

Symbiogenesis, natural selection, and the dynamic Earth

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Abstract One century ago, Constantin S. Mereschkowsky introduced the symbiogenesis theory for the origin of chloroplasts from ancient cyanobacteria which was later supplemented by Ivan E. Wallin's proposal that mitochondria evolved from once free-living bacteria. Today, this Mereschkowsky–Wallin principle of symbiogenesis, which is also known as the serial primary endosymbiosis theory, explains the evolutionary origin of eukaryotic cells and hence the emergence of all eukaryotes (protists, fungi, animals and plants). In 1858, the concept of natural selection was described independently by Charles Darwin and Alfred R. Wallace. In the same year, Antonio Snider-Pellegrini proposed the idea of shifting continents, which was later expanded by Alfred Wegener, who published his theory of continental drift eight decades ago. Today, directional selection is accepted as the major cause of adaptive evolution within natural populations of micro- and macro-organisms and the theory of the dynamic Earth (plate tectonics) is well supported. In this article, I combine the processes and principles of symbiogenesis, natural selection and the dynamic Earth and propose an integrative 'synade-model' of macroevolution which takes into account organisms from all five Kingdoms of life.

Keywords Darwin · Dynamic Earth · Macroevolution · Natural selection · Symbiogenesis · Synade-model

Introduction

The Russian botanist and cytologist Constantin S. Mereschkowsky (1855–1921), the English naturalist Alfred Russel Wallace (1823–1913), and the French geographer Antonio Snider-Pellegrini (1802–1885) became some of the founding fathers of novel concepts and theories in the emerging evolutionary sciences. One century ago (January 1909), Mereschkowsky wrote the preface of his landmark paper on symbiogenesis and the origin of higher organisms, such as plants, which was published one year later (Geus and Höxtermann 2007). In 1858, the principle of natural selection was proposed independently by Wallace and Charles Darwin (1809–1882) (Beccaloni and Smith 2008; Kutschera 2003, 2008a). In the same year, the concept of shifting continents was discovered and published by Snider-Pellegrini (LeGrand 1988; Levin 2003).

In this article, which marks the 100th and 150th anniversaries, respectively, of these major publications, I describe the original hypotheses of Mereschkowsky, Wallace and Snider-Pellegrini as well as their developments into established scientific theories. In addition, I briefly discuss the general significance of the scientific work of these naturalists. In the last section I combine the facts presented here and deduce a descriptive "synade-model" of macroevolution that takes into account representative taxa from all five kingdoms of life on Earth.

The Mereschkowsky–Wallin principle of symbiogenesis

In a remarkable paper published in 1905, C. S. Mereschkowsky concluded that the chloroplasts (plastids) of green algae and land plants were once free-living cyanobacteria. This endosymbiotic hypothesis for the origin of plant

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organelles was based on several lines of evidence—data from the literature, and novel microscopic observations by the author (Mereschkowsky 1905). In his preface to a subsequent article (signed 11 January 1909), which was published in the following year, Mereschkowsky (1910) wrote that his intention was to introduce a new theory on the origin of the organisms on Earth. He explicitly pointed out that the attempts of Charles Darwin, Ernst Haeckel and others to solve this problem have been unsuccessful, because not all pertinent facts were available when these naturalists published their books (Darwin 1859, 1872; Haeckel 1877). He argued that so many novel findings in the fields of cytology, biochemistry and physiology have accumulated, notably with respect to lower (unicellular) organisms since Darwin's era, the time has come to propose a new theory.

Based on the principle of symbiosis (i.e., the union of two different organisms whereby both partners mutually benefit), Mereschkowsky (1910) coined the term *symbiogenesis theory*. The principle of symbiogenesis, as envisioned by Mereschkowsky, is based on an analogy between phagocytosis of extant unicellular eukaryotes such as amoebae (Fig. 1a) and hypothetical processes that may have occurred millions of years ago in the oceans of the young Earth. Mereschkowsky's symbiogenesis hypothesis explained the origin of the chloroplasts from ancient cyanobacteria and hence gave insight into the first steps in the evolution of the plant kingdom (Sapp et al. 2002).

Six years after Mereschkowsky's death, the Russian cytologist Ivan E. Wallin (1883–1969) proposed that the mitochondria of eukaryotic cells are descendants of ancient, once free-living bacteria (Wallin 1927). In addition, he suggested that the primary source of genetic novelty for speciation events was a periodic, repeated fusion of bacterial endosymbionts with eukaryotic host cells. However, this second hypothesis of Wallin is not supported by empirical data (Kutschera and Niklas 2005).

Evolutionary origin of multicellular organisms

Endosymbiotic events that occurred ca. 2,200–1,500 million years ago (mya) in the oceans gave rise to the first eukaryotic cells (Fig. 1b). Today, they are described within the framework of the serial primary endosymbiosis theory for cell evolution, which is supported by a solid body of empirical data (see Margulis 1993, 1996 for classic reviews and Kutschera and Niklas 2004, 2005 for more recent accounts).

The capture of an ancient α -proteobacterium by a nucleus-containing (eukaryotic) host cell that resembled extant amitochondriate protists occurred probably only once in evolution. After a subsequent intracellular

