Can We Understand Evolution Without Symbiogenesis?

Francisco Carrapiço

…symbiosis is more than a mere casual and isolated biological phenomenon: it is in reality the most fundamental and universal order or law of life.

Hermann Reinheimer (1915)

Abstract This work is a contribution to the literature and knowledge on evolution that takes into account the biological data obtained on symbiosis and symbiogenesis. Evolution is traditionally considered a gradual process essentially consisting of natural selection, conducted on minimal phenotypical variations that are the result of mutations and genetic recombinations to form new species. However, the biological world presents and involves symbiotic associations between different organisms to form consortia, a new structural life dimension and a symbiont-induced speciation. The acknowledgment of this reality implies a new understanding of the natural world, in which symbiogenesis plays an important role as an evolutive mechanism. Within this understanding, symbiosis is the key to the acquisition of new genomes and new metabolic capacities, driving living forms' evolution and the establishment of biodiversity and complexity on Earth. This chapter provides information on some of the key figures and their major works on symbiosis and symbiogenesis and reinforces the importance of these concepts in our understanding of the natural world and the role they play in the establishing of the evolutionary complexity of living systems. In this context, the concept of the symbiogenic superorganism is also discussed.

Keywords Evolution · Symbiogenesis · Symbiosis · Symbiogenic superorganism · New paradigm

F. Carrapiço (✉)
Centre for Ecology Evolution and Environmental Change (CE3C);
Centre for Philosophy of Science, Department of Plant Biology, Faculty of science,
University of Lisbon, Lisbon, Portugal
e-mail: fcarrapico@fc.ul.pt

N. Gontier (ed.), *Reticulate Evolution*, Interdisciplinary Evolution Research 3,
DOI 10.1007/978-3-319-16345-1_3

1 Introduction

The idea of evolution applied to the biological world was used for the first time in the eighteenth century (1779) by the Swiss naturalist and philosopher Charles Bonnet (Bowler 1975), who developed this concept in the context of egg fertilization by spermatozoon. In his work, the author considers that the egg contains the embryo preformed with all the parts of the future organism present, the sperm cell being the trigger for such development. The unfolding of the pre-existent embryo was called "evolution" (Rieppel 2011). However, the use of this term in a more modern sense began to emerge when new data were obtained from different expeditions around the world carried out by French and English naturalists in the eighteenth and nineteenth centuries. These data, which included geological and biological information on different continents, undermined the official version of the Earth's formation and its age, as well as the universal tenet of the creation of species, questioning the validity of the biblical version and building a new tree of life on a dynamic planet (Mayr 2001; Kutschera 2011).

The first modern scientific ideas on evolution were presented in 1809 by Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck, in his book *Philosophie Zoologique, ou Exposition des Considérations Relatives à l'Histoire Naturelle des Animaux*. The latter envisioned evolution as a progression from less to more complex organisms, where the notion of progression was represented by a straight line (Lamarck 1809). The shift from the belief in a static approach to a dynamic understanding of the evolution of the natural world was brought about by the publication of Alfred Wallace's works and especially, in 1859, by Charles Darwin's book *On the Origin of Species by means of Natural Selection or the Preservation of Favored Races in the Struggle for Life* (Darwin 1859). Influenced by the works of Thomas Malthus and Charles Lyell, Darwin built a theory that contributed to change radically the idea of constancy of species, which allowed for the development of the theory of common descent and the challenging of the natural theology principles that had ruled natural science for centuries (Kutschera 2011).

At the beginning of the twentieth century, new scientific data were published by several authors, among them the German biologist, Theodor Boveri, and the American biologists, Thomas Hunt Morgan and Hermann Joseph Muller (Reif et al. 2000), contributing to a new understanding of the evolution concept. Among these data, the discovery of the nature and role of the chromosome in heredity—which lays at the core of the chromosome theory of inheritance—was of primordial importance. Further research, namely in mathematical and field studies population genetics, developmental biology, biogeography, and paleontology, contributed to a better understanding of evolution and the formation of evolutionary synthesis, which constituted the core of the synthetic theory of evolution. This theory was based on five evolutionary factors: mutation, recombination, selection, isolation, and drift (Reif et al. 2000). In 1942, Julian Huxley published *Evolution: The Modern Synthesis*, opening a new chapter on the understanding of evolution, merging the Darwinist ideas with new concepts in genetics and evolutionary biology, developed previously by authors such as John B.S. Haldane and Theodosius Dobzhansky (Huxley 1942). The same year, Ernst Mayr published *Systematics and the Origins of Species, from the Viewpoint of a Zoologist* (Mayr 1942), an important work on modern evolutionary synthesis. It was the beginning of the neo-Darwinist period, which is still considered the mainstream approach to evolution studies.

Bearing this background in mind, this work is a contribution to the literature and knowledge on evolution, which takes into account the biological data obtained in the last few years. This chapter tries to find new answers to old questions, which neo-Darwinism in its "ivory tower" has not been able to cope with, having driven evolutionary science to a dead end regarding some topics in the field, reinforcing the importance of symbiogenesis to understand the natural world and in the establishment of evolutive complexity of living systems.

2 Roots and Paths of Symbiogenesis

Evolution is traditionally considered as a gradual process essentially consisting of natural selection conducted on minimal phenotypical variations, which are the result of random mutations and genetic recombinations to form new species. However, "Mutation accumulation does not lead to new species or even to new organs or new tissues," and "99.9 % of the mutations are deleterious" (Margulis and Sagan 2002).

In contrast, the biological world presents and involves symbiotic associations between different organisms to form consortia, a new structural life dimension and a symbiont-induced speciation. This reality implies a new understanding of the natural world, in which symbiogenesis plays an important role as an evolutive mechanism, with symbiosis as the key to the acquisition of new genomes and new metabolic capacities, which drives living forms' evolution and the establishment of biodiversity on Earth (Margulis and Sagan 2002). So, we can say that "Symbiosis is simply the living together of organisms that are different from each other" (Margulis and Sagan 2002) and symbiogenesis can be seen as the "origin of evolutionary novelty via symbiosis" (Margulis 1990). Even one of the well-known neo-Darwinists of our time, Richard Dawkins, in his book *The Selfish Gene* (Dawkins 1976, p. 182), introduced the idea that "Each one of our genes is a symbiotic unit" and "We are gigantic colonies of symbiotic genes." Nevertheless, he refused to admit that symbiosis and co-operation can have a crucial role in nature and reinforced the importance of gene selfishness in the evolutive process.

It was only with Peter Corning's work, *The Co-operative Gene…* (Corning 1996), that these ideas moved to a new level of understanding, highlighting co-operation and saying that "Synergy is a multi-leveled phenomenon that can take many different forms," and "has played a significant causal role in the evolution of complexity."

In a certain way, "Co-operation represents an often advantageous survival strategy" and in "a complex organism or superorganism [it] represents a collective survival enterprise" (Corning 1996, p. 205). It was also this author who in his book *Holistic Darwinism* clarifies the relation between symbiosis and synergy, saying

> That symbiosis refers to relationships of various kinds between biological entities and the functional processes that arise from those relationships. Synergy, on the other hand, refers to the interdependent functional effects (the bioeconomical pay offs) of symbiosis, among other cooperative phenomena. In short, all symbioses produce synergistic effects, but many forms of synergy are not the result of symbiosis (Corning 2005, p. 82).

