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EDITORIAL

Darwin's legacy

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Introduction

The year 2009 has been a year of numerous commemorations of both scientific and non-scientific achievements that contributed to the advancement of human kind. Protestants celebrated the 500th anniversary of the birth of Calvin; literary critics celebrated the 200th anniversary of the poet Edgar Allan Poe; and the musical genius Felix Mendelssohn-Bartholdy was also born 200 years ago. 2009 further marked the bicentennial of the birth of Louis Braille, the inventor of Braille; and Abraham Lincoln, the 16th president of the United States, who founded the National Academy of Sciences. Pierre Curie, famous for his work on radioactivity that he conducted together with his wife Marie Curie, was born 150 ago; as was John Dewey, a philosopher and psychologist who is recognized as one of the founding fathers of both pragmatism as well as functional psychology.

UNESCO and the International Astronomical Union dubbed 2009 the International Year of Astronomy (IYA2009, http://www.astronomy2009.org/). By doing so, astronomers celebrated the 400th anniversary of Galileo Galilei's telescopic observations as well as the publication of Johannes Kepler's *Astronomia nova* wherein he formulated the first two laws of planetary motion. 2009 also marked the last of a 3-year-long celebration of Planet Earth http://www.yearofplanetearth.org/, another UNESCO-governed initiative.

However, for evolutionary biologists and philosophers of science, 2009 will be largely remembered for its worldwide commemorations of the 200th anniversary of the birth of Charles Darwin, and the 150th anniversary of the publication of his magnum opus *On the origin of species by means of natural selection.*[1] In order to pay tribute to Darwin's major contribution to the advancement of evolutionary science, the International Union of Biological Sciences and the International Union of History and Philosophy of Science have called the year 2009 the Darwin Year http://darwin-year-2009.org/index.html.

Given that so many scientific discoveries were commemorated, COPUS, the Coalition on the Public Understanding on Science, called out 2009 as the Year of Science http://www.yearofscience2009.org/home/, in the hope to pay equal tribute to both the field of biology as well as astronomy.

2009 was indeed a year of biology. Somewhat overshadowed by the big Darwin celebrations, smaller-scaled events were held to commemorate the 200th anniversary of the publication of Lamarck's *Philosophie Zoologique*; and the 150th anniversary of the death of Alexander von Humboldt, the father of biogeography. In 1910, Constantin Mereschkowsky wrote his article on symbiogenesis entitled 'The Theory of Two Plasmas as the Basis of Symbiogenesis, a New Study for the Origins of Organisms'. The

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[1] A complete listing of all Darwin commemorations can be found at: http://darwin-online.org.uk/2009.html.

article was published in the German *Biologisches Zentralblatt*, the journal that would later evolve into the current *Theory in Biosciences*. Somewhat forgotten, but equally important for the field of symbiogenesis, was the 200th anniversary of the birth of Pierre-Joseph Van Beneden, a Belgian paleontologist and zoologist famous for distinguishing parasitism from commensalism. Finally, Henry Bergson, known for inventing the currently rejected notion of *élan vital*, was born 150 years ago.

In order to memorialize the important role these biologists played in the advancement of our understanding of the evolutionary process, a 2-day international conference was organized entitled: *Evolution today and tomorrow, Darwin evaluated by contemporary evolutionary and philosophical theories* http://cfcul.fc.ul.pt/coloquios/darwincolloquium/coloquiodarwin.htm. The conference was organized by The Centre for Philosophy of Science of the University of Lisbon (Portugal), in collaboration with the Centre for Environmental Biology of the same university, and the Lisbon Centre for Applied Psychology.

The articles presented here are a spin-off of this conference. The current volumes contain the peer-reviewed articles of a selection of the plenary and invited speakers, as well as those of scholars who were additionally invited to contribute to the volumes.

Contrary to most of the 2009 Darwin conferences, *Evolution today and tomorrow* did not exclusively focus on the impact that Darwin's theory of natural selection had on modern evolutionary biology and philosophy of biology. Rather, natural selection was examined in relation to the theories of symbiogenesis and punctuated equilibria. Emphasis was put on the controversies over the pace of evolution, the different species concepts that are associated with different evolutionary theories, and the units and levels of evolution debate. The articles that grew out of these debates are bundled in Part A of this double issue.

The conference additionally focussed on the current implementation of Neodarwinian thinking in the human and social sciences. The philosophical implications of this implementation were also the topic of investigation. The resulting articles make up Part B.

Setting the stage

> It is more than thirty years [for us it is 150 years] since *the Origin of Species* was written, but for many these questions are in no sense answered yet. In owing that it is so, we shall not honour Darwin's memory the less: for whatever may be the part which shall be finally assigned to Natural Selection, it will always be remembered that it was through Darwin's work that men saw for the first time that the problem is one which man may reasonably hope to solve. If Darwin did not solve the problem himself, he first gave us the hope of a solution, perhaps a greater thing. How great a feat this was, we who have heard it all from childhood can scarcely know. (Bateson, cited in Schwartz 1999, p. 196)

As is well known, Darwin developed his ideas on evolution after a 5-year-long travel around the world on Her Majesty's Ship Beagle. During this journey, Darwin was greatly struck by the enormous morphological variation there exists within and between species, which at times made it difficult for him to distinguish between mere variations of the same species, and different species altogether. At the same time, he was also astonished by the great affinity in features, which sometimes exists between different species, and within members of the same species (Burrow 1972).