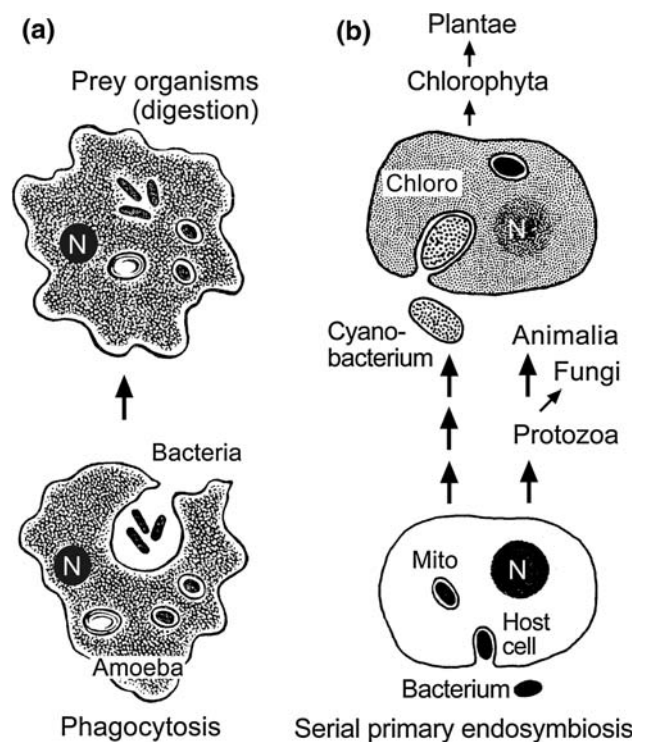


Fig. 1 Phagocytosis and primary serial endosymbiosis. In phagocytosis, which is a kind of cellular eating, an eukaryotic cell such as an amoeba engulfs prey organisms (bacteria), packages it in a food vacuole and digests it (a). Diagrammatic rendering of the symbiogenetic origin of mitochondria and chloroplasts during the proterozoic (ca. 2,200–1,500 million years ago, see Fig. 7) according to the serial primary endosymbiosis theory (b). A free-living α -proteobacterial ancestor (*Bacterium*) is engulfed by an eukaryotic host cell with nucleus (N) and reduced (domesticated) to an organelle (mitochondrion, Mito). Millions of years later, this heterotrophic cell engulfs and domesticates an ancient cyanobacterium, which evolved into a chloroplast (Chloro). The phylogeny of the multicellular Fungi, Animalia and Plantae via unicellular ancestors (Protozoa, Chlorophyta) is indicated. Mitochondria and chloroplasts multiply in the cytoplasm of their host cell and are inherited from the parent cell

domestication process, the once free-living α -proteobacterium was reduced to an organelle for the production and export of energy-rich adenosine triphosphate (ATP). In a subsequent primary endosymbiotic event an ancient cyanobacterium was engulfed, domesticated and finally enslaved to become a photosynthetic, green organelle (chloroplast). These acquisitions of an α -proteobacterial and a cyanobacterial endosymbiont (i.e., the ancestral mitochondrion and chloroplast, respectively), organelles that multiply in the cytoplasm by binary fission and are inherited via the egg cell, were momentous events in the history of life on Earth. Molecular phylogenetic analyses of plastid and nuclear genes led to the conclusion that only a single, ancient primary plastid endosymbiosis had persisted (Cavalier-Smith 2000; Reyes-Prieto et al. 2007).

All multicellular organisms consist of eukaryotic cells, which are much more complex than prokaryotes (bacteria, cyanobacteria). Without the emergence of mitochondria- and chloroplast-containing eukaryotic cells via serial primary endosymbiosis (i.e., symbiogenesis) the biosphere would exist exclusively of prokaryotes, but no protists, chlorophytes (green algae) and their multicellular descendants could have evolved (Fig. 1b). Hence, animals (including humans), fungi and plants emerged as a result of ancient invasions of prokaryotes into primitive eukaryotic cells. This merger of two cell types to create novel unicellular organisms (the Mereschkowsky–Wallin principle of symbiogenesis) was a key macroevolutionary process in the development of life on Earth (Margulis 1993, 1996; Niklas 1997; Kutschera and Niklas 2005, 2008; Reyes-Prieto et al. 2007; Bowman et al. 2007; Kutschera 2008b).

It should be noted that ancient secondary endosymbiotic events, i.e., the incorporation and enslavement of unicellular algae by heterotrophic eukaryotic host cells, resulted in chimeric “monster organisms” such as euglenids and dinoflagellates. Today, these photosynthetic protists represent the majority of extant phytoplankton in marine and freshwater ecosystems of the Earth and are the dominant photosynthetic primary producers in the oceans (Cavalier-Smith 2000; Knoll 2003; Reyes-Prieto et al. 2007; Kutschera and Niklas 2008; Falkowski and Isozaki 2008).

The Darwin–Wallace principle of natural selection

In February 1858, during a stay in the Malay Archipelago, Alfred R. Wallace connected the concept of Robert Malthus (1766–1834) on the limits of population growth to the well-known fact of biological variability. He postulated a new mechanism that may explain the phylogenetic development of new phenotypic variants and species in natural populations of animals based on these findings. Since Wallace had begun an ongoing correspondence with Charles Darwin 2 years earlier, he sent off a summary of his ideas. Darwin, as the well-known story goes, had been working on a very similar concept over the past 20 years, and, like Wallace, was impressed by the thesis of Malthus. He was shocked when he read the phrase “The life of wild animals is a struggle for existence” and, as a result, contacted the geologist Charles Lyell (1797–1875) to ask for advice. Lyell and the botanist Joseph Hooker (1817–1911) decided to publish Wallace’s “Ternate-essay” together with some unpublished fragments from Darwin’s manuscripts on natural selection and the principle of artificial selection by man. These papers were read at the next meeting of the Linnean Society on July 1, 1858 and published in Volume 3 of the *Proceedings of the*

Linnean Society London on August 20 of the same year (Shermer 2002).

Based on the original articles (Darwin and Wallace 1858), the principle of natural selection (Fig. 2a) can be summarized as follows:

1. Overproduction (doctrine of Robert Malthus):

C. Darwin: “Every being (even the elephant) breeds at such a rate that in a few years ... the surface of the earth would not hold the progeny of one pair”.

A. R. Wallace: “A simple calculation will show that in fifteen years each pair of birds would have increased to nearly ten millions”.

2. Struggle for life/existence and variability:

C. Darwin: “Only a few of those annually born can live to propagate their kind (struggle for life) ... individuals ... will be occasionally born with slight variation”.

A. R. Wallace: “The numbers that die annually must be immense ... those that prolong their existence can only be the most perfect in health and vigour (struggle for existence) ... varieties do frequently occur”.

3. Transformation of species:

C. Darwin: “Each new variety or species, when formed, will generally take the place of, and thus exterminate, its less well-fitted parent”.

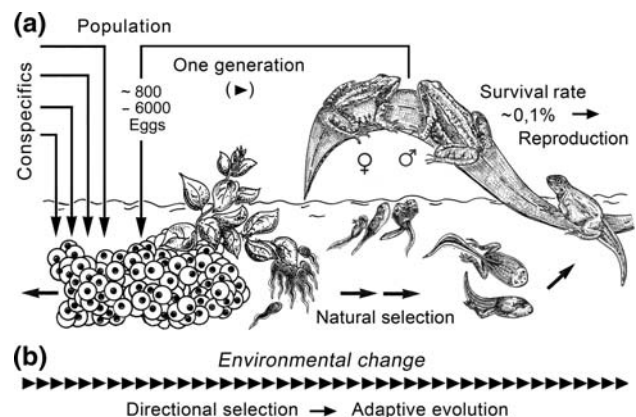


Fig. 2 Illustration of the Darwin–Wallace principle of natural selection, one of the basic concepts of modern biology (a). Under optimal environmental conditions, waterfrogs (members of the *Rana esculenta*–*R. lessonae* species complex) produce thousands of fertilized eggs per pair. However, due to the limited supply of resources, there is competition among the individuals that differ in heritable traits, which leads to a struggle for existence (or life). As a result, natural selection, i.e., the elimination of the less favourable (unfit) variants within the population, leads to the survival and reproduction of the best adapted animals (on average two individuals among thousands of conspecifics). In natural populations, the average survival rate from the egg stage to first reproduction is about 0.1% (data from Thurnheer and Reyer 2000). Gradual changes in environmental conditions (b) can cause adaptive phenotypic evolution by directional natural selection. Arrowhead one generation

A. R. Wallace: “A new variety would be in all respects better adapted to secure its safety, and to prolong its individual existence and that of the race”.