As Yves Sciama states in his article "Penser coopération plutôt que competition (Think cooperation instead of competition)," it is important to consider as the main project for twenty-first century biology, "*Repenser le vivant à partir de la notion de symbiose* (Rethinking the living from within the notion of symbiosis)" (Sciama 2013).

Despite these open-minded ideas related to a more co-operative and synergistic approach to the evolutive process, symbiosis and symbiogenesis have been considered by the majority of the scientific community as "stepdaughters or stepsons" of evolutionary theory (Pereira et al. 2012), or in the case of symbioses, as biological jokes (Selosse 2000). This reveals a limited understanding of evolutive process and does not correspond to the reality of the facts nor to the structure of the web of life on our planet. The symbiogenic view also enables a coherent conceptual and epistemological rupture with some evolutionary ideas of the past, indicating and building a new approach to understanding the development and evolution of life. To comprehend this new approach and paradigm to the evolution process and diversity of life on our planet, we must go back in time and begin our narrative when the first modern scientific ideas on evolution appeared, namely after *The Origin of Species* by Darwin in 1859. On the topic of origins, let us start at the beginning…

The year of 1867 is better known for the publication of the first volume of *Das Kapital* by Karl Marx, but it was also in that year that Simon Schwendener, a Swiss botanist, proposed at the Swiss Natural History Society annual meeting, held in Rheinfelden, an interesting dual hypothesis. In order to explain the nature of lichens, this hypothesis indicated that they are an association of two organisms, a fungus and an alga, behaving as "master and slave" (Honegger 2000). The idea that an organism could be formed by two or more genetically separate organisms living together and working as one unit was regarded as so unusual at the time that it was largely rejected by the scientific community. The dual hypothesis was a revolutionary concept for the biology of the nineteenth century, as well as a rupture in the traditional concept of an organism. The proposal, however, was not easily accepted, as can be seen from the example of William Nylander's book *Les Lichens des Environs de Paris*, published almost 20 years after Schwendener's statement. In his book, Nylander states that "*On sait bien aujourd'hui que la formule 'les lichens sont des champignons vivant en symbiose avec des algues' est une assertion de pure fantaisie ou une calomnie* (Today, we know very well that the formula 'lichens are fungi living in symbiosis with algae' is an assertion resting on pure fantasy, or a calumny)" (Nylander 1896).

Another example of this situation was the living experience of Beatrix Potter who worked with lichens at the end of the nineteenth century and who was not allowed to continue her scientific work because she supported Schwendener's ideas, vand also because she was a woman. The traditional English scientific community was not supportive of her work (Sapp 1994; Taylor et al. 1995). However, as society lost a scientist, it gained a children's story writer. *Peter Rabbit and his Friends* probably did more for the establishment of an environmentally friendly behavior for new generations than many of her co-fellows who rejected her as a scientist.

The next important step was the introduction of the symbiosis concept by the German naturalist Heinrich Anton De Bary in 1878, which was based on studies of the nature of lichens and the role of algae and fungi in this association. He also used the example of the aquatic fern *Azolla* to develop this concept, referring to the permanent presence of the cyanobacterium *Anabaena azollae* in the leaf cavity and in the sexual structures of this plant. He further expanded on this presence by explaining that at no stage of its life cycle is the fern free from cyanobacterium and that the latter is in no way harmful to *Azolla* (Carrapiço 2010a). This concept was presented in a communication entitled "Ueber Symbiose" (About Symbiosis), at the Congress of Naturalists and German Doctors in Cassel (De Bary 1878), and was defined as "the living together of unlike named organisms," which is at present the best definition for this phenomenon (Carrapiço 2010a). However, it is important to note that this concept follows two previously introduced concepts. The first was mutualism, which was put forward by Pierre-Joseph Van Bénéden in 1875, and constituted an application of Pierre-Joseph Proudhon's social ideas to the animal kingdom (Van Bénéden 1875; Boucher 1985). The second concept was symbiotismus, which was introduced by Albert Bernhard Frank, in 1877, in a publication on the biology of lichens (Frank 1877). This author, who is better known for the study and introduction of the term "mycorrhiza" in 1885, defined symbiotismus in a similar way to De Bary's symbiosis in 1878. In 1879, De Bary published a new article related to this subject entitled "Die Erscheinung der Symbiose" (The Phenomenon of Symbiosis). In both works, De Bary considers the association *Azolla–Anabaena* to be a classic example of van Bénéden's mutualistic cases applied to the plant kingdom. Even though this association was previously studied by Eduard Strasburger in 1873, De Bary noted, as already mentioned, that no stage of the life cycle of the fern was free of the cyanobacteria and that they did no harm *Azolla*.

In 1895, the Danish botanist Eugenius Warming published *Plantesamfund* (*Ecology of Plants*) and considers the *Azolla–Anabaena* association an example of mutualism and an exception to normal behavior in plant communities: "In plant community egoism reigns supreme" (Sapp 1994).

In 1902, Petr Kropotkin published *Mutual Aid. A Factor of Evolution*. This work was written while in exile in England, and argues that, despite the Darwinian concept of the survival of the fittest, co-operation rather than conflict is the main factor in the evolution of species. Kropotkin, better known as a leader of the anarchist movement, developed his ideas of the natural world based on the experience he lived during a five-year expedition in Siberia (1862–1867). He was also influenced by the work of the Russian zoologist Karl Kessler, who in 1879 presented a paper entitled "On the Law of Mutual Aid" at the Society of Naturalists of St. Petersburg (Kropotkin 1902; Todes 1989).

However, the main core of the symbiogenic ideas was developed by the Russian biologist Constantin Merezhkowsky during his stay as professor at Kazan University (1902–1914) where he conducted research on symbiotic associations, namely on lichens. His research, however, goes well beyond these organisms. Between his stay in Kazan and his death in Geneva in 1921, this author published several papers on the origin of chloroplasts and the role of symbiosis in evolution (Sapp et al. 2002). In particular, in 1905 he published the article "Uber Natur und Ursprung der Chromatophoren im Pflanzenreich" (On the Nature and Origin of Chromatophores in the Plant Kingdom) where, for the first time, coherent scientific arguments showed that plastids arose from free-living cyanobacteria (Martin and Kowallik 1999; Merezhkowsky 1905). In 1909, he published "The Theory of two Plasms as Foundation of Symbiogenesis, New Doctrine on the Origin of Organisms" in Russian (Merezhkowsky 1909). The German version was published one year later. As a professor at Kazan University, Constantin Merezhkowsky developed this work introducing the concept of symbiogenesis as "The origin of organisms by the combination or by the association of two or several beings which enter into symbiosis." In this paper, he introduced not only new concepts on symbiogenesis and evolution, but he also developed some important ideas about the origin of life, namely related to the role of extremophiles in that scenario. A new classification of the living world was proposed using associations between organisms (Fig. 1; Merezhkowsky 1909).

In 1920, several months before committing suicide in Geneva, Constantin Merezhkowsky published the article "La Plante Considerée comme un Complexe Symbiotique" (The Plant Considered as a Symbiotic Complex) where the author developed his previous ideas on the symbiotic origin of chloroplasts and nucleus. In opposition to contemporary views of the time (Guilliermond 1918), Merezhkowsky defended that chloroplasts did not evolve from mitochondria or protoplasm, but from free-living cyanobacteria, as he had presented in 1905 (Merezhkowsky 1920).