These morphological features can be either beneficial or detrimental for those organisms, depending on how well they help organisms to obtain environmental resources such as food. Resources tend to be limited, and features can either help or disable an organism in its 'struggle for existence'.

Furthermore, Darwin (1859) was convinced that the variation displayed was hereditary, and that heritable traits were transmitted during reproduction.

It follows that organisms can only transmit their heritable features to the next generation when they are able to survive long enough to reproduce. Organisms that are disabled in their features, and that are subsequently unable to make it in the struggle for existence, die out without being able to reproduce, or they reproduce less often than others. In other words, they are not favoured by the environment. It follows that maladapted organisms are naturally weeded out, while adaptive organisms, i.e. organisms that are able to survive long enough in the environment to reproduce, are naturally 'preserved'. The subtitle of Darwin's *Origin* talks about *The preservation of favoured races in the struggle for existence*, which is just another way of stating that adapted organisms are naturally selected by the environment wherein a struggle for resources takes place.

As a consequence, organisms appear to be a perfect fit for their environment, and adaptation can be measured by the number of successful descendents (called fitness).

Because adaptive traits get naturally selected, and maladaptive traits die out, the variational traits get reshuffled over subsequent generations, resulting in descent with modification. In the long run, this modification can become so enormous that the gap with the parental species has become sufficiently wide to recognize the descendents as part of a new species. Furthermore, maladaptation can lead to extinction. Thus species are neither morphologically fixed nor unchangeable, rather they evolve into new species or 'transmutate' as Darwin called it, or they die out.

This, in a nutshell, is the great contribution Darwin made to the advancement of biological science.

Simple as these ideas may seem at first sight, they are far from it. The last 150 years have been characterized by vigorous scientific debate and intensive research into how exactly we have to test and interpret these great ideas of adaptation, struggle for existence, natural selection, descent with modification and transmutation of species.

Darwin's biggest stumbling block was *how* variation occurred. He wrote at a time that genes had yet to be discovered, and he had no idea how information could be passed on to future generations. In order to explain the transmission of existing features, and to explain the origin of novel features, he invoked ideas such as the blending of gemulles (which were presumed hereditary particles), pangenesis, and Lamarck's ideas of use and disuse and the inheritance of acquired characteristics. He further assumed, partly because he endorsed the idea that hereditary traits could blend, that evolution was a slow and gradual process and that therefore, numerous intermediates lined up between species. However, the fossil record could not help in verifying this idea, because no such intermediates were found. Rather, different species appeared to arise rather abruptly in the fossil record.

In the years to follow, different research fields originated that were put to use to test and prove the theory of evolution by means of natural selection. As a result, different elements of Darwin's original formulation of the theory were reformulated or abandoned (such as the ideas of blending or Lamarckian inheritance), and new elements were added to the theory. In the 1930s, the Modern Synthesis was formed, which provided scholars with the standard paradigm of how evolution by means of natural selection occurred. Neodarwinians, as the founders of the synthesis are called, combined Mendelian hereditary laws with modern genetics and de Vries' mutation theory. With the Modern Synthesis, evolutionary biology was also mathematized and an interest was developed in population biology. Today, the evidence for the occurrence of evolution is now so abundant that we can say that evolution is a fact of nature. And that evolution occurs by means of natural selection is abundantly clear. Nonetheless, debate continues over what exactly it means for something to evolve by means of natural selection.

Evolution by means of natural selection, a meta-theoretical analysis

In its modern Neodarwinian version, evolution by means of natural selection has come to imply that small, genetic variations that are phenotypically displayed by organisms, and that are caused by chromosomal rearrangements and random mutations, are positively selected for in relation to the environment when adaptive. Over time, the natural selection of favourable traits gradually leads to the diversification from the original species up to the point that a new species evolves.

However, what does this mean exactly? What assumptions are made when natural selection is formulated as such? On a meta-level, evolution by means of natural selection, as defined by Neodarwinians, implies the following:

- Natural selection is always active: there is always a scarcity of resources which results in a constant struggle and a constant favouring of the fit over the unfit, and species, therefore, also constantly evolve by means of natural selection;
- Natural selection occurs slowly and gradually (at a constant rate): mutations are chance events, and the possible selection and transmission of adaptive mutations are confined to the germ line and always require the emergence of a new generation, making evolution a timely event;
- Because of the requirement of germ line transmission of novel traits, the origin of new species occurs as a vertical process: species either evolve themselves out of existence by evolving into new ones (anagenesis); or they split off from older species (cladogenesis);
- Natural selection occurs at the interface of a phenotype and the environment: in other words, the phenotype is the unit of selection, and evolution by means of natural selection occurs at the level of the environment.

Today, advances in the study of evolution have called many of the above made assumptions into question. The following criticisms can be objected:

(1) Because genes are the stuff that organisms and ultimately evolution is built upon, population genetics and later molecular genetics have been dominating all theorizing on how evolution by means of natural selection occurs. The exclusive focus on the distribution of genetic traits has resulted in the idea that microevolution (small random genetic changes) suffices to explain macroevolution (the evolution of species). This gene and mutation-centred idea has been put forward to the neglect of the role of the organism, the environment and species.

