Hist. Phil. Life Sci., 24 (2002), 413-440

Symbiogenesis: The Hidden Face of Constantin Merezhkowsky

Jan Sapp

Centre interuniversitaire de recherche sur la science et la technologie
Université du Québec à Montréal
Case postale 8888, succursale Centre-ville
Montréal, Québec, Canada

Francisco Carrapiço

Centro de Biologia Ambiental
Departamento de Biologia Vegetal
Faculdade de Ciências da Universidade de Lisboa
Bloco C2, Campo Grande, 1749-016 Lisboa, Portugal

Mikhail Zolotonosov

191028, St. Petersburg,
Nevsky prospect, 70, Russia

ABSTRACT - Constantin Merezhkowsky is celebrated today for his theory of symbiogenesis, postulated in the early decades of the twentieth century, particularly that chloroplasts were symbiotic cyanophytes (cyanobacteria). While biologists point singularly to what they see as his heroic achievement, its neglect and subsequent rediscovery, we introduce a broader and much more complex perspective on his science, his troubled life and career. We present a view of Merezhkowsky as zoologist, anthropologist, botanist, philosopher, and novelist. We explain the genesis of his theory of the origin of chloroplasts and of nucleus and cytoplasm as symbionts, as well as his depiction of the geo-chemical context of the origins and early evolution of life on earth. We also disclose his sordid social and political activities, his eugenics and racist writings, his paedophilia, and his metaphysics. Finally, we describe the context of his elaborate suicide in 1921.

Introduction

Constantin Sergeevich Merezhkowsky (1855-1921) is well-known today as a champion of symbiogenesis.[1] He is celebrated especially for his arguments, in the first decades of the Twentieth Century, that chloroplasts had originated as *Cyanophyceae*. Ignored, or denounced as speculative, ideas about the symbiotic origin of cell organelles have

[1] 'Mereshkowsky' is the spelling of his name he used in nineteenth-century British published papers. In German publications it is 'Merezhkowsky'; in publication in French the spelling was 'Mérejkovsky', but in manuscripts in French he spelled his name 'de Mereschkovsky.'

0308-7298/90 $ 3.00 © 2002 Taylor and Francis Ltd

had a renaissance beginning in the 1970s with new molecular evidence that chloroplasts and mitochondria each has their own DNA and protein synthesis apparatus.[2] Merezhkowsky's papers of 1905 and 1909/10 long forgotten, ridiculed or marginalised have now received worldwide acclaim; he is now loudly acclaimed today as the 'founding father' of symbiogenesis (Martin and Kowallik 1999; Khakhina et al 1993; Margulis 1993; Dyer 1994). While biologists have applauded his heroic theoretic achievements, historians have placed him in the context of the history of research on symbiosis in evolution more generally (Sapp 1994; 2003b).

Here we offer a broader contextual overview of Merezhkowsky's complex career, first as a young student in St Petersburg, then his travels in northern Russia, France, Germany and the United States in the Nineteenth and early Twentieth Centuries. We trace his interest in chloroplasts to his studies of the natural history of protists, especially diatoms and their classification. We also emphasize his symbiotic theory of the origin of the nucleus and cytoplasm as well as the geochemical context he offered for the early evolution of life on earth. Finally, we place Merezhkowsky's scientific life in the larger context of his metaphysical, spiritualist beliefs, his paedophilia, and socio-political activities during turbulent times in Russia. We explore how these relate to the larger philosophical meaning he gave to symbiogenesis, and we describe the context of his elaborate suicide in 1921.

Marine Expeditions to Lichens

Merezhkowsky was born July 23, 1855 (August 4, Western calender) in Warsaw then part of the Russian empire. His father, Sergey Ivanovich Merezhkowsky (1823-1908) was a high official of the Czar's court office; toward the end of his career he served as secret counsellor (Zolotonosov 2003).[3] He was a self-centred and conservative man, and in Constantin's student days, he and his father quarrelled over political issues. Constantin, at that time, ideologically supported Russian revolutionaries; he was also fond of the writings of Herbert Spencer and of atheism. His father disapproved of his choice to enter the natural sciences, wishing he would enter the faculty of law instead, so as to become an official clerk.

[2] Since 1980 there have been more than 200 citations to Mereshkowsky's papers of 1905 and 1910. Science Citation Index. (Mereshkowsky 1905 ; 1910 ; 1920c).

[3] Constantin was the eldest son; he had five brothers and three sisters.

Fig. 1 – Constantin Merezhkowsky. From *Prjamoj Put*, April 1911, p. 1101.