It should be mentioned that another Russian botanist, Andrey Famintsyn, contemporary of Merezhkowsky and also working in the symbiotic field, published in 1907 *On the Role of Symbiosis in the Evolution of Organisms*, where he developed the idea that symbiosis has an important evolutionary, or even adaptive, meaning (Khakhina 1992; Sapp 1994; Sapp et al. 2002; Corning 2005). He states that the increasing complexity of the organization and function of organisms during the process of evolution may occur not only through the differentiation of simpler, early forms, but also on the basis of symbiotic unification of independent organisms into a living unit of a higher order (Khakhina 1992). In his point of view, the idea that symbiosis could be involved in evolution was important to understand the origin of life on Earth and its development (Khakhina 1992).

The same year that Constantin Merezhkowsky published his last work, Hermann Reinheimer published a book entitled *Symbiosis. A Socio-Physiological Study of Evolution* (Reinheimer 1920). The author points out the importance of specific interrelations in the development of organisms as a whole, giving us a holistic perspective on organismal evolution:

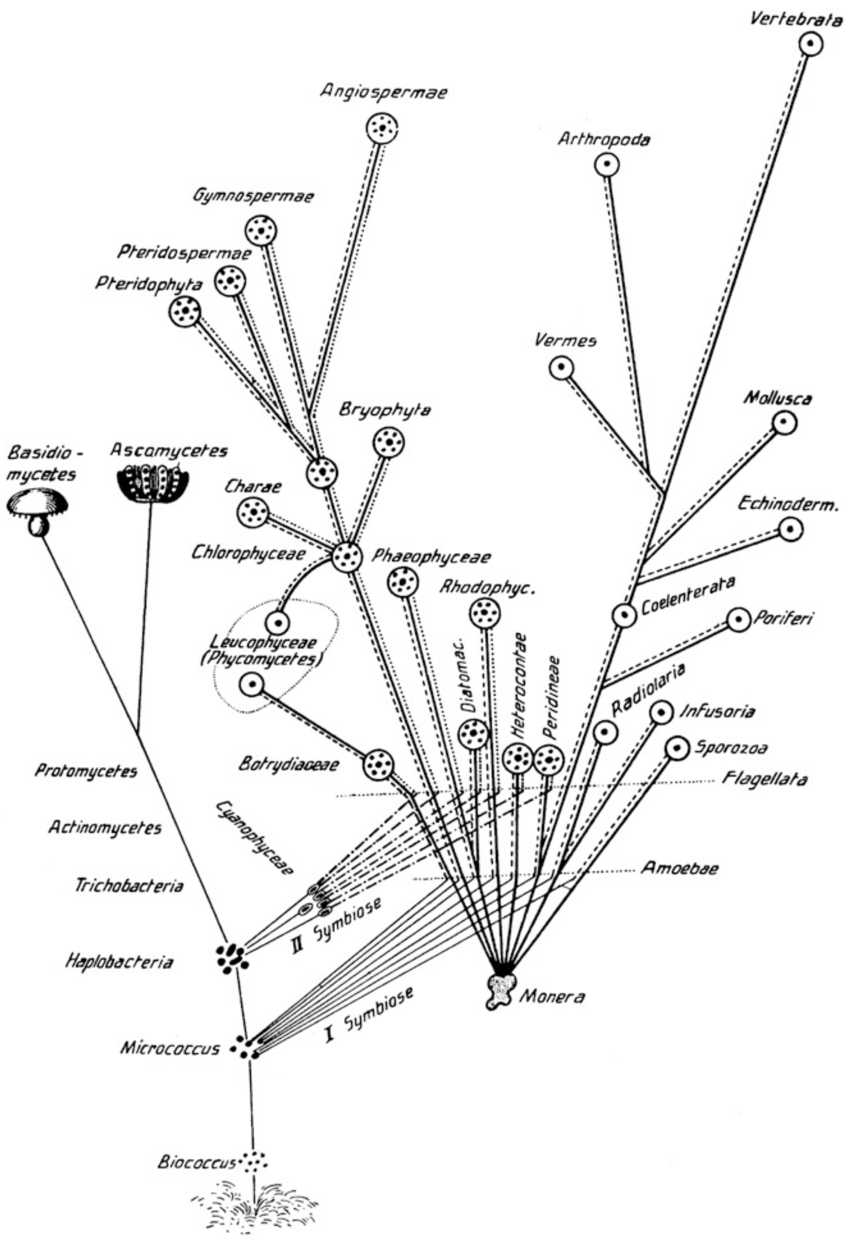

Fig. 1 The tree of life proposed by Constantin Merezhkowsky in 1909. In this, the organization of the living world is presented using, for the first time, associations between prokaryotic and eukaryotic organisms

> The main conclusion which I wish to enforce is that the normal relations between organisms, more particularly those having regard to food, involve, quite indispensably, a stupendous amount of systematic biological reciprocity, so that upon all organisms, be they high or low in the scale of life, there devolve definitive duties and obligations, on pain of degeneration or destruction, viz., to contribute in their several ways to the welfare of the organic family as a whole. (…) I regard the totality of organisms as a kind of world-society, the various species and families of plants and animals being the individuals of which this worldsociety is made-up.

This author, who lived in Surbiton (London) until the 1950s, is not particularly well known among biologists, which is strange given that he wrote 19 books during his life, several of them related to evolution and symbiogenic topics. His first book was published in 1909 with the title *Nutrition and Evolution*. A year later, he published *Survival and Reproduction. A New Biological Outlook*. It was in his three following books that Reinheimer developed his ideas about co-operation in a more coherent way: symbiogenesis, symbiosis, and evolution. The third book, published in 1913 and titled *Evolution by Co-operation. A Study in Bio-Economics*, is a good example of these ideas. In the preface of the book he mentions: "To the study of the physiological and combined economic factors productive of 'general stability and efficiency'—the study of biological eugenics—freed from the misleading side-issues of 'single peculiarities,' I have devoted myself for some years, and in so doing, I claim to be contributing to and furthering Darwin's work" (Reinheimer 1913). He was an evolutionist, but also believed in eugenics, which was usual in that period among many of Darwin's supporters. One of the main ideas of this book is the significance of what he calls "bio-economics" in evolution, including the importance of co-operation and mutuality in the evolutionary process rather than the "struggle for existence." These ideas were further developed in his next book published in 1915 and entitled *Symbiogenesis; the Universal Law of Progressive Evolution*. The word symbiogenesis was used without any reference to Merezhkowsky's work, which means that he either eventually omitted the work of the Russian biologist or that he did not have knowledge of his works, namely that of 1909. Although Merezhkowsky published this work in German in 1910 and Reinheimer knew the language, its diffusion was very limited and probably did not reach the United Kingdom. However, it is interesting and intriguing to notice the use of the same term.

To understand the nature of the content of Reinheimer's book and the way he perceived biology, we transcribe parts of the introduction that are relevant for the nature of our work. On page XIII he mentions:

> The first chapter is particularly devoted to the subject of symbiosis, which is generally defined as a physiological partnership between individuals of different species, but which is of far more universal meaning and occurrence than is suggested by this definition. The term must be particularly applied also to the wider bio-economic form of co-operation which underlies evolution and unites all organisms in one vast web of life.