(2) Darwin had already recognized that besides adaptive and maladaptive traits, organisms can display neutral traits that appear to have no use in the struggle for existence. He recognized the existence of such neutral traits as a major challenge to his theory. How could these neutral traits have evolved when selection was

constantly active? The only answer could be that sometimes selective pressures are loosened and no struggle for existence occurs. Interested in how traits originate and how they migrate within and across populations (how they are distributed over space and time), population geneticists came to realize that not all traits are selected and spread as a consequence of their adaptive values. Genetic drift theory and neutral evolution, first introduced by Wright (1932) and later elaborated upon by Kimura (1968, 1983), explain how the transmission of traits from parents to offspring is mostly the result of random sampling and thus of stochastic processes. Because causation can be attributed to genetic drift, we can call it an evolutionary mechanism just as natural selection is one. And the recognition that several evolutionary mechanisms can be active, requires that we investigate how these mechanisms alternate one another. A further major consequence of the theory of genetic drift is that evolution is not necessarily characterized by an increase in fit between an organism and its environment, and that consequently, evolution is not necessarily progressive.

(3) When selection pressures are strengthened or loosened, this can tamper with the rate of evolution. It follows that the evolutionary rate, although perhaps gradual, is not constant. The idea of gradualness implies that intermediates need to be found between species. As Darwin already noted, the fossil record often does not show the remains of such intermediates between different species. The fossil record has, therefore, been called incomplete, and the field of palaeontology has been considered useless in helping to prove evolution. Eldredge and Gould (1972) however argued that the gaps in the fossil record need to be taken at face value. That is, the gaps are real and they provide us with an empirical observation that can tell us something about evolution. The authors introduced the theory of punctuated equilibria to explain the rapid occurrence of new species in the fossil record without the apparent presence of intermediates. According to the theory of punctuated equilibria, evolution is characterized by long periods of stasis wherein no permanent evolutionary changes occur, which are punctuated by short periods of rapid change. During these long periods of stasis, new variations can occur (due to random mutations), but drift and the size of a population often make it impossible for these novelties to become fixed. In other word, even when there is variation over long periods of time, speciation will not automatically occur. Microevolutionary processes such as genetic mutations, taken on their own, are incomplete to explain the origin of new species (macroevolution). Rather, the theory of punctuated equilibria suggests that additional explanations need to be sought to explain how speciation occurs. One of these additional explanations is the role of the physical environment. Climate changes or natural barriers between populations (allopatric speciation) can facilitate if not induce speciation. This in turn has strong consequences for how we understand species and the process of speciation, because punctuated equilibria suggests that species are real entities and speciation events are real as well.

(4) Zooming in on the role of the environment, we can argue that for a long time, the study of the environment was only relevant in so far as it gave the scene where selection and speciation can occur. The environment was considered to be of a purely physical nature, and to be external to the organism. Systems theory and ecological thinking would undo of this assumption by arguing that the environment of an organism is by and large made up of other organisms (Van Valen 1973). Lewontin (2000) would argue that organisms can, to a greater or lesser extent, construct their own environment through a process called niche construction. And organisms can change their phenotypes in relation to a changing environment, a process that is called phenotypic plasticity by West-Eberhard (2003). These theories have significantly blurred the once distinctive barrier between organism and environment.
Epigeneticists and evolutionary developmental biologists (evo–devo) brought to light that the internal milieu of an organism, and non-genetic factors, are highly relevant for the origin and evolution of species (Goodman and Coughlin 2000). During the formation of the Modern Synthesis, a firm line was drawn between ontogeny, the development of the individual from conception until death; phylogeny, the evolution of species; and the external environment, the place where evolution occurred. Today, scientists undo of all these boundaries. Notions of eco–devo or ecological developmental biology (Gilbert 2001), and even eco–evo–devo are introduced from within a systems theoretical perspective. Evolution is understood as a hierarchical process, it occurs at several levels of biological organisation. These organisational levels are determined by both upward and downward causation (Campbell 1974): the parts determine the whole, but the whole also determines the parts in new ways. Biological systems are probably unique in portraying emergent properties.

(5) The adaptive status of a trait is not fixed, rather it can change. Dependent on environmental changes,

adaptive traits can become maladaptive, or neutral traits can become adaptive. The function of a trait is not constant either, since the function of a trait can be put to use in a rather different context than the context in which it evolved; or a non-functional trait can require a function in the course of evolution. The latter are the processes identified as co-optation and exaptation by Gould and Vrba (1982).