A comparative analysis of the papers published by Darwin and Wallace (1858) revealed that these naturalists did not publish the same ideas (Kutschera 2003). For instance, Wallace rejected Lamarck’s principle of an inheritance of acquired characteristics with reference to the long neck of the giraffe, a concept that Darwin (1859, 1872) integrated into his book *On the Origin of Species*. Since Darwin’s monograph of 1859, in which the theory of descent with modification by means of natural selection was described in detail, soon became a best- and long-seller, the contribution of Wallace was overshadowed by that of his colleague.

In his most influential book entitled *Darwinism*, Wallace (1889) discussed the “problem of the Origin of Species”, coined the phrase “the Darwinian theory of natural selection” and wrote that “I am the advocate of pure Darwinism”. His own significant contributions to the development of the “Darwin–Wallace principle of natural selection” (Kutschera 2008a) is only briefly described in his book. However, since Wallace (1889) rejected the idea of an inheritance of acquired characteristics and fully incorporated the discoveries and principles described by the German zoologist August Weismann (1834–1914), he became one of the founding fathers of the Neo-Darwinian theory of biological evolution (Mayr 1984, 2001; Kutschera and Niklas 2004, 2008).

The “Darwin–Wallace principle of natural selection”, which can be viewed as a process that results from differences in lifetime reproductive success (fitness) among individuals in expanding populations of organisms, has been confirmed in numerous field and laboratory studies, ranging from bacteria to humans (Endler 1986; Bell 1997; Futuyma 1998; Eldredge 1989; Seeley 1996; Gould 2002; Grant and Grant 2002; Majerus 2009; Majerus and Mundy 2003; Altwegg and Reyer 2003; Kutschera and Wirtz 2001; Kutschera and Niklas 2004; Hendry 2005; Carroll 2006; Gregory 2008; Berner et al. 2008).

A quantitative example that illustrates the strength of natural selection in free-living populations of water frogs, based on the data of Thurnheer and Reyer (2000), is depicted in Fig. 2a. During periods of gradual environmental change or under the influence of predators, directional selection can lead, over the course of many generations, to descent with modification (adaptive phenotypic evolution) (Fig. 2b). However, the more prominent case mentioned above—how the giraffe gradually evolved its long neck—has only recently been analyzed in the wild. In an elegant study, Cameron and du Toit (2007) demonstrated that competition from other herbivores, such as kudu, is the cause for giraffes eating leaves high in the

trees. Hence, interspecific competition, and therefore natural selection, was one of the “driving forces” for the evolution of the unique body form of the giraffe.

According to Klingsolver and Pfennig (2007) natural selection can be defined as the non-random differential survival and reproduction of phenotypically different individuals in populations of organisms. Those variants that do have more surviving offspring have a higher individual (Darwinian) fitness than their less productive competitors (Jost 2003). Directional phenotypic selection in nature (Fig. 2b) has been measured in the field and may be sufficiently strong enough to cause significant evolutionary change within a relatively short time period (in some case studies, less than one hundred generations, see Majerus 2009; Majerus and Mundy 2003). Moreover, Klingsolver and Pfennig (2007) provide evidence indicating that, in animal populations, competition for mates (i.e., sexual selection) appears to be stronger than natural selection acting on traits that influence survival or fecundity, but more work is required to corroborate this hypothesis.

In another article on the same topic that was published when Klingsolver and Pfennig’s account appeared in print, Nei (2007) concluded that phenotypic evolution is primarily driven by mutations of genes that interact with each other during the development of the individual and that natural selection is of secondary importance. Unfortunately, Nei (2007) largely ignored genetic recombination as a generator of phenotypic variability as well as the comprehensive list of empirical studies on the strength of natural (and sexual) selection in nature. Hence, his conclusion that natural selection is not a major cause of evolutionary change in extant populations of animals is questionable.

Okasha (2006) has described in detail how natural selection in populations of animals (including humans) can occur at different levels of organization—it may favour traits that are good for the individual as well as for a group of organisms (i.e., a sub-population). A discussion of the units of the selection in nature, which forms the core of the “multilevel selection theory”, is beyond the scope of this article.

Directional natural selection in the fossil record

Numerous empirical investigations have unequivocally shown that directional natural selection (Fig. 2b) in extant populations of organisms (bacteria, animals, plants etc.) is a major cause of adaptive evolution (Endler 1986; Bell 1997; Grant and Grant 2002; Altwegg and Reyer 2003; Kutschera and Niklas 2004; Carroll 2006; Klingsolver and Pfennig 2007; Berner et al. 2008). However, several statistical analyses of fossils have failed to reveal that natural selection had a strong influence on the evolution of

phenotypic traits. For instance, the gradual change in shell morphology in the Pliocene–Holocene Turkana Basin malacofauna may reflect biological invasions, but no traces of a “struggle for life” are apparent in these fossils (Van Bocxlaer et al. 2008). Hence, some paleobiologists are not convinced that directional selection was the causative agent which shaped the phenotype and life cycle in some well-documented groups of fossil organisms (Hunt et al. 2008). In this section, I describe four case studies that provide evidence for natural selection in the fossil record of life.

It has long been known that, at least in animals, body size correlates with a number of fitness components. According to Cope’s rule there is a tendency for species within a taxonomic group to evolve, over millions of generations, a larger body size. Although exceptions are known, Cope’s rule has been documented in the fossil record of several animal and plant taxa. A remarkable example is pterosaurs, flying diapsid reptiles which first appeared about 220 mya and became extinct at the end of the Cretaceous (65 mya) (Benton 2005, 2009). Early pterosaurs such as *Eudimorphodon* (wingspan ca. 0.4 m) were relatively small animals; the last members of this group were giants (*Quetzalcoatlus*, with a wingspan of up to 13 m). According to Klingsolver and Pfennig (2007), pterosaurs underwent their largest increase in body size during the Cretaceous period (144–65 mya), only a few million years after the first birds appeared (about 150 mya). There is circumstantial evidence to suggest that the cause for this increase in body size over hundreds of thousands of generations was competition from birds, and hence directional natural selection (Klingsolver and Pfennig 2007).