On pages XIV and XV he defines symbiogenesis as

> By symbiogenesis I mean the production and increase of values throughout organic life by means of a symbiotic principle of co-operation or reciprocity between different organs

> of the individual, but evolved and complex body, as well as between different organisms in a species or different species, genera, orders, etc., even in the last and most fundamental way between plant and animal in the web of life. By the term symbiosis I refer to that obvious phenomenon of co-operation of parts and organisms as they occur, while by symbiogenesis I mean the principle underlying such symbiosis and indeed all instances of mutuality in the progressive transmutation of biological values generally. Symbiosis, further, may be domestic when it is between the organs of one organism and between the members of a family; biological when it refers to physically separate partners, even when widely separated and unconscious of partnership.

And on pages XVI and XVII he states:

> The grand importance of symbiosis consists in the fact that it evolves and safeguards those very modes of reciprocal differentiation which we must recognise as the universal means of the creation and elaboration of physiological and psychological values, including those which perhaps may be more especially regarded as genetic in character and influence. In other words, symbiosis is more than a mere casual and isolated biological phenomenon: it is in reality the most fundamental and universal order or law of life. So much so is this the case that I claim the great principle underlying all Creative Life, all Progressive Evolution to be that of "Symbiogenesis"; i.e., the mutual production and symbiotic utilisation of biological values by the united and correlated efforts of organisms of all descriptions. It is a well-known saying of Aristotle that the City exists for the sake of its good citizens, and I would apply it to the biological society, which also exists for its "good" citizens—those organisms, namely, which by symbiotic endeavour at once earn the right of biological citizenship and contribute to the welfare, permanence and progress of their "society."

At last, a sentence that summarizes his ideas related to symbiosis: "… Biologically speaking, I should say: 'La symbiose fait la force.'" This was said when he argues that "l'union fait la force" (Reinheimer 1915).

A final note about this author and his background. As we previously mentioned, Reinheimer is almost unknown among the authors working on symbiontology, especially taking into consideration the number of works he published related to this area of science. In many of these works, he used expressions that were ahead of his time, such as "web of life", "bio-economics", and "antibiotics". To understand how some of his works were not well accepted by established biologists, we transcribe a sentence included in a review of his 1915 book, which was authored by the American biologist William L. Tower, from the University of Chicago, and published in *The American Journal of Sociology*: "… in the whole book nothing to commend it, nor any possible escape from characterizing it as the least logical, worst constructed, most inaccurate and irrational book upon evolution that has appeared in a long time" (Tower 1916). Reinheimer was born in Germany (Hesse), but he was naturalized as a British citizen in 1901. In 1911, the England Census reported that he was 38 years old, single, and worked as a self-employed stockbroker. He lived in London (Surbiton) until the 1950s and subscribed to an alternative view of society, with the majority of his books being published by editors associated with anarchism, metaphysics, theosophy, and vegetarianism. A good example of alternative editors is the publisher Charles William Daniel, an anarchist and pacifist who founded his own company in 1902 for editing books on such topics. Another example is John M. Watkins, a publisher involved in the subjects of mysticism and metaphysics. Although Reinheimer refers to his occupation as stockbroker, his knowledge of natural sciences and namely of evolution suggest that he had a biological background, despite there being no indication that he had any affiliation with academia in England.

Several other authors were related to the development of symbiogenic ideas in biology during the first decades of the twentieth century. Among them, we must refer to the French biologist Paul Portier who published *Les Symbiotes* in 1918. In this work, Portier developed the idea that all organisms are constituted of an association of different beings. In the particular case of mitochondria, he argues that those cell organelles were symbiotic bacteria, which the author calls "symbiotes" (Portier 1918; Sapp 1994). He also refers to the positive role of these prokaryotic organisms in the human body at a time when germ theory was the mandatory rule in biology and medicine. These ideas shocked the French scientific community that reacted negatively. The following year, Auguste Lumière published a critical response in the book *Le Mythe des Symbiotes* (Lumière 1919).

In the United States, Ivan Wallin, working at the University of Colorado, developed similar ideas to Portier's concepts, and in 1923 and 1927 published two important works on the subject. The first, titled *The Mitochondria Problem*, emphasized the symbiotic origin of these organelles against the cytoplasmic point of view. In the second work, titled *Symbionticism and the Origin of Species*, the author defends the importance of symbiotic mechanisms in evolution, with emphasis on the symbiotic origin of mitochondria. Wallin also underlines the importance of microsymbiosis in this process, pointing out the idea "That bacteria, which are popularly associated with disease, may represent the fundamental causative factor in the origin of species" (Wallin 1923, 1927; Sapp 1994). He considers symbioticism as a mechanism of speciation, suggesting that the primary source of genetic novelty for speciation was the periodic repeated fusion of bacterial endosymbionts with host cells (Taylor 1979). Although he claims that it was possible to cultivate mitochondria outside of the cell, like Portier did in 1918, these data were incorrect as they resulted from culture contamination. It was only after his death, in 1969, that evidence began accumulating that his theory was partially correct concerning the bacterial origin of mitochondria, and the prokaryotes' role in evolution. *Symbionticism and the Origin of Species* was published in 1927, the year in which Hermann J. Muller published the paper "Artificial Transmutation of the Gene" in *Science*. This article opened the way to the explanation for species formation under the neo-Darwinian theory, showing that X-rays could dramatically increase the frequency of gene mutations in *Drosophyla*, and overshadowed Wallin's explanation of bacteria as a factor of speciation (Muller 1927; Wallin 1927; Sapp 1994; Brucker and Bordenstein 2012).

Another author, who must be referred to, is the Russian biologist Boris Kozo-Polyansky, who published an important book in 1924 entitled *A New Principle of Biology: An Essay on the Theory of Symbiogenesis*. This book gave symbiosis a determinant role in evolution, building the bridge between symbiogenesis and the Darwinian theory, and introducing the idea of the organism as a consortium (Kozo-Polyansky 2010). This concept was initially presented in 1873 by the German botanist Johannes Reinke, to refer to the relationship between the fungi and algae in lichens (Reinke 1873; Sapp et al. 2002). According to Kozo-Polyansky, the theory of symbiogenesis was a theory of selection relying on the phenomenon of symbiosis (Khakhina 1992).

All these ideas had criss-crossed in an elegant and outstanding way in the 1967 work of Lynn Margulis published in the *Journal of Theoretical Biology* under the title "On the Origin of Mitosing Cells" (Sagan 1967). In this paper, a theory of the origin of eukaryotic cells was presented, explaining the transition bridge between the prokaryotic and the eukaryotic levels of biological organization. Mitochondria, basal bodies of the flagella and chloroplasts, are considered to have derived from free-living prokaryotes, and eukaryotic cells are seen as the result of the evolution of ancient symbioses. All this pioneering work formed the basis of serial endosymbiotic theory, and it constituted the beginning of both remarkable work and contributions to the rehabilitation and development of symbiogenic ideas applied not only to the cellular world, but also to the construction of a new biology for the twenty-first century. Furthermore, it represented a clear and sustained rupture with the traditional neo-Darwinian understanding of biological evolution. Beginning with eukaryotic cell formation, symbiogenesis appears to be the main evolutionary mechanism in the establishment and maintenance of different ecosystems, as well as the foundation for biodiversity on Earth, based on rather sudden evolutionary novelties, and not in conventional gradualism or mutagenic processes (Carrapiço 2010b).