(6) The requirement of germ line transmission of novel traits, together with the resulting emphasis on evolution being vertical, has resulted in the neglect of hybridization, lateral or horizontal gene transfer and symbiogenesis as possible evolutionary mechanisms. Nonetheless, we now know that the latter are indeed mechanisms that can introduce novel traits, and that can even lead to the origin of new species. Symbiogenesis, as an evolutionary mechanism, was first brought to the attention by Constantin Merezhkowsky (1910), and it was later independently rediscovered by Wallin (1927) and Margulis (1970, 1998). It is now widely recognized that the cell organelles present in eukaryotic organisms evolved out of the merging of nucleated cells with different prokaryotes. Margulis further argues that the first nucleated cells also originated as the result of the merging of different prokaryotes. In fact, the field of symbiogenesis today is a fast rising one, with implementations reaching as far as botany, insectology, virology and zoology (Sapp 2003). It now becomes abundantly clear that every organism alive today is the result of symbiogenetic mergers; it undergoes lateral gene transfer through contact with parasites, or through bacterial or viral infections; and it lives, to a great or lesser extent, in symbiosis with other creatures.

(7) All of the above has resulted in major theoretical reconceptualisations of evolutionary terminology. What is an 'organism', 'species', 'environment', and 'evolutionary mechanism'?

Organisms used to be regarded as homogeneous (even sterile), well-demarcated, passive entities that evolved as a whole, in an ever-changing environment that actively selects the adaptive ones. Organisms were unable to change their evolutionary faith. Today, we know that organisms can, to some extent, actively construct both their external environment (via niche construction), as well as internal environment (through immunological processes that allow or block parasites to enter, and that allow to create conditions that are different from the external milieu). Symbiogenetic studies have further made it necessary to consider most if not all organisms as superorganisms, because organisms have a heterogeneous nature: they are made up of different organisms with which they function as an emerging whole. A crucial question then becomes how these different structures are able to combine and function as a whole.

The species concept has also been the subject of serious reconsideration. Adhering to natural selection and acknowledging that it is a gradual and automatic process where intermediates successively follow one after the other, necessitates that one understands 'species' as unreal, theoretical constructs that merely facilitate theory-formation. Microevolutionary events occur incessantly and as a consequence populations constantly change. Species are not fixed entities. Indeed, Darwin himself adhered to a nominological species concept, arguing that species' boundaries are arbitrarily drawn by us humans, because species are non-existent. A consequence of punctuated equilibria and its introduction of macroevolutionary processes is that species are considered real entities that have clear spatial and temporal boundaries. Mayr's (1942) biological species concept, the concept most associated with the Modern Synthesis, takes the possibility to hybridize and produce fertile offspring as prime criteria to belong to the same species. The symbiogenetic species concept as defined by Margulis and Sagan (2002, p. 94), on the other hand, takes the possibility of lineage crossing as an identifying criteria of different species. Moreover, symbiogenesis implies that just like organisms, species too are not homogenous entities, but rather are formed through the interaction of different species, if not altogether through the incorporation of different gene sets and whole organisms (such as microbes). Finally, the acknowledgement of the existence of species makes it necessary to ask whether species themselves are units of evolution.

The environmental concept has also undergone significant changes through time. Focus has shifted from understanding the environment as a monolithic whole, to recognizing the heterogeneous nature and multilayeredness of the environment. An environment is dividable into many different habitats, and an environment can include physical forces such as climate change or gravitational forces, and biological elements such as other organisms. The internal milieu of an organism also creates an environment that can be the scene of evolution. As the quintessential location of where evolution by means of natural selection occurs, the environment is the major level of evolution. Recognizing the heterogeneous nature of the environment has, therefore, implied recognizing multilevel evolution.

Finally, the nature of an evolutionary mechanism has been subject to revision. Natural selection has been criticized by physicists for its lack of predictive value. They state that selection cannot provide us with a law of nature. The recognition of different mechanisms has made us realize that mechanisms are not constant forces like physical forces appear to be. Rather, their workings are dependent on a series of conditions. We need to identify those conditions. Mechanisms also not merely provide us with a mode of evolution, they also have consequences for theories on evolutionary rates, and the recognition of different mechanisms has made us contemplate the nature of their interaction: how do different mechanisms work together? Or do they alternate one another? These are just a few of the major questions in need of an answer.

(8) Finally, since the introduction of natural selection, the application range of evolutionary theory has widened immensely. As a consequence, the following research questions have been raised. What entities can evolve? Where does this evolution occur? How does it occur? Answers to these questions have been sought in the units and levels of selection debate. Today, however, we search not only for the units and levels of selection. We also search for the units, levels and underlying mechanisms of all sorts of evolution (the evolution of life, the brain, culture, …). Darwin saw evolution as something that occurs primarily through natural selection, and this selection occurred at the interface between an organism and an environment. Dawkins (1976, 1982) argued that organisms are mere vehicles. The true units of evolution were the genes. Many evolutionary biologists and philosophers of science have further argued that these genes can be selected at many levels.

One of the consequences of acknowledging evolution as a fact of nature has been that everything in the organic world can only be the result of some kind of evolutionary process. Recognizing the heterogeneous nature of an individual implies that several parts of the individual can evolve faster or slower and by means of different evolutionary mechanisms. In other words, the organism is a unit of evolution itself decomposable into subunits that are also subjected to evolution. This calls out for the recognition of multiple units of evolution. Recognizing the heterogeneous nature of the environment implies that multilevel selection (Maynard Smith and Szathmáry 1995; Okasha 2005) can occur. Recognizing the heterogeneous nature of evolutionary mechanisms again implies that multilevel evolution (rather than merely selection) can occur and that even multi-mechanism evolution can occur: evolution occurs through a combination of different mechanisms (Gontier, this volume).