Pterosaurs and birds are not the only vertebrates that evolved the capability for flight. For instance, flying fish (Exocoetidae) can glide for 200 m or more through the air above the water, using their oscillating tale and the enlarged wing-like pectoral fins. Othenio Abel (1875–1946), the founding father of palaeobiology (Kutschera 2005, 2007), was the first to document that flying fish occurred in the fossil record as early as ca. 220 mya (Triassic). One of Abel’s well-preserved fossil species, the flying fish *Thoracopterus*, is depicted in Fig. 3a, b. Numerous studies on extant populations of exocoetids have shown that these oceanic vertebrates fly to escape large, aggressive predators like dolphins, sharks and marine mammals. These and other facts led to the conclusion that the evolution of gliding in extant and extinct flying fish was driven by predatory attacks from below and hence may document the occurrence of directional natural selection millions of years ago (Kutschera 2005).

Another striking example for predator-driven macroevolution in marine animals was described by Baumiller and Gahn (2004), who analyzed the intensity of predation through geological time. The authors selected fossilized

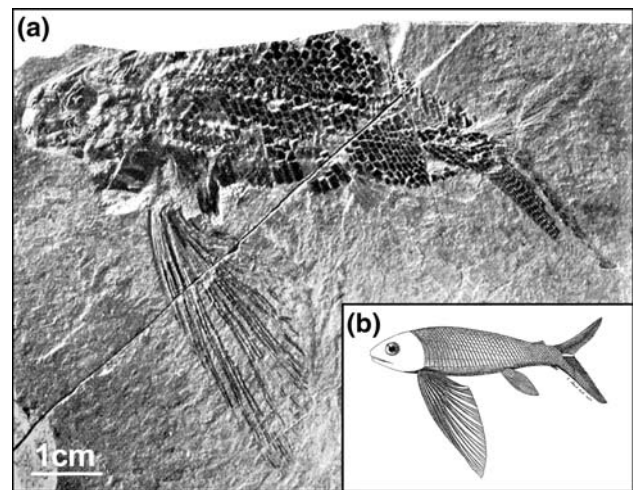


Fig. 3 Reproduction of the original fossil of the flying fish *Thoracopterus niederristi* (Triassic) (a) and reconstruction of its phenotype (b). Since all extant groups of flying fish (Exocoetidae) investigated so far use their gliding ability to escape from aquatic predators it is likely that the evolution of flight, which was associated with the enlargement of the pectoral fins and the asymmetrical tail lobes, may have been caused by predation and hence natural selection (adapted from Abel 1906)

crinoids (Fig. 4a), marine stalked filter-feeders, as model organisms and determined the frequencies of arm-regeneration during the Middle Paleozoic. About 100 my before the “Middle Paleozoic revolution”, a time period when predators such as sharks and fish diversified (ca. 380 mya), fewer than 5% of fossilized crinoids displayed damaged, re-growing arms. Millions of years later, more than 10% of the crinoid echinoderms were growing replacement arms. Baumiller and Gahn (2004) concluded that, because extant crinoids are regularly attacked by fish etc., predation was the predominant cause of arm-regeneration in these fossil invertebrates. Since most of the individuals survived these non-lethal attacks, natural selection for antipredatory traits is one possible consequence of these aggressive biological interactions that occurred during the Paleozoic.

The most convincing quantitative case study that documents directional selection in evolving populations of extinct animals is based on the 21,500-year record of defensive armament in fossil sticklebacks (fish of the genus *Gasterosteus*) from an ancient Nevada lake. Hunt et al. (2008) have shown that, over an evolutionary time of about 7,800 generations, three skeletal features (the number of dorsal spines, the size and structure of the pelvis and the number of ‘touching pterygiophores’) changed in a similar fashion. This evolutionary trend in the defensive armament of fossil sticklebacks is attributed to natural selection, presumably because of a change in predation intensity (Hunt et al. 2008).

In summary, the case studies described above indicate that directional natural selection is not only a reality in

populations of extant organisms, but may also have been a major “driving force” during the history of life on Earth.

The Snider–Wegener concept of the shifting continents

In 1669, the Danish anatomist, geologist and Catholic priest Nicolaus Steno (1638–1686) established some of the fundamental principles of paleontology and stratigraphy. Steno was one of the first to identify fossils as remnants of once living organisms and argued that rock strata are analogous to the pages in a history book (Fig. 4a, b). Based on these and other insights, Steno concluded that the surface of the Earth was not static, but dynamic and that the fossil record represents a chronology of living beings (organisms) that inhabited our planet in different eras of Earth’s history (Cutler 2003). Therefore, the scientific publications of Steno mark the beginning of historical geology.

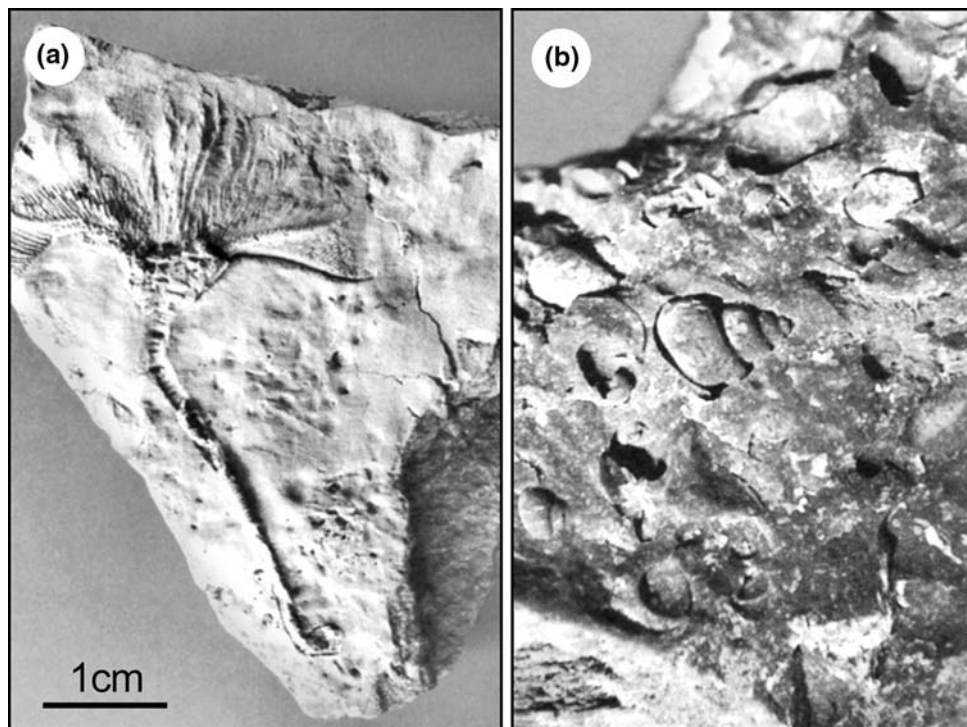
In spite of Steno’s early work, which indicated that the surface of our planet may be dynamic, the hypothesis of a static Earth prevailed. In 1858, the year before the publication of Darwin’s *Origin of Species*, Antonio Snider-Pellegrini proposed that identical plant fossils found in European and North American coal deposits may be explained if the two continents were once connected together during the Pennsylvanian period. In his book *The Creation and its Mysteries Unveiled*, Snider-Pellegrini (1858) published two maps of the Earth, depicting the