Among the numerous works published by Lynn Margulis, we would like to refer to two important works that changed the way biology is seen and understood nowadays. The first, published in 1970, is *Origin of Eukaryotic Cells*, considered a landmark in the understanding of the origins of eukaryotic cells. In the well-expressed words of John M. Archibald in a recent commemorative review published on the 40th anniversary of its publication, "This influential book brought the exciting and weighty problems of cellular evolution to the scientific mainstream, simultaneously breaking new ground and 're-discovering' the decadesold ideas of German and Russian biologists" (Archibald 2011). The other book is *Acquiring Genomes. A Theory of the Origin of Species*, in which Margulis and her co-author Dorion Sagan provide a solid critique of neo-Darwinism and identify the acquisition of new genomes involving symbiogenic processes as the main driving force in evolution, not random mutations (Margulis and Sagan 2002) (Fig. 2). These ideas include new research themes in order to develop the understanding of the evolutionary process and the complexification of life, namely the existence of horizontal DNA transfer between organisms and the mechanisms to explain it. These new paradigms in biology and in the evolution of biodiversity include bacteria and virus–host symbiosis and their composite dynamics in the establishment of the symbiogenic web of life (Sapp 2003; Carrapiço 2010b; Villarreal and Ryan 2011).

At the same time that the 1967 Margulis' article was published, an oft-forgotten short paper by the Norwegian microbiologist Jostein Goksoyr appeared in *Nature,* providing a similar endosymbiotic theory for the origin of eukaryotic cells (Goksoyr 1967). In this paper, the author suggested that the evolutionary development of the eukaryotic photosynthetic cell was based in prokaryotic forms. He

Fig. 2 The author of this chapter with Lynn Margulis at the Gulbenkian Foundation in Lisbon in 2009

also suggested that this evolution could have been of a polyphyletic nature, as stated in the conclusion of his work:

> A further logical conclusion is that the eucaryotic cell which developed would take its genetic material mainly from the procaryotic forms making up the coenocytic system. Such coenocytic systems may develop a number of times, from different procaryotic forms. Present-day eucaryotic organisms do not necessarily, therefore, have to be developed from one original species. This might even explain some of the rather puzzling parallels that exist between groups of procaryotic and eucaryotic organisms.

Before concluding this part of the text, we would like to refer to the work of the Canadian biologist F.J.R. (Max) Taylor, a renowned expert on dinoflagellates, who has published several papers on cell evolution and endosymbiosis theory (Taylor 1974, 1976, 1979). He was also one of the first researchers to understand the significance and importance of symbiotic bacteria in the origin of chloroplasts and mitochondria in eukaryotic cells and independently to develop similar ideas to Margulis' serial endosymbiosis theory, as well as the role of symbiosis in evolution. His ideas were ahead of his time as we can see in the 1979 work *Symbioticism Revisited: A Discussion of the Evolutionary Impact of Intracellular Symbioses*:

> From the evolutionary standpoint, a symbiotic event represents the union of two or more previously divergent genomes into a new coevolutionary unit. The subsequent fate of this unit will depend on both the survival effectiveness of the new unit interacting with external selective forces, and also the continued integrative and competitive interactions between the two symbionts.
>
> In terms of genetic novelty symbiosis represents a quantum leap of a magnitude far greater than that arising from intrinsic sources such as mutation, hybridization or ploidy changes. The component species can exist independently, but the structure formed by the union of the two may be equal or more successful than the individual species. Integrative factors are therefore crucial in intracellular symbioses (Taylor 1979).

Although we have referred mainly to the symbiogenic studies applied to the biological field, symbiogenesis can be related to other scientific fields beyond biology and evolution, such as in social studies. One pertinent example is the work of Nathalie Gontier from 2007, which states that "Besides the obvious application of the universal scheme in micro-evolutionary symbiosis studies and the origin of eukaryotic beings, it will be argued that universal symbiogenesis can also include the study of viruses and their hosts, hybridization, and even extra-biological phenomena such as culture and language" (Gontier 2007). We believe that economics, medical sciences, and education may also potentially benefit from this theory's application.

3 The "Big One" and the Concept of the Symbiogenic Superorganism

The concept of superorganic evolution was first introduced into the scientific literature by Herbert Spencer in 1876, in the first volume of *The Principles of Sociology* (Spencer 1876). Although the term "superorganism" was not used explicitly, the work implied the existence of a new approach to the classical concept of organism, with consequences at both the biological and social levels. In 1911, the American entomologist William Morton Wheeler, in his paper, "The Ant-Colony as an Organism," compared ant society to an organism when observing the biology and social behavior of these insects in colonies. However, it was only in 1928 that he concluded in his book *The Social Insects, Their Origin and Evolution* that the "insect colony or society may be regarded as a super-organism and hence as a living whole bent on preserving its moving equilibrium and integrity." In this case, the entire colony acts in unison as an independent "creature," feeding itself, expelling its wastes, defending itself, and looking out for its future (Wheeler 1911, 1928). The idea of the superorganism was applied to different levels of biological organization and was subsequently developed by other authors, such as Wilson (1975), Wilson and Sober (1989), Sapp (2003), Corning (2005), Carrapiço (2006a, 2010a, b), and Holldobler and Wilson (2009). Based on these ideas, we have introduced the concept of the *symbiogenic superorganism* (Carrapiço 2012b), applied to new entities or consortia formed by the integration of individual organisms, that possess characteristics that go beyond the sum of the individual properties of each element of the association, resulting in the development of new attributes and capacities as an integrated whole. In this process, these new entities also agglutinate and dynamize synergies not present in the individual organisms. This symbiogenic process also involves genetic sharing at the level of the organisms constituting the consortium, forcing the genomes to be incurred by synchronization and harmonization processes. These processes are aimed at establishing a proper functioning for the new organism as a whole. It indicates that the association depends not only on the intrinsic symbiont–host's properties, but also on the internal and external system environmental conditions. By way of example, a single organism formed by the association of two composite organisms could be demonstrated by way of mathematical formula. The result, however, would not be

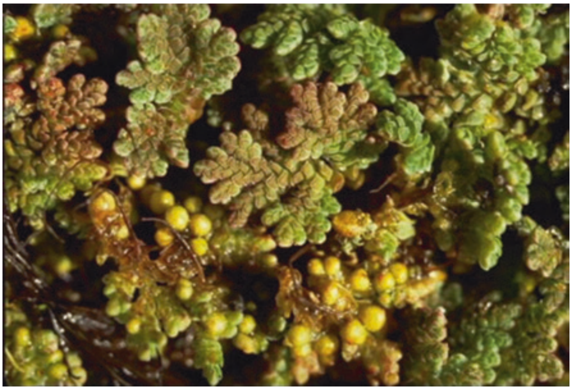

Fig. 3 Sporophyte of *Azolla filiculoides* showing overlapping scale-like bilobed leaves and numerous microsporocarps (*yellow small spheres*)

1 + 1 = 2, but 1 + 1 = a larger 1, characterized by the following principles: (a) the new organism is formed by different species of organisms that work towards a common goal; (b) this new entity is a polygenomic one, in which the different genomes operate together in a complementary and synergistic way for the whole; (c) the parts and units of this entity modify themselves qualitatively, compared to the same units when isolated; and (d) the final outcome is not the mere qualitative and/or quantitative sum of the units that constitute the consortium, but acquire new collective synergies and characteristics. In reality, this phenomenon is widespread in nature and allows a coherent reconceptualization of the traditional epistemological concepts of the past, helping to form a new evolutionary approach to the web of life as well as a contribution to a new idea for the organism concept.