This has widely expanded the range of natural selection and evolutionary thought. Evolutionary thinking is not merely relevant for biology, or for understanding the evolution of organisms. Group-level behaviours such as culture, or products of biological organisms such as cognition or epistemology, are now considered to be the outcome of evolution. Therefore, they must be explainable by the mechanisms of evolution. Evolutionary biology today is expanded to include evolutionary psychology, evolutionary epistemology, evolutionary anthropology, archaeology, economics, etc.

In conclusion, the concept of evolution has itself evolved. The above, however, should not be read as a rejection of either Darwin's or Neodarwinian thinking. If anything, it demonstrates Darwin's genius, for the past 150 years of evolutionary thinking have revolved around how exactly we are to interpret the evolutionary concepts first introduced by him. Although evolution might occur faster than Darwin predicted, he first made us recognize that evolution occurred *tout court*. Vertical evolution, for example, might need to be complemented by horizontal evolutionary mechanisms, but it is only by recognizing such a thing as vertical evolution to begin with that we have come to identify horizontal evolution as another possibility. Through the recognition of microevolutionary events, we were able to distinguish macroevolutionary events, and we can now begin the search for its underlying mechanisms.

The complexification of evolution

The above makes it obvious that evolutionary studies nowadays are characterized by a severe complexification of research questions. Many new disciplines have evolved, which developed new techniques to observe, test and theorize on the evolution of life. The different contributions that make up these volumes zoom in on some of the most pertinent research questions. A brief summary of the articles follows.

Part A examines natural selection, drift, punctuated equilibria and symbiogenesis from a historical, scientific and philosophical perspective.

Special attention is given to the different species concepts that are associated with these mechanisms.

The first two articles of Part A present a short historical review of microevolutionary experiments conducted on fruit flies, followed by the results of a 20-year-long and ongoing domestication experiment with *Drosophila subobscura*. Darwin was oblique on how novel and existing variation originated and how it was hereditarily transmitted.

The introduction of Weismann's germ plasm theory together with Weismann's barrier, the rediscovery of Mendelian genetic laws, the development of the chromosome and gene theory, the adherence to de Vries' mutation theory, and the cracking of the genetic code in the fifties of the previous century, have all contributed to the development of the field of population and molecular biology. Molecular biology is by far the most appropriate field by which we can study microevolutionary events and it is also in this biological domain that questions centre around what the ultimate role is that can be attributed to natural selection and drift. Many of the formulated hypotheses can be tested experimentally, especially on organisms such as fruit flies, because they have a very short life cycle which enables scientists to have a quick insight into how variation evolves across multiple generations.

Margarida Matos begins by lining out the pros and cons of lab-based experimental evolution and explains how the field can lend insight into real-time evolutionary events. Thereafter, she reviews how experimental studies with *Drosophila melanogaster* were conducted to test the role different habitats can play in sympatric speciation. Such experiments make it clear that habitat selection can result in reproductive isolation which in turn enhances genetic divergence and thus it can ultimately lead to sympatric speciation. Matos goes on and examines experiments conducted on the same fruit flies to investigate the process of ageing. The evolutionary theory of ageing states that the strength natural selection has on an organism declines with age, and thus that natural selection is not uniformly active on the organism during its different life phases. Such a hypothesis can be tested by reversing evolution. Scientists have created experimental settings wherein later age cycles of *Drosophila melanogaster* were preferred, and this resulted in a decline of the rate by which these organisms aged.

Marta Santos and co-workers zoom in on 20-year-long domestication experiments conducted on *Drosophila subobscura*. These experiments investigate just what it means for an organism to become adapted to a new environment, and how organisms adapt to captivity in general. More specifically, natural populations of these species of fruit flies were domesticated in the lab and it was investigated how well they adapted to their new surroundings under captivity. The results obtained from these studies univocally report that when placed in a new environment, the selection pressure is high and the evolutionary rate by which characters change is faster. This rate subsequently declines, a tendency that is echoed in molecular analyses of microsatellites. After foundation, a slow temporal decrease in genetic diversity can be witnessed. Also, a loss in chromosomal polymorphisms in the long-established populations of fruit flies is distinguished. The studies demonstrate that the experimentally induced, real-time evolution of fruit flies happens through a fine balancing between natural selection and genetic drift in relation to population size. It concludes that adaptive evolution is a local event.

A basic tenet of the Modern Synthesis has been that these microevolutionary events are sufficient to explain macroevolution. Small random genetic mutations will gradually lead to the diversification of populations and, over generations, this will lead to speciation. Evolutionary change is constant and evolution by means of natural selection becomes inevitable. Punctuated equilibria argues that macroevolution, i.e. speciation, needs to be distinguished from microevolution and that the latter, taken on its own is insufficient to explain speciation events. Change is punctuated by periods of stasis. Stasis, i.e. no change, becomes problematic and in need of scientific explanation. Two articles investigate the relation between gradualism and punctuated equilibria.