continents before and after the separation. Although the author referred to fossil plants when he proposed his concept of continental drift, Snider-Pellegrini’s primary source of inspiration was the book of Genesis in the Bible. Accordingly, he claimed that the continents were originally “created as one large piece of rock” and were blasted apart on the “sixth day” by volcanic vapours that rose through a hypothetical fissure between America and Africa (LeGrand 1988).

Snider-Pellegrini’s (1858) fanciful maps (he wrapped South America around the horn of Africa), combined with his supernatural stories like “Noah’s flood”, which was an integral part of his concept, did not convince the geologists of his time. Accordingly, the hypothesis of a static Earth prevailed again. It was the German scientist Alfred Wegener (1880–1930) who provided solid evidence for a naturalistic theory of continental drift that later revolutionized geology. Like Snider-Pellegrini (1858), Wegener examined the maps of the globe and concluded that most of the extant continents seem to fit together like a puzzle. For instance, the West African coastline fits into the east coast of South America and the Carribean Sea; a similar fit is apparent across the Pacific. Even more striking results were obtained when the submerged continental shelves were compared rather than the continents.

Based on these geographical and a number of geological observations, Wegener proposed, in his book *The origin of the continents and oceans* (1929), that the current, isolated continents were once compressed into a single proto- or

Fig. 4 Fossils of marine animals from the Cretaceous, collected on a hill in the centre of Germany. The crinoid (*Chelocrinus*), a sessile echinoderm with numerous arms (a) and snails (*Omphaloptycha*) (b) lived in a shallow marine habitat about 248 millions of years ago (adapted from Bös and Kunz 2002)



super-continent which he called Pangaea (“all lands”) (Fig. 5a). Wegener (1929) suggested that Pangaea covered about half of the Earth’s surface and was surrounded by one giant ocean called Panthalassa (“universal sea”). In addition, he noticed that some animal and plant fossils from the Paleozoic age are very similar, despite the fact that they were found on different continents. He suggested that these terrestrial organisms once lived together when the continents were united and formed his hypothetical land mass Pangaea. Wegener’s drift theory, which was summarized in his monograph of 1929, provided a novel explanation for the formation of mountains via the compression and upward folding of the edges of moving continents. Moreover, he postulated that “earthquakes and volcanism are without doubt caused by continental drift” (Wegener 1929, p. 185).

However, Wegener’s theory lacked a convincing geological mechanism to explain by which forces the large continents could drift across the surface of the Earth, as postulated by his novel concept. This inability to provide an adequate explanation for the physical forces responsible for the drift of the continental land masses and the prevailing assumption that the Earth was immovable (static) resulted in the ignorance and dismissal of Wegener’s theory.

During the late 1960s, Snider’s and Wegener’s forgotten concepts were re-discovered, supported by independent lines of evidence from geology and paleobiology, and expanded into the concept of the dynamic Earth (LeGrand 1988; Irving 2005; Nield 2007; Steinberger 2008).

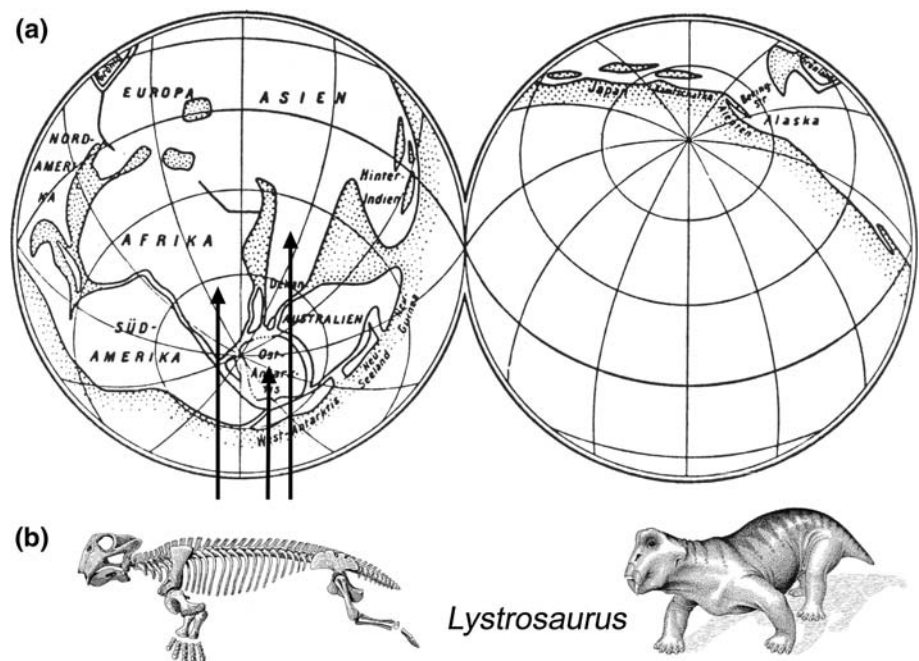
Plate tectonics and the dynamic Earth

Forty years ago, part of the upper jaw of a 200-my-old mammal-like reptile of the genus *Lystrosaurus* was discovered at Coalsack Bluff in the Transantarctic Mountains. This discovery of a fossilized terrestrial vertebrate in frozen sediments of Antarctica was a sensation—the story was announced in 1969 to the world from the front pages of leading Newspapers. Why was this fossil find so important?