Constantin began his studies in natural science at the University of St. Petersburg in 1875. The following summer, he went on an expedition to the White Sea whose flora and fauna were almost completely unknown. His main interest was in 'marine invertebrate animals;' he discovered a 'new genus of hydroids' and he described other new species of hydra from the Zoological Museum of the St. Petersburg Academy (Merezhkowsky 1877; 1878c; 1878b).[4] In 1877, he published studies on the Protozoa of Northern Russia, and later, he reported on some new and 'some little-known species of Infusoria': two from the White Sea, three from the Black Sea, and two from the Bay of Naples (Merezhkowsky 1877; cited in 1881b, 215). His interest in protists began with his discovery of what he had thought was a new species of sponge in 1878. He named it *Wagnerella borealis* in honour of his 'master', Professor Nicolas Wagner. Three years later, following his observations of other specimens in the Bay of Naples and studies of the preparations of German biologist Paul Mayer, Merezhkowsky concluded that, in fact, the protoplasmic mass of the organism was not formed by cells but was actually only a single cell. *Wagnerella* thus belonged to the class protozoa (Merezhkowsky 1878; 1881d).

Merezhkowsky's career was unsettled between 1880 and 1902. After graduating with the diploma of *Kandidat* (with distinction) in Natural Sciences in 1880, he travelled to France and Germany where he visited with well-known naturalist and marine zoologist Henri Lacaze-Duthiers (1821-1901) in Paris, founder of the biological station at Roscoff (1872), and he visited with famed cell pathologist Rudolph Virchow (1821-1902) in Berlin. Virchow was well known not only for his book, *Die Cellularpathologie* of 1858, but in later life he devoted himself to archaeology and anthropology. Virchow formed a close friendship with Heinrich Schliemann, the discoverer of the site of Troy, and he had accompanied Schliemann to Troy the year before Merezhkowsky arrived (Brackman 1974). Merezhkowsky turned to anthropology for a while, becoming a member of the *Société d'Anthropologie de Paris* in 1881, and publishing papers on Sardinian and American sculls (Merezhkowsky 1882b; 1882c; 1882d; 1883b).

Merezhkowsky also investigated animal pigments during the early 1880s, publishing his preliminary work in France, where he became a member of *Société Zoologique de France* (Merezhkowsky 1881; 1881c; 1882; 1883a; 1883c). After a public defence of his research on animal pigments, at the University of St. Petersburg in December 1883, and

[4] The hydroids, collected and preserved by Mereshkowsky, are kept today in the Zoological Institute of the Russian Science Academy, St. Petersburg.

after two test lectures he was permitted to deliver lectures on zoology as *Privatdocent*. He married Sultanova Olga Petrovna that year. But three years later, he and his wife suddenly left St. Petersburg to live in the Crimea. In 1891, he worked as a pomologist supervising the fruit-tree gardens of Livadia and Massandra, and he conducted research on grape varieties. In 1898, he left the Crimea, travelled to the Russian Biological Station in Villefranche near Nice for a few months, and then to the United States where he remained until 1902 conducting research, first at the Biological Station of San-Pedro in Los Angeles, and then at Berkeley University. During this period, he focussed especially on describing and classifying the unicellular algae, diatoms which he had begun in the Black Sea.

Merezhkowsky offered a new classification when he divided diatoms into two divisions those which are mobile and those which are immobile (Merezhkowsky 1901; 1902). Diatoms had been classified exclusively on the basis of dead shells, but he argued that such classification needed to be supplemented by studies of their internal cellular organization: 'New genera, based on cell-contents, will be founded, new groups established, and the affinities of the diatoms will prove to be very different from what is now supposed to be true' (Merezhkowsky 1901b, 185). While in the United States, he published a series of papers on the classification of diatoms with famed Swedish chemist, Per Theodor Cleve (1840-1905) from the University Uppsala, renowned for his discovery in 1879 of the rare-earth elements holmium and thulium. Cleve had turned to biology in the 1890 with oceanographic expeditions on which he investigated freshwater algae, plankton, and especially diatoms.[5] He and Merezhkowsky reclassified some standard diatoms based on Merezhkowsky's descriptions of their internal organization: chloroplast (chromatophore) number and structure characteristics (pyrenoid and endochrome) (Cleve and Merezhkowsky 1902).[6] The true structure of chloroplasts became an issue of considerable significance for Merezhkowsky's symbiotic arguments.