These ideas can be included in the concepts of holobiont (the host with its symbionts as a whole) and hologenome (the sum of the genetic information of the host and its microbiota), developed by several authors (Zilber-Rosenberg and Rosenberg 2008; Guerrero et al. 2013). These principles are similar to the symbiome concept introduced in 2003 by Jan Sapp (Sapp 2003; Carrapiço 2006b). The symbiome concept reinforces the principle that eukaryotic organisms are not genetically unique entities, and the concept of individual must be seen as a complex biological ecosystem, composed of multiple interdependent parts living symbiotically. It is at the symbiome level, composed of an integrated multigenomic genetic pool, that natural selection acts (Carrapiço 2006b). In a recent book, John Archibald explores and elaborates these related topics in an elegant way (Archibald 2014).

Some examples of these kinds of consortia are lichens, termites, and their symbionts, the symbiotic system *Azolla–Anabaena*–bacteria (Carrapiço 2006a, 2010a, b), and in many animal bodies, including humans, with their microbiota community (Sapp 2003). All of these relationships can be considered as constituting symbiogenic superorganisms.

In the case of *Azolla* (Fig. 3), the superorganism is constituted of the association of two types of prokaryote organisms (cyanobacterium and bacteria) living symbiotically inside the leaf cavity of the fern (host). This implies and involves the development and acquisition of new metabolic and organic capabilities and also genome sharing by the partners in syntony with the host, to establish a new level of organization, extending beyond the capability of each individual forming the association. One good example of this can be found at the pathway of the biological nitrogen fixation present in this symbiotic system and shared by the different elements of the consortium. Another is at the level of sexual reproduction of the fern, involving cooperative and synchronous efforts, taking into consideration that the cyanobacterium and the bacteria are also involved and incorporated in this process (Carrapiço 2010a). Due to these latter characteristics, this association can be considered both as an example of a hereditary symbiosis and a synergistic complex biological system, with the symbionts always present in the fern's life cycle, suggesting a phylogenetic parallel co-evolution of the associated partners with the fern.

4 The Symbiogenic Theory of Evolution

The biological world presents and involves symbiotic associations between different organisms to form consortia, a new structural life dimension and a symbiont-induced speciation. This implies a new understanding of the natural world, in which symbiogenesis plays an important role as an evolutive mechanism, with symbiosis being the key for the acquisition of new genomes and new metabolic capacities, which drives living forms' evolution and the establishment of biodiversity on Earth. One good example of the importance of symbiosis in evolution can be found in plant transition from aquatic to terrestrial environments. In a recent work, Lipnicki (2015) states that symbiosis played a very important role in the crucial stages of the transition of life onto land, namely through lichenization and mycorrhization. In this sense, explanations of evolutionary changes must include an integrated synergistic co-operation between organisms, in which symbiosis acts, not as an exception, but as the main rule in nature, based on rather sudden evolutionary novelty and the increased complexity of living systems (Carrapiço 2010b; Corning 2005, 2014; Corning and Szathmáry 2015; Reid 2007). These ideas constitute the development of novel concepts for a better understanding of life on our planet and beyond, including the foundation of a new biological theoretical framework that can integrate and explain the dynamical organismal interactions and synergistic relationships present on Earth and in other planets. In this sense, we would like to share in this work a set of principles that could be integrated into a new approach to the evolutive process, helping to build a symbiogenic theory of evolution (Carrapiço 2006a, 2010b, 2012a, b). This theory includes Darwinian principles, but does not limit itself to the latter in its attempt to promote and explain the development, organization, and evolution of the biological world in a symbiogenic and synergistic sense. To integrate these ideas in the scientific literature, we need to develop a new approach to the analysis of evolution based on six themes: (1) Darwinian principles, (2) symbiosis concept, (3) symbiogenesis as an evolutive mechanism, (4) serial endosymbiotic theory,

(5) horizontal gene transfer and other genetic recombinations, and (6) epigenetic changes. These tenets should be considered as a contribution to a new epistemological perception of the natural world and also to the understanding of the true complexity, organismal interactions, and relationships present in the different ecosystems on Earth.

5 Conclusion

Life is evolution, a dynamic continuum existing unbroken since its emergence. Nevertheless, we must go beyond the traditional approaches to the understanding of evolution based on competition and gradualism, and integrate symbiogenic, synergistic, and co-operative principles as potential sources of evolutive novelty and quick transition. In symbiotic relationships, the central aspect is the creation of evolutive novelty (metabolic, anatomical, and organismal), which also involves the sharing of genomes among the organisms constituting the consortium, forcing these genomes to be incurred by synchronization and harmonization aimed at the proper functioning of the new organism as a whole. All these data should be incorporated into a new field of biological science, symbiogenic developmental biology, or informally, *symbio-devo*, merging symbiogenic evolution with developmental biology. These ideas imply the development of novel concepts for a better understanding of life and the emergence of complexity in nature, including the foundation of a new biological theoretical framework that can integrate and explain the dynamical organismal interactions and synergistic relationships present on Earth. This reality can be embodied and built in a symbiogenic theory of evolution. The development of such a theory could contribute towards a new epistemological approach to symbiotic phenomena in evolution specifically, and indeed biology in general, presenting new perspectives that allow for a better understanding of the web of life on our planet and beyond.

6 Main Milestones in Symbiogenic Studies Until 2003

1840 Pierre-Joseph Proudhon (1809–1865) develops the idea of *mutualism* applied to the social and political arena in the book *Qu'est-ce que la propriété* (What is Property?).

1867 Simon Schwendener (1829–1919) proposes in the Swiss Natural History Society annual meeting held in Rheinfelden (Switzerland) the dual hypothesis to explain the nature of lichens, indicating that they are an association of two organisms, a fungus and an alga, behaving as "master and slave."

1873 Johannes Reinke (1849–1931) refers to the relationship between the fungi and the algae in lichens as a *consortium.*

1875 Pierre-Joseph van Bénéden (1809–1894) introduces the *mutualism* concept for the animal kingdom in the work *Les Commensaux et les Parasites dans le Règne Animal* (*The Commensals and the Parasites in the Animal Kingdom*).

1877 Albert Bernhard Frank (1839–1900) introduces the term *symbiotismus* in a publication on the biology of lichens. This concept is similar to the symbiosis one introduced one year later by Anton De Bary.

1878 Heinrich Anton De Bary (1831–1888) introduces the concept of *symbiosis* (from Greek, meaning "living together") as "the living together of unlike named organisms" in a communication entitled "Ueber Symbiose" (On Symbiosis) during a meeting at Cassel (Germany) of the Congress of German Naturalists and Physicians. De Bary used this term when discussing the presence of the cyanobacteria in the leaf cavity of *Azolla* and also about the nature of lichens and the role of the alga and fungus in this association.

1883 Andreas Schimper (1856–1901) reports on the nature and growth of starch grains showing that they arise in specific organelles, which he named *chloroplasts*. He also noted the proliferation of these organelles through division, suggesting their symbiotic origin.

1885 Albert Bernhard Frank introduces the term "micorrhizen" *mycorrhiza* (fungus root) in a paper entitled "Ueber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze" (On the Nourishment of Trees Through a Root Symbiosis with Underground Fungi) in the *Berichte der Deutschen Botanischen Gesellschaft*, to describe the mutualistic associations between soil fungi and plant roots.

1893 Roscoe Pound (1870–1964) publishes in the journal, *The American Naturalist.* "Symbiosis and Mutualism." based on the communication with the same title read at the Botanical Seminar of the University of Nebraska on December 17, 1892.