Lystrosaurus (“shovel reptile”) (Fig. 5b) is an extinct genus of Early Triassic Period therapsids, which survived the end-Permian mass extinction 251 my ago (see Fig. 7). These animals became widespread in the early Mesozoic, when representatives of this group were the dominant component in tetrapod assemblages in South Africa, India and China (Benton 2003, 2005; Botha and Smith 2007). The abundant occurrence in Antarctica of fossils representing the *Lystrosaurus* fauna confirmed the close connection between this continent and Africa in the early Triassic. Since these pig-sized land vertebrates were unable to cross the oceans, these fossils confirmed Wegener’s theory of continental drift and convinced most of the doubters.

It is documented that the majority of reptiles and amphibians disappeared at the Permian-Triassic boundary (Benton 2003; Retallack et al. 2007). At this time (ca. 251 mya), world-wide explosive volcanism contributed to the most drastic era of mass extinction in the history of life (i.e., natural selection at the level of individuals and

Fig. 5 The theory of continental drift as proposed by Alfred Wegener. His classical reconstruction of the ancient Earth shows all land masses united in the hypothetical proto-continent Pangaea (a) (adapted from Wegener 1929). The later discovery of fossilized bones of the mammal-like reptile *Lystrosaurus* in 200 million year old deposits of Africa, Antarctica and India (Triassic) (b) provided convincing proof for Wegener’s theory (adapted from Botha and Smith 2007)



species). According to Carroll (2000), the coalescence of the land masses that formed Pangaea (Fig. 5a) might have restricted the heat flow from the core of the Earth, leading to the catastrophic volcanic eruptions at the end of the Permian.

With its short snout and other unique anatomical features, *Lystrosaurus* (Fig. 5 b) was obviously better adapted than most of its competing vertebrate species for the oxygen shortages that resulted from world-wide volcanism and other effects caused by the dynamic land mass of Pangaea (Benton 2003; Bralower 2008). The *Lystrosaurus*-data, together with the discovery of Permian fern leaves of the genus *Glossopteris* in sediments of South America, Africa, India, Australia and Antarctica provides solid paleontological proof of the former existence of Wegener's hypothetical proto-continent Pangaea. These findings, supplemented by new geological data on mid-oceanic ridges etc., led to the theory of plate tectonics, which is also known under the more popular term of the "dynamic Earth" (Nield 2007).

It is known that the supercontinent Pangaea existed during a 100-my-year period, from the Permian into the Jurassic. Detailed maps of this giant pole-to-pole land mass and its subsequent break-up into Gondwanaland and Laurasia were published in the 1980s (Probst 1986; Levin 2003; Gradstein et al. 2004; Irving 2005) (Fig. 6a–c). Numerous studies have shown that the break-up of Pangaea had far-reaching consequences for the evolution of terrestrial organisms (Pielou 1979)—from dinosaurs to leeches. The fossil record documents the relatively uniform dinosaurian faunas of the late Triassic and Jurassic (representative genera: *Pisanosaurus*, *Plateosaurus*, *Coelophysis*) which was later replaced by highly differentiated, phenotypically distinct faunas during the Cretaceous, with genera that inhabited Gondwanaland (South America/Africa) and Laurasia (Fig. 6b) (Sereni 1999). After the extinction of the dinosaurs at the end of the Cretaceous (65 mya), placental mammals (Placentalia) diversified and, within less than 20 my, became the dominant terrestrial vertebrates on Earth (Benton 2005). Plate tectonics explains the evolutionary diversification of the major clades of these mammals (Wildman et al. 2007; Benton 2009). During the Jurassic, the first non-specialized mammals (Eutheria), represented by *Eomaja*, originated on Pangaea. The first split between placental clades occurred during the Cretaceous when Gondwanaland and the northern continent of Laurasia became divided. Diversification among placental mammalian orders was complete by the early Cenozoic (Eocene) (Fig. 6c). Blood-feeding terrestrial leeches (Haemadipsida), soft-bodied annelids for which no unequivocal fossils are known (Kutschera and Wirtz 2001), diversified during the break-up of Gondwanaland. For instance, Madagascar and Australia are characterized by a

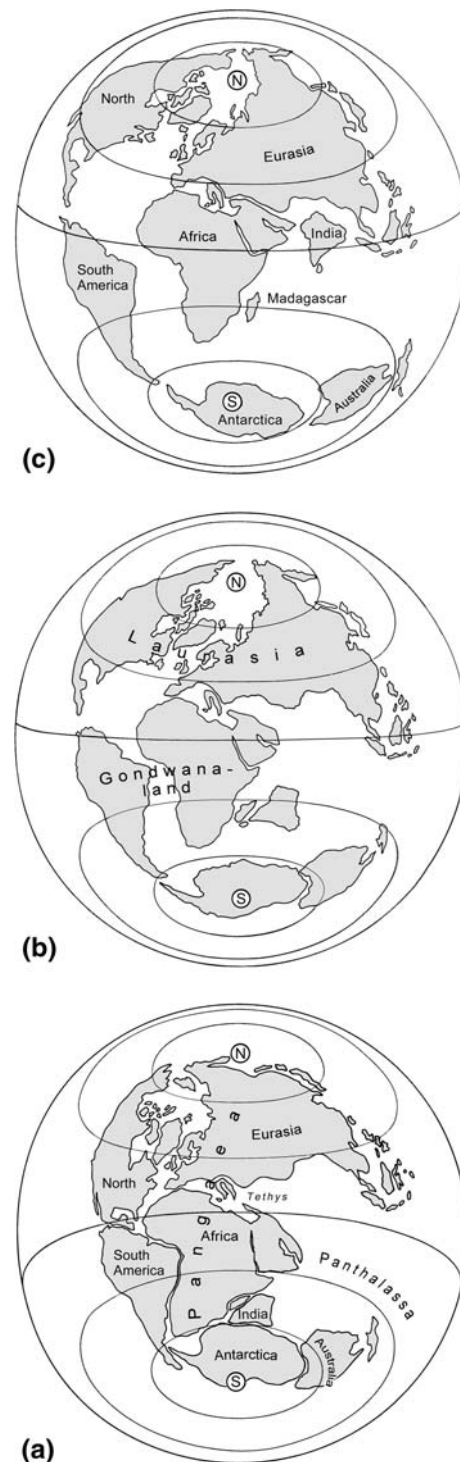


Fig. 6 The ancient super continent Pangaea (a) (Permian ~299 to 251 mya). Pangaea, which was inhabited by tetrapods of the genus *Lystrosaurus* broke up into Laurasia and Gondwanaland (b) (Cretaceous ~145 to 65 mya). Further plate motion eventually resulted in the more recent positions of the continents (c) (Eocene ~40 mya). Many studies have documented that the macroevolutionary patterns in most lineages of organisms were determined by these geological processes. mya Millions of years ago, N North Pole, S South Pole (adapted from Probst 1986)

unique fauna of terrestrial leeches that can only be understood in the light of biogeographical patterns caused by the dynamic Earth (Kutschera et al. 2007; Borda et al. 2008).