For a long time, punctuated equilibria has been associated with the fossil record and with the field of palaeontology. However, nowadays, due to large-scale genome-sequencing programs of whole species, molecular evolution can also be put to use to examine the basic assumptions of punctuated equilibria in a neontological context. The article of Melanie Monroe and Folmer Bokma does exactly that. The authors investigate how genomic sequences of whole clades allow to test the assumptions that long-term periods of stasis are alternated by short periods of rapid change *during* speciation. Several mechanisms have been put forward to explain the phenomenon of stasis. Monroe and Bokma review the following: stabilising selection, organismal plasticity, rapid adaptation and hyperstable niches, niche or habitat tracking, and the impossibility for new variations to become established into new species. Through their analysis, they demonstrate how the study of stasis brings forth a whole new set of research questions previously unrecognized as such by the founders of the Modern Synthesis. The authors focus on their own study which revolves around mammal and bird phylogeny to demonstrate that evolution can be concentrated in speciation events rather than that it occurs gradually through time. Moreover, during speciation, lineages accumulate variance at a higher rate; thus, during speciation there is an acceleration of the evolutionary rate.

A consequence of punctuated equilibria is that both species and speciation events are considered real phenomena in nature. Derek Turner takes a philosophical approach and investigates what else is suggested by the theory of punctuated equilibria. He argues that punctuated equilibria suggests, but does not imply, that species selection occurs. One of the epistemological questions that, therefore, need to be looked into is the following: when a theory A suggests a theory B, does this provide proof for theory B? Does this imply that theory B is correct? In other words, does the fact that punctuated equilibria suggest that there is such a thing as species selection, also provide proof that species selection occurs? His answer is negative, because according to Turner, punctuated equilibria concerns the pace of evolution, while species selection concerns the mode of evolution. Nonetheless, this does not rule out that species selection cannot occur. As a theory, species selection is merely distinguishable from punctuated equilibria. The author goes on to investigate how other theories have suggested species selection as well.

The following two articles are on symbiogenesis. Symbiogenesis was first recognized to be an evolutionary mechanism by Merezhkowsky (Sapp et al. 2002). Unfortunately, this mechanism has long been neglected by the mainstream biological community, partly due to the success of selectionist approaches. Nonetheless, it is now a well-established fact that evolution by symbiogenesis occurs, and that it occurs quite differently from the way in which evolution by means of natural selection proceeds.

Symbiogenesis leads to speciation, and this speciation occurs rapidly. This is the major conclusion Jan Sapp comes to after reviewing the historical origin and scientific insights of symbiotic studies. Symbiosis was first brought to the attention by de Bary, who argued that it could be a mode of saltational change. However, historically, symbiosis has often been examined in relation to parasitism, commensalism and mutualism. More often than not it has been conflated with either one of the latter. The concept of symbiosis indeed has severe consequences for how we understand organisms and species. Its recognition introduces concepts such as 'symbiotic superorganisms' or 'interspecies supraorganisms'. New wholes are made up of different parts that function in integrative ways which lead to novel properties and functions. With Merezhkowsky, symbiogenesis finally became recognized as an evolutionary mechanism. Wallin would go so far as to argue that evolutionary novelty is introduced by symbiogenesis, while natural selection results in the preservation or weeding out of that novelty. This idea was reinforced by Margulis when she demonstrated the symbiotic origin of eukaryotic organelles. Today, we know that symbiogenesis can be hereditary, as is shown by cases such as *Wolbachia*. Sapp, therefore, concludes that the tree of life is highly reticulated and symbiogenesis as well as horizontal gene transfer should be treated with the same amount of attention that is bestowed on natural selection.

Francisco Carrapiço homes in on the evolutionary and epistemological consequences of a symbiogenetic evolutionary view. Symbiosis and horizontal gene transfer between species can lead to rapid speciation as well as rapid adaptation to the environment. He further provides us with insights on the mechanism of hereditary symbiosis based on his own research of *Azolla*. *Azolla* is a fern that floats on the surface of fresh-water environments. The leaf cavities of *Azolla* hosts a whole community of different prokaryotes that help the fern to survive and prosper. Carrapiço argues that *Azolla* can be understood as a superorganism, and the leaf cavity as a unit of this symbiotic association. The symbiotic interaction allows the superorganism to establish a new level of organisation that extends beyond the capacities that the individual parts have.

A comparison of natural selection to punctuated equilibria and symbiogenesis makes the following questions quite pertinent: What is a species and how do species originate? Two articles zoom in on species concepts.

John Wilkins provides us with a historical and philosophical analyses of the species concept debate. He traces the word all the way back to Aristotle. Nowadays, it is a commonly held assumption that with the introduction of Darwin's *Origin of species*, natural scientists first abandoned the idea that species are real, that they have fixed essences and that they carry essential properties. However, Wilkins demonstrates that this idea of species' essences has never really been endorsed either by Aristotle himself or by naturalists that preceded Darwin. He traces this 'essentialist story' back to an article that was written by John Dewey. Wilkins argues instead that naturalists, before and after Darwin, have endorsed, what he calls, a generative conception of species. Species have the characterisation of generativity: progeny resemble parents, the like bring forth the like.