1893 Shosaburo Watasé (1862–1929) gives the lecture "On the Nature of Cell-Organization" before the Biological Club of the University of Chicago, on February 7 of this year, where he defends the idea of the eukaryotic cell as a symbiotic community, and published the following year in the *Biological Lectures of Marine Biological Laboratory of Woods Hall.*

1897 Albert Schneider publishes in the *Minnesota Botanical Studies,* "The Phenomena of Symbiosis," and redefines symbiosis as "a contiguous association of two or more morphologically distinct organisms, not of the same kind, resulting in a loss or acquisition of assimilated food-substances."

1899 Herbert Spencer introduces in his revised and enlarged second volume of *The Principles of Biology* the idea of symbiosis as a division of labor, a synthesis of a complementary physiological functions, resulting from early divergence in the history of life.

1902 Petr Kropotkin (1842–1921) publishes *Mutual Aid. A Factor of Evolution*. In this work, Kropotkin argues that despite the Darwinian concept of the survival of the fittest, co-operation rather than conflict is the main factor in the evolution of species. The book was written while he was in exile in England.

1904 Theodor Heinrich Boveri (1862–1915) suggests that the nucleated cells arose from a symbiosis of two kinds of single plasma-structures, Monera, in a fashion that a number of smaller forms, the chromosomes, established themselves within a larger one which is called the cytosome. In conclusion, the chromosomes would be independent elementary organisms that live symbiotically in the cytoplasm. This idea was further deeply developed by Constantin Merezhkowsky.

1905 Constantin Sergeevich Merezhkowsky (1855–1921) publishes the article "Uber Natur und Ursprung der Chromatophoren im Pflanzenreich" (On the Nature and Origin of Chromatophores in the Plant Kingdom) where, for the first time, coherent scientific arguments show that plastids arose from free-living cyanobacteria.

1907 Andrey Sergeevich Famintsyn (1835–1918), a Russian botanist contemporary of Merezhkowsky, publishes "On the Role of Symbiosis in the Evolution of Organisms," where the author developed the idea that symbiosis has an important evolutionary, or even adaptative, meaning.

1909 Publication of "The Theory of Two Plasms as Foundation of Symbiogenesis, New Doctrine on the Origin of Organisms" in Russian. The German version is published one year later. Constantin Merezhkowsky writes the work during his stay at Kazan University, introducing the concept of symbiogenesis as "The origin of organisms by the combination or by the association of two or several beings which enter into symbiosis." In this paper, he introduces not only the new concepts in the symbiogenesis field, but he also develops some important ideas about the origin of life, namely related to the role of extremophiles in that scenario. A new classification of the living world is proposed using symbiotic criteria.

1910 Frederick Keeble (1870–1952) publishes *Plant-Animals. A Study in Symbiosis*, a study of the biology of two marine worms, *Convoluta roscoffensis* and *Convoluta paradoxa*, and their algae symbionts.

1913 Hermann Reinheimer publishes *Evolution by Co-operation. A Study in Bio-economics.*

1915 Hermann Reinheimer publishes *Symbiogenesis: The Universal Law of Progressive Evolution*, reinforcing the idea that natural co-operation was as strong a force in evolution as Darwinian natural selection.

1918 Paul Portier (1866–1962) publishes *Les Symbiotes*. In this work, Portier develops the idea that all organisms are constituted of an association of different beings. In the case of mitochondria, he argues that those organelles are symbiotic bacteria that the author calls "symbiotes."

1920 Constantin Merezhkowsky publishes in the *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France* (*Nantes*), "La Plante Considerée comme un Complexe Symbiotique" (The Plant Considered as a Symbiotic Complex) where the author develops his previous ideas on the symbiotic origin of chloroplasts and nucleus. In opposition to all the current views at the time, Merezhkowsky defends that chloroplasts have not evolved from mitochondria or protoplasm, but from free-living cyanobacteria.

1920 *Symbiosis: A Socio-physiological Study of Evolution* is published by Hermann Reinheimer. In the book, the author points out the importance of the specific interrelations in the development of organisms as a whole, giving us a holistic perspective of organismal evolution.

1921 Constantin Merezhkowsky commits suicide in a room of the Hotel des Familles in Geneva, Switzerland, after several years of exile (January 9).

1921 Paul Buchner (1886–1978) publishes his first book entitled *Tier und Pflanze in Intracellular Symbiose* (*Animals and Plants in Intracellular Symbiosis*).

1922 Maurice Caullery (1868–1958) publishes *Le Parasitisme et la Symbiose*, translated into English in 1952 with the title *Parasitism and Symbiosis.*

1923 George H.F. Nuttall (1862–1937) publishes in the journal, *The American Naturalist,* the article, "Symbiosis in Animals and Plants."

1923 Lemuel Roscoe Cleveland (1892–1969) publishes in the *Proceedings of the National Academy of Sciences* the article "Symbiosis between Termites and their Intestinal Protozoa" referring for the first time to the symbiotic nature of the intestinal flagellates of termites.

1923 Ivan Emmanuel Wallin (1883–1969) publishes in *The American Naturalist*, "The Mitochondria Problem," emphasizing the symbiotic origin of these organelles against the cytoplasmic point of view. He joined the University of Colorado in 1918 and the next year became professor of anatomy, a position he held for 32 years.

1924 Boris Kozo-Polyansky (1890–1957) publishes in Russian the monograph "A New Principle of Biology: An Essay on the Theory of Symbiogenesis." In this work, Kozo-Polyansky tries to integrate the symbiogenesis theory with the Darwinian one.

1927 Ivan Wallin publishes *Symbionticism and the Origin of Species*, where the author defends the importance of symbiotic mechanisms in evolution, with emphasis on the symbiotic origin of mitochondria. Wallin also emphasizes the importance of microsymbiosis in this process, pointing out the idea that "Bacteria, which are popularly associated with disease, may represent the fundamental causative factor in the origin of species."

1952 Joshua Lederberg (1925–2008) publishes an article in the journal *Physiological Reviews* entitled "Cell Genetics and Hereditary Symbiosis," where he introduces the term *plasmid* to describe extranuclear genetic structures that can reproduce independently. In the same article, he defends a symbiogenic approach to the origin of mitochondria and chloroplasts, pointing out the similarities between known bacterial symbionts and those organelles.

1962 The definitive proof of DNA in chloroplasts is made by Hans Ris (1914–2004) and Walter Plaut (1931–) suggesting that chloroplasts originate from endosymbiotic cyanobacteria as was postulated by Constantin Merezhkowsky. The work titled "Ultrastructrure of DNA-Containing Areas in the Chloroplast of *Chlamydomonas*" is published in *The Journal of Cell Biology.*

1963 The First International Conference on Symbiosis titled "Symbiotic Associations" takes place in London (April), held by the Society for General Microbiology in its Thirteenth Symposium.

1963 René Dubos (1901–1982) and Alex Kessler publish in the *Proceedings of the 1st International Conference on Symbiosis* the article "Integrative and Disintegrative Factors in Symbiotic Associations."

1963 Margit Nass and Sylvan Nass found DNA fibers in mitochondria, reinforcing the symbiotic origin of these organelles. These results are published in two papers of *The Journal of Cell Biology.*

1967 Lynn Margulis (1938–2011) publishes in the *Journal of Theoretical Biology* the article "On the Origin of Mitosing Cells." In this paper, a theory of the origin of the discontinuity between eukaryotic and prokaryotic cells is presented. Mitochondria, basal bodies of the flagella and chloroplasts, are considered to have derived from free-living cells, and the eukaryotic cell is seen as the result of the evolution of ancient symbioses.