The theory of plate tectonics can be summarized as follows (Nield 2007; Steinberger 2008). Underneath the crust of the Earth, which is called the lithosphere (a solid array of tectonic plates, 5–40 km in thickness) is a malleable layer of heated rock known as the asthenosphere, which is maintained at high temperature by the natural radioactive decay of heavy chemical elements such as Uranium, Thorium, and Potassium. Since the radioactive source of heat is localized deep within the mantle of the planet, the viscous-fluid asthenosphere constantly circulates as convection currents underneath the rock-solid lithosphere. This internal heat of the Earth, which is created primarily by the radioactive decay of Uranium (Hopkins et al. 2008), is not only the cause of plate movements, but also the source of lava we observe in volcanoes and the actively changing oceans. Moreover, where plates collide, over millions of years, large mountain ranges such as the Himalayas, are pushed up. If one tectonic plate sinks below another, deep oceanic trenches and chains of marine and terrestrial volcanoes are formed. As a result, islands and hence new habitats for terrestrial organisms may be created by these geological processes. The most spectacular example is, in addition to the famous Galapagos Archipelago, the volcanic island Anak Krakatau in Indonesia, a land mass that established itself permanently above sea level in 1930. This newborn island, which contains an active volcano, has been colonized by a number of plant, bird, bat and insect species and currently serves as a “natural laboratory” for the study of island biogeography (Guo 2008).

Since earthquakes occur by far most commonly along plate boundaries and rift zones, it has been concluded that these seismic vibrations are the result of plate movements (LeGrand 1988; Nield 2007). Major earthquakes that occur along subduction zones are especially devastating, because they can trigger tsunamis (“harbour waves”). These seismic sea waves, which may either be caused by earthquakes, submarine landslides, or sometimes by the eruptions of island volcanoes, can destroy all plant and animal life on coastal areas. However, most terrestrial and aquatic bacteria, organisms that represent more than 50% of the protoplasmic biomass of the Earth (Whitman et al. 1998; Pearson 2008), usually survive these catastrophes.

It should be noted that Wegener’s original theory of 1929, which proposed a causal link between continental drift and volcanism/earthquakes, was wrong in one decisive point: the shifting continents do not plough through the ocean floor, as proposed by him. According to our new view of the dynamic Earth, both continents and the ocean floor form solid plates, which “float” on the asthenosphere.

This underlying rock is under such enormous heat and pressure that it behaves like a viscous fluid. Hence, both the continents and oceanic crust of the mobile Earth move. In view of these novel insights, Wegener’s term “continental drift” is no longer appropriate (Nield 2007).

In summary, these facts show that the dynamic Earth (Fig. 6a–c) has not only created and modified most terrestrial and aquatic habitats through the aeons of geological time, but also destroyed entire groups of organisms via volcanic eruptions and the associated release of poisonous gasses such as SO₂, SO₃ and CO₂ (mass extinctions, see Benton 2003, 2005; Retallack et al. 2007; Kring 2007; Bralower 2008).

Finally, it should be mentioned that two recent reports indicate that the Neoproterozoic “snowball ice age”, which ended about 635 my ago, may have been causally related to a long-term build-up and subsequent decline of volcanic CO₂ in the atmosphere, which reached up to 350 times the current level. A second cause for de-glaciation and warming of the “snowball Earth” could be a catastrophic release of methane hydrates (Bao et al. 2008; Kennedy et al. 2008). A recent study indicates that plate tectonics may have started more than 4,000 mya (during the Hardean aeon) (Hopkins et al. 2008), but more work is required to support this hypothesis. The geological studies summarized above show that the dynamic Earth was not only operative during the evolution of organisms that lived in the post-Cambrian era (the Phanerozoic), but also in the Precambrian, when unicellular microbes and algae-like forms of life dominated the biosphere (Knoll 2003; Levin 2003; Westall 2009).

Darwin, Mereschkowsky, and the five Kingdoms of life

When Darwin (1859) published his famous book *On the origin of species*, systematic biology (taxonomy) was still in its infancy. Throughout this great work, which delivered the organizing principle of modern biology—descent with modification or evolution—to the scientific community of the nineteenth century, Darwin referred to animals and plants. Only at the end of the last chapter he mentioned, with reference to “lower algae”, animal–plant-like intermediate forms of life, such as freshwater flagellates of the genus *Euglena*, from which all organic beings may have descended (Darwin 1872). It has recently been shown that Darwin’s classical “Proto-Euglena-hypothesis” is no longer acceptable (Kutschera and Niklas 2008). Hence, in Darwin’s time, animals, plants and some lower organisms (“infusoria”) were the model organisms of choice to deduce the principles of evolution. Bacteria, amoebae and many other micro-organisms described by nineteenth century naturalists are not mentioned by Darwin (1859, 1872).

Today we know that prokaryotic microbes (bacteria and cyanobacteria) represent the majority of life forms on Earth. Numerous studies have shown that more than 50% of the protoplasmic biomass on this planet consists of archae-, eu- and cyanobacteria (Whitman et al. 1998; Pearson 2008).

The botanist and cytologist Mereschkowsky (1905, 1910) was one of the first to integrate, in addition to animals and plants, bacteria, cyanophytes (i.e., cyanobacteria), green algae, amoebae (Protists), fungi and other “lower organisms” into an evolutionary scheme that was summarized under the term sybiogenesis—the origination of organisms by the combination of two or several living beings which enter into symbiosis. Hence, the Russian biologist was one of the founding fathers of a “several Kingdom-principle” that incorporated all known forms of life.

Today, the organisms on Earth are usually classified according to the “Five-Kingdom-System” (Margulis 1996; Barnes 1998; Margulis and Schwartz 1998), which is comprised of (1) the Monera (Bacteria or Prokaryotae), (2) the Protoctista (protists, like algae and amoebae), (3) Animalia (animals, including humans), (4) Fungi (moulds, yeasts and mushrooms) and (5) Plantae (bryophytes, ferns and seed plants). According to this classification scheme (Fig. 7) we distinguish between prokaryotic microbes, unicellular micro-organisms that consist of small bacterial cells (Kingdom 1) and the eukaryotes (Kingdoms 2–5), micro- and macro-organisms that are composed of much larger eukaryotic cells, which are defined by the presence of a nucleus (see Fig. 1).

