. MacMillan, London
- Weismann A (1892) *Das Keimplasma. Eine Theorie der Vererbung*. Fischer, Jena, Germany
- Wellnhofer P (2002) Die befiederten Dinosaurier Chinas. *Naturwiss Rundschau* 55:465–477
- Whitman WB, Coleman DC, Wiebe WJ (1998) Prokaryotes: the unseen majority. *Proc Natl Acad Sci USA* 95:6578–6583
- Wilf P, Johnson KR, Huber BT (2003) Correlated terrestrial and marine evidence for global climate changes before mass extinction at the Cretaceous-Paleogene boundary. *Proc Natl Acad Sci USA* 100:599–604
- Woese C (2002) On the evolution of cells. *Proc Natl Acad Sci USA* 99:8742–8747
- Wood B (2002) Hominid revelations from Chad. *Nature* 418:133–135
- Xu X, Zhou Z, Wang X, Kuang X, Zhang F, Du X (2003) Four-winged dinosaurs from China. *Nature* 421:335–340
- Zhang J (2003) Evolution by gene duplication: an update. *Trends Ecol Evol* 18:292–298
- Zhou Z, Zheng S (2003) The missing link in *Ginkgo* evolution. *Nature* 423:821–822
- Zimmer C (1998) *At the water's edge: macroevolution and the transformation of life*. Free Press, New York