Filipe Costa and Gary Carvalho explain how the recent bar-coding initiative of life provides us with a different, pragmatic way of identifying species. At present, different labs all over the world are in the process of sequencing the same, pre-defined fragment of DNA that is present in a mitochondrial gene of all animals, and they are examining a different 'barcode' for plants and fungi. This 'barcode' can subsequently be used to identify and classify species, and it can also provide us with some comparative insights on the evolution of eukaryotic beings. For one, the barcode initiative allows for a fast identification of cryptic (sibling) species and can, therefore, help form hypothesis of the nature of morphological stasis in related species. It further allows to draw conclusions on the patterns of molecular divergence and the rate of nucleotide substitution.

The acknowledgement that species are real entities has not only given way to the formulation of different species concepts, it has additionally introduced the possibility that species might be units of selection in their own right. Two articles analyse the units and levels of evolution debate.

A conceptual analysis of what it means for something to be a species or a unit of selection is provided by André Levy. Different species concepts ultimately provide us with different ways to draw the tree of life. Levy reviews the different systematic ways to draw phylogenies. Numeral taxonomists preferred to highlight patterns of morphological similarity, while cladists preferred to draw trees based on phylogenetic relationships. Both endeavours got synthesized by evolutionary systematics that combined morphological similarity with evolutionary information. Endosymbiogenesis additionally demonstrates that the tree of life is highly reticulated. In the second part of the article, Levy zooms in on the concept of 'unit' of selection. Traditionally, the unit of selection has been considered the phenotype. Dawkins, however, argued that the unit of selection is the gene, while the organism is a mere vehicle that carries these genes. Genes are replicating entities, and Dawkins thus argues that something can only be a unit of selection when it is replicated. Other functional requirements have been given to units of selection, such as their interacting capacities (Hull's concept of an interactor). In relation to the adaptation debate, a distinction has been made between the manifestor and the beneficiary of the adaptation.

Nathalie Gontier takes a more pragmatic approach to the units and levels of evolution debate. The acknowledgement of different evolutionary mechanisms, different evolutionary rates and different environmental settings has made us realize that the whole of an organism does not evolve simultaneously in a homogenous environment according to one single constant evolutionary mechanism. Rather, different parts of the organism (e.g. its symbionts), or even different parts of the genome, evolve according to different mechanisms, and follow their own, often different pace of evolution. Moreover, it is not always clear whether a certain feature, environment, event, etc. is either a unit or a level of evolution; and nor is it clear under what circumstances an evolutionary mechanism becomes active or ceases to be so. Given this multiplicity of evolutionary mechanisms, and given that there are several units of evolution and several levels where evolution can occur, how can we identify these units, levels and mechanisms of evolution? Gontier proposes to step away from metaphysical and functional definitions of units, levels and mechanisms of evolution and argues that one should identify units based on levels and mechanisms; levels based on units and mechanisms; and mechanisms based on units and levels. Three heuristics are provided that allow for such a pragmatic identification of units, levels and mechanisms of evolution, and it is explained how evolutionary epistemology can investigate the conditions under which evolutionary mechanisms occur.

Most of the molecular studies that are presently conducted could not have been done without the help of the computer. Part A, therefore, closes with a look into how computation studies can advance biological investigations.

Luís Correia describes how evolutionary algorithms allow for a firm testing of natural selection, especially in regard to optimisation problems. In addition, studies on co-evolution and symbiosis can be modelled and tested by making use of computer simulations. Finally, attention is given to advances made in the field of Artificial Life.

Today evolution is such a widely recognized fact that its implications far outreach the field of biology. Human evolution as well as behaviours displayed by human beings can only be understood from within an evolutionary context. Darwin (1871, 1872) already applied his ideas of natural selection to human evolution in his books *The Descent of Man*, and *The expression of the emotions in man and animals*. Part B, therefore, zooms in on the application of Neodarwinian thinking in the human and social sciences.

Ian Tattersall begins the volume with an outline of hominid evolution and the difference between anatomical and behavioural modernity. Modern behavioural features such as tool making are already present in different hominid species even though they are not anatomically modern in the same way as human beings are. Moreover, a puzzle brought forward by the archaeological record is that the same tool technologies are often associated with different hominid species. This demonstrates that cultural evolution follows a different pace than the physical evolution of hominids, and that cultural evolution is marked by a tendency to resist change (stasis or tradition is thus a typical feature of culture). Tattersall further argues that although many innovative behaviours are shared with other hominid species, humans have unique symbolic capabilities. As a species, human beings reached anatomical modernity long before they displayed signs of this modern symbolic behaviour. An implication is that symbolic behaviour must have evolved as an exaptation, and that symbolic behaviour is an emergent property.

One major symbolic innovation that is associated with our species is the capacity to have language. António Bracinha Vieira examines how the different tool technologies associated with our hominid ancestors can provide us with insights into the origin of language. He argues that the use and the manufacture of tools requires cognitive capacities that are similar to syntactic and lexical capacities. A co-evolution might have occurred between the origin of tools and the origin of language. More specifically, the introduction of specific tool types such as Oldowan pebble tools or Auchelean bifaces requires that the manufacturer has a clear cognitive image in mind of the tool that he is about to make, and this tool might have received a name. The manufacture of complex tools requires that one follows a series of well-defined behavioural rules which are comparable to the syntactic rules that allow us to structure words into sentences. Vieira further provides us with neurological evidence that points in the direction of a co-evolution between tool making and language. The long periods of stasis, wherein the same tool types are made by different hominid species across geographically distinct regions, implies that the tool prototypes were culturally transmitted and that there might have been some type of cultural group selection process involved. He argues that the origin of language far precedes our own species, and that it might have evolved as an exaptation of tool making capacities.