1967 At the same time that Margulis' 1967 article was published, an oft-forgotten short paper by the Norwegian microbiologist Jostein Goksoyr (1922–2000) appeared in *Nature,* providing a similar endosymbiotic theory for the origin of eukaryotic cells.

1969 Ivan Wallin submitted a short paper titled "Symbioticism in the Light of Recent Cytological Investigations" to *Science* magazine. This paper was rejected without any comments.

1970 Lynn Margulis publishes the book, *Origin of Eukaryotic Cells: Evidence and Research Implications for a Theory of the Origin and Evolution of Microbial, Plant and Animal Cells on the Precambrian Earth,* in sequence with her previous article. Using information from cellular and molecular biology, she promotes the serial endosymbiotic theory for the origin of the eukaryotic cells.

1972 Kwang W. Jeon publishes in the journal, *Science,* a short article entitled "Development of Cellular Dependence on Infective Organisms: Micrurgical Studies in Amoebas" about the role of intracellular symbionts on cellular divergence and variation.

1975 James Lovelock (1919–) and Lynn Margulis propose the Gaia hypothesis, supporting the idea that Earth is a complex self-regulatory, flexible living system.

1976 Richard Dawkins (1941–) writes *The Selfish Gene*, redefining the concept of symbiosis to include relations between individuals of the same species. He also introduces says that there is no selection for "the good of species" and "we are gigantic colonies of symbiotic genes."

1979 Liya N. Khakhina publishes in Russian the book, *Problema Simbiogeneza: Istoriko-Kritichesky Ocherk Issledovany Otechestvennykh Botanikov*, translated into English in 1992 as *Concepts of Symbiogenesis. A Historical and Critical Study of the Research of Russian Botanists*, and edited by Lynn Margulis and Mark McMenamin, an important contribution to the knowledge of the history of symbiosis research in Russia.

1981 Lynn Margulis publishes *Symbiosis in Cell Evolution: Life and its Environment on the Early Earth*. In this book, the author presents a modern synthesis of the mechanisms and processes of cell evolution, offering a coherent explanation of how eukaryotic cells evolved from bacterial ancestors by a series of symbioses. In this sense, the origin of the eukaryotic cell is perceived as a special case of a general phenomenon, the evolution of microbial associations.

1982 Christian de Duve (1917–2013) suggests that peroxisomes arose from aerobic bacteria that were adopted as endosymbionts before mitochondria.

1985 Douglas H. Boucher (1950–) edits *The Biology of Mutualism. Ecology and Evolution*. This book develops the point of view that the mutually beneficial interactions between species are just as important as competition and predation, and how mutualisms affect population dynamics and community structure.

1987 David C. Smith and Angela E. Douglas publish *The Biology of Symbiosis*. This important textbook was primarily aimed at filling a gap in the symbiosis literature to base a course in the field for the biology curricula at the university level.

1988 The Microcosmos Project begins. This project co-ordinated by Douglas Zook and Lynn Margulis at the University of Boston aims at the use of the microorganism world for a more earth-conscious approach to education, with particular interest in co-operative biological systems and the maintenance of species diversity.

1991 The book *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis* is published. It is edited by Lynn Margulis and René Fester.

1991 Francisco Carrapiço (1951–) publishes in the journal *Plant and Soil* the article "Are Bacteria the Third Partner of *the Azolla-Anabaena* Symbiosis?" presenting data showing that bacteria existing in the *Azolla* leaf cavities and megasporocarps follow a developmental pattern identical to the cyanobacteria *Anabaena azollae* and can be considered the third partner of the symbiotic association.

1994 Jan Sapp (1954–) writes *Evolution by Association. A History of Symbiosis*, an important scientific landmark in the history of symbiosis theory.

1994 Angela Douglas publishes *Symbiotic Interactions*, considering that "The common denominator of symbiosis is not mutual benefit but a novel metabolic capability, acquired by one organism from its partners."

1996 Peter Corning (1935–) publishes in the *Journal of Evolutionary Theory* the article "The Co-operative Gene: On the Role of Synergy in Evolution," an important contribution to understanding evolution in a more synergistic and cooperative way.

1997 The International Symbiosis Society (ISS) is founded on April 15 at the Second International Symbiosis Congress in Woods Hole, United States.

1998 Lynn Margulis publishes *Symbiotic Planet. A New View of Evolution*, a personal and autobiographical journey to the science and symbiosis world.

1998 Douglas Zook in the article, "A New Symbiosis Language," published in the *ISS Symbiosis News*, proposes a new definition for symbiosis: "Symbiosis is the acquisition and maintenance of one or more organisms by another that results in novel structures and metabolism. Some symbiotic evolution may involve partner genetic exchanges."

1999 William Martin and Klaus V. Kowallik publish in the *European Journal of Phycology* the annotated English translation of Merezhkowsky's (1905) paper "Uber Natur und Ursprung der Chromatophen im Pflanzenreich" (On the Nature and Origin of Chromatophores in the Plant Kingdom).

2000 Surinder Paracer and Vernon Ahmadjian write *Symbiosis. An Introduction to Biological Associations.*

2000 Rosmarie Honegger publishes in the journal, *The Bryologist,* the article, "Simon Schwendener (1829–1919) and the Dual Hypothesis of Lichens."

2000 Marc-André Selosse writes *La Symbiose: Structures et Fonctions, Rôle Ecologique et Évolutif.*

2002 The book *Cyanobacteria in Symbiosis* is edited by Amar N. Ray, Birgitta Bergman, and Ulla Rasmussen. It is a reference work in the field of plant–cyanobacteria interactions and nitrogen biological fixation.

2002 Joseph Seckbach (1934–) edits *Symbiosis: Mechanisms and Model Systems*, providing in a clear and broad way the inter- and multidisciplinary dimension of the interspecific relationships, and their mechanisms of work and evolution.

2002 Lynn Margulis and Dorion Sagan (1959–) publish *Acquiring Genomes. A Theory of the Origins of Species*. In this work, the authors point out that the acquisition of new genomes involving symbiogenic processes is the main driving force in evolution, not random mutations, and include a solid criticism of neo-Darwinism.

2002 Jan Sapp, Francisco Carrapiço, and Mikhail Zolotonosov (1954–) publish in the journal of *History and Philosophy of the Life Sciences* the article, "Symbiogenesis: The Hidden Face of Constantin Merezhkowsky," revealing the controversial dimension of his life and work.

2003 Jan Sapp introduces the terms *symbiomics* and *symbiome* in his new book *Genesis. The Evolution of Biology*, revealing a new approach to the understanding of this science in an evolutive perspective, reinforcing its symbiogenic component. In this work, the author points out an important and innovative idea that

> Every eukaryote is a superorganism, a symbiome composed of chromosomal genes, organellar genes, and often other bacterial symbionts as well as viruses. The symbiome, the limit of the multicellular organism, extends beyond the activities of its own cells. All plants and animals involve complex ecological communities of microbes, some of which function as commensals, some as mutualists, and others as parasites, depending on their nature and context.

Acknowledgments I am grateful to Nathalie Gontier and Maria Helena Costa for their encouragement in the development of this work and to Helena Carrapiço and Ben Farrand for the English revision of the text. Also, a word of gratitude to Jonathan Bujak for helping to obtain information about Hermann Reinheimer related to the 1911 England Census, and to Padmavathi Jayajeevan for the excellent work in publishing this chapter.

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