Conclusions: The synade-model of macroevolution

Our current view of the history of life on Earth is depicted in Fig. 7. It is documented that, after the emergence of life via hypothetical proto-cells about 3,800 mya, bacteria and later cyanobacteria dominated the aquatic habitats on Earth (Knoll 2003; Schopf 2006; Westall 2009). Via the evolutionary “invention” of oxygenic photosynthesis, ancient cyanobacteria created the oxygenic atmosphere that emerged about 2,200 mya (Knoll 2003; Fischer 2008). Sybiogenesis (i.e., primary endosymbiosis) was the key macroevolutionary event that gave rise to the first eukaryotic micro-organisms: mitochondria-containing heterotrophic cells without, and photoautotrophic microbes with domesticated/enslaved cyanobacteria (chloroplasts) (Figs. 1, 7).

Directional natural selection of the best adapted individuals in expanding populations of pro- and eukaryotic micro- and macro-organisms not only “shaped” the evolving phenotypes, but was also involved in the

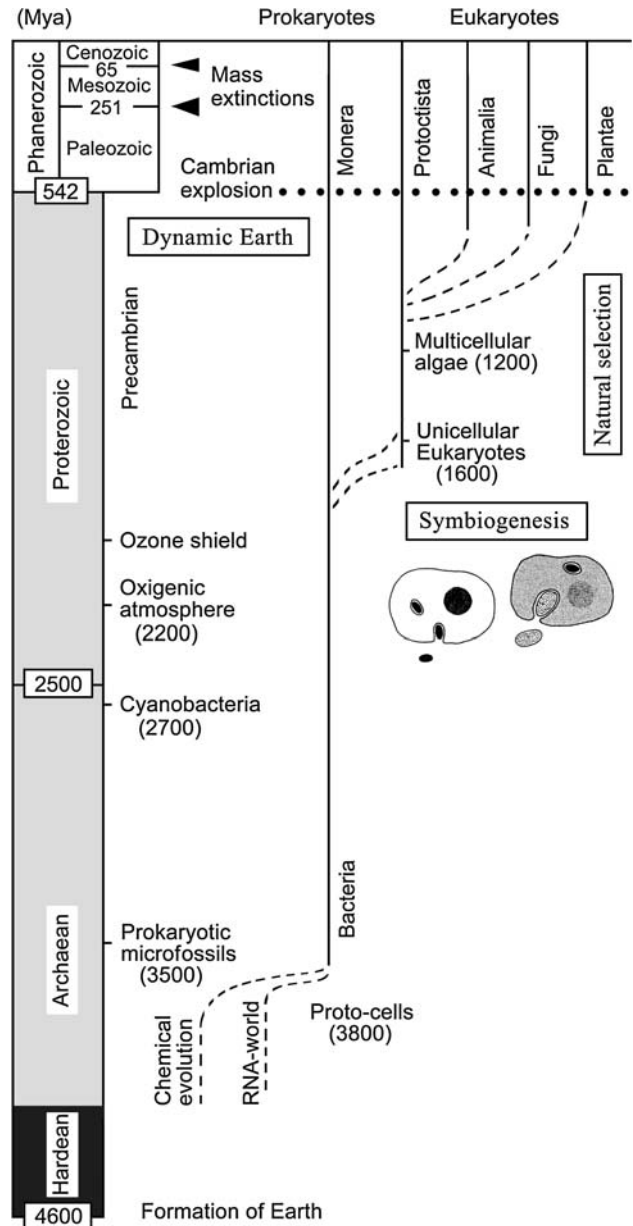


Fig. 7 Geological time scale with key events and processes in the history of life. According to this scheme, sybiogenesis (primary endosymbiosis), natural selection and the dynamic Earth (plate movements and associated phenomena like volcanism) caused, shaped and determined the phylogenetic development of all forms of life (synade-model of macroevolution). Note that the first bacteria evolved ca. 3,500 mya. Today, the descendants of these earliest prokaryotic microbes represent the dominant group of organisms on Earth (Kingdom Monera, syn. Bacteria). *Mya* Millions of years ago

diversification of life (Dobzhansky 1955; Mayr 1984, 2001; Bell 1997; Klingsolver and Pfennig 2007). The dynamic Earth, i.e., plate movements, the associated formation of mountains and deep oceans as well as volcanism, created new habitats and niches for the evolving populations of organisms in all five Kingdoms

of life. At a large scale, the major environmental changes responsible for adaptive evolution via directional selection (Fig. 2b) were caused by plate tectonics. In addition, the climate of the planet has been modified via changes in oceanic and atmospheric chemistry and global topography (Storey et al. 2007; Jablonski 2008; Benton 2009). Mass extinctions, which eliminated the last trilobites and the dinosaurs about 251 and 65 mya, respectively, were to a large extent caused by volcanism, although extra-terrestrial factors such as meteorite impacts may also have contributed to these global catastrophes (Serenio 1999; Benton 2003, 2005; Kring 2007; Bralower 2008; Jablonski 2008).

As shown in Fig. 7, symbiogenesis, natural selection and the dynamic Earth were the key processes or factors that caused and determined the course of evolution on this ever changing planet. Therefore, I propose an integrative “synade-model” of macroevolution, which is a general theory that consists of a set of fundamental principles, but does not make specific predictions (Scheiner and Willig 2008; Gregory 2008). It should be noted that neither Darwin (1859, 1872) nor the architects of the Synthetic Theory of the 1950s had incorporated symbiogenesis and the dynamic Earth into their corresponding set of explanations of evolutionary change (Dobzhansky 1955; Mayr 1984, 2001; Futuyma 1998; Eldredge 1989; Gould 2002; Haffer 2007; Levit et al. 2008). These major processes and factors of biological evolution were re-discovered and refined during the post-synthesis-era of evolutionary biology (Carroll 2000; Kutschera and Niklas 2004; Kutschera 2008b).

Finally, it should be mentioned that without the internal heat of the Earth, which is driven primarily by radioactive decay of heavy, naturally occurring elements such as Uranium (Hopkins et al. 2008), no continental land masses may ever have existed. Hence, without the dynamic Earth, life would probably still be restricted to the oceans and no land plants and terrestrial animals would ever have had a chance to evolve.

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