Another major symbolic innovation associated with our species is art. Jan Verpooten and Mark Nelissen state that the origin of art provides Neodarwinian views with a challenge: the creation of art does not appear to provide its maker with direct survival benefits and in so far as it does not, the behaviour might even be considered maladaptive. How then could it have evolved? The authors argue that art evolved as an exaptation of biological adaptations. Human beings, for example, have an inborn capacity to recognize faces, a behaviour that is most likely an adaptation for it helps children distinguish their caregivers from strangers. The origin of portrait art and our fascination with it, might have evolved as a side-effect of our biological capacity to be attracted to faces. Art, in other words, exploits pre-existing sensory sensitivities and can evolve as long as the costs are not to heavy for the organism that bears them. They obtain the concept of sensory exploitation from sexual selection theory, a theory indeed first introduced by Darwin in parallel to his idea of natural selection. The origin of art also demonstrates the presence of cultural evolution because the production of art requires the learning of a series of skills. These cannot be re-invented anew or acquired single-handedly during the life-time of a individual. The authors remain undecided on whether art itself can be considered an adaptation.

Besides understanding human evolution, and human behaviour such as language and art, as the direct outcome of the evolutionary process, we can also apply evolutionary methods as epistemological tools that can be of use for human and social sciences. The last two articles demonstrate how this is the case in the field of linguistics and political science.

In the *Origin*, Darwin already drew parallels between the evolution of species and the evolution of languages. Both were argued to evolve according to a selectionist process. This resulted in a temporary cross-fertilisation between the field of historical linguistics and evolutionary biology. Remnants of this cross-fertilisation can still be found in the use of phylogenetic trees by both linguists and biologists to portray the evolution of languages and species. James Steele and Anne Kandler investigate the differences and similarities between trees that display the genetic dispersal of humans and their languages, as well as the virtues and vices of such macroevolutionary comparisons. It is often assumed by such comparisons that the genetic dispersal of human populations runs parallel with the evolution of the languages these populations speak. They focus on the shift from Gaelic to English in the Scottish highlands. A shift occurred from the former to the latter language, because the speakers shifted to a different language. The demographic tree did not die out, it simply transferred to another branch on the linguistic tree. This example of language shift, therefore, is at odds with standard ideas that require there to be a congruence between the biological and the cultural tree. They, therefore, argue that language shifting requires additional cultural explanations such as selective cultural migration (due to marriage, trade, political integration, etc). Moreover, their research shows that horizontal transmission process can nonetheless be displayed as tree models.

The last article, written by Orion Lewis and Sven Steinmo, investigates how evolutionary jargon can be introduced in political sciences. When natural selection was first introduced, it quickly gave way to notions such as Hebert Spencer's 'survival of the fittest', racism, eugenetics, and developmental laws of culture. These ideas, however, are not necessarily conclusions that need to be drawn from the theory of evolution by means of natural selection. Rather, racial ideas or ideas on eugenetics rely on misinterpretations of the evolutionary process. These ideas are thus both politically as well as biologically incorrect and it is no-one's wish to revitalize them. Nonetheless, just as the evolution of cognition, tool manufacture, language and culture can be regarded as an evolutionary process, so can political history be regarded as an evolutionary process. Indeed, accepting evolution as a fact of nature, and accepting that all behaviour displayed by individuals is the consequence of some kind of evolutionary process, makes the line between mere history and evolution fuzzy, for what is evolution more than a description of natural history (or vice versa)? Lewis and Steinmo demonstrate how the field of political science has been dominated by a reductionist philosophy that has its roots in mechanical, Newtonian physics and mathematical reductionism. This results in a search for political laws and a growth of rational-choice theory to explain political change. They argue that this approach is at odds with how political history truly evolves, and the authors plead for an introduction of evolutionary ontology that can underlie the epistemological questions framed in their field. Political systems, they argue, are complex adaptive systems that are hierarchically structured and that undergo evolution at multiple levels. Evolutionary theory can further provide us with explanations of why organisms display certain types of social behaviour such as cooperation or altruism; why they form groups and social institutions; why they have a tendency to obey social rules; or where moral sentiments might come from.

In conclusion, the past 150 years are marked by an evolution of evolution. Evolution today forms part and parcel of our everyday life and the consequences of an evolutionary world view have only recently impregnated all layers of scientific thinking. At present, it is unclear how far an evolutionary approach will take us in solving the problems considered in the human and social sciences. And although natural selection is today accompanied by other evolutionary mechanisms such as stasis or symbiogenesis, many evolutionary mechanisms are probably still waiting to be discovered. This is the case because accepting evolution equals accepting that there is no such thing that came into existence without evolution. Therefore if something did not evolve by a known evolutionary mechanism such as natural selection, drift or symbiogenesis, then it must have evolved by another evolutionary mechanism. The full consequences of an evolutionary view are, therefore, still to be felt, and the legacy of Darwin continues.

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