Merezhkowsky returned to Russia in the summer of 1902 and was appointed to the position of curator of the zoology museum at Kazan University. The following year, he passed his *Magister* with a dissertation in botany 'On the Morphology of Diatoms'.[7] He was appointed *Privatdocent* in botany 1904. The year before, he had begun to associate

[5] Cleve developed a method for determining the age and order of late glacial and post-glacial deposits from the types of diatom fossils in the deposits. This use of diatoms was subsequently applied to determining the origin of ocean streams.

[6] Throughout this paper, we use the term chloroplast for 'chromatophore' (used by Merezhkowsky).

[7] The *Magister* is equivalent to an American Master's degree.

his studies of the morphology of diatoms, the internal organization of cells, chloroplasts, nucleus and cytoplasm with symbiosis. His turn to symbiosis, like that of so many others, began with research on lichens.

Symbiogenesis

The dual nature of lichens as fungi and algae, first reported by Swiss botanist Simon Schwendener in 1867, had led several biologists to consider the role of symbiosis in evolution (Schwendener 1867; Sapp 1994). Lichens showed how new organisms could be synthesized out of two different kinds of organisms living in intimate association. Herbert Spencer had used the lichen symbiosis as microcosm of his super-organismic outlook on life. He saw it as a 'communistic arrangement' based on a division of labour between the plant and animal (Spencer 1889, vol. 2, 399-400).[8] But interpretations of the relationship between algae and fungi varied, as botanists employed a variety of anthropomorphic metaphors: Schwendener viewed the lichen in terms of slavery, by a fungal master over captured algae, Johannes Reinke interpreted the relationship as a consortium (Reinke 1873).

Famed German biologist Anton de Bary coined the term symbiosis in 1879 as a neutral word simply to mean the living together of two or more differently named organisms - to embrace a continuum of relationships from parasitism to mutualism (De Bary 1879). The term s*ymbiotismus* had been used the previous year by Albert Bernard Frank, remembered today especially for his pioneering studies of the symbiosis between fungus and roots of plants which he called 'mycorrhiza' (Frank 1885). Beginning in the 1880s, there was evidence of algae living inside protozoa, and in the tissue of sponges, hydra and certain worms. The symbiosis of nitrogen-fixing bacteria in the root nodules of legumes was also shown to be a widespread phenomenon (Sapp 1994).

When such examples of symbiosis were considered in light of new cytological evidence of the physical continuity of chloroplasts, they led many researchers to suggest that various parts of the cell (nucleus, cytoplasm, chloroplasts, mitochondria and centrioles) had evolved as symbionts. That chloroplasts might have arisen as independent symbiotic organisms had been mentioned by many biologists in the 1880s and1890s including de Bary's former student Andreas Schimper, Schwendener's former student Gottlieb Haberlandt as well as Reinke, and Ernst Haeckel in Germany, Ray Lankaster in England, and Albert

[8] For historical discussions of the different meanings of symbiosis see Sapp, 1994, 25-28.

Schneider, Edmund B. Wilson, and Shôsaburô Watasé in the United States among others (Sapp 1994). Merezhkowsky recalled that the idea had come to him 'in a completely spontaneous way' after reading Schimper's classic paper of 1885 (Mérejkovsky 1920c). Schimper had also suggested that chloroplasts may have arisen by symbiosis in his famed paper of 1883 in which he coined the term 'chloroplast':

> If it can be conclusively confirmed that plastids do not arise de novo in egg cells, the relationship between plastids and the organisms within which they are contained would be somewhat reminiscent of a symbiosis. Green plants may in fact owe their origin to the unification of a colourless organism with one uniformly tinged with chlorophyll (Schimper 1883, 112-113).

Ideas about the role of symbiosis in evolution were known in Russia as they were elsewhere.[9] In the late 1880s and early 1890s, well-known plant physiologist Andrei Famintsyn (1835-1918) at the University of St. Petersburg, inspired by the dual nature of lichens, conducted experiments to extract and culture Zoochlorella and Zooxanthella from lower animals with the idea that if he were successful, he would hope to culture chloroplasts (chromatophores) from plant cells (Famintsyn 1889b; 1891; 1889; 1892).[10] Merezhkowsky's relationship with Famintsyn was strained, to say the least. He had begun communicating with him when he was in the United States. In 1901, Famintsyn refused to publish his paper on the organization and affinity of Diatoms in the journal of the St. Petersburg Academy. On May 7, 1903, Merezhkowsky wrote to him, mentioning his own interest in chloroplasts:

> I am very interested in the significance of chromatophore grains (whether they are organs or independent organisms) and plan to work further in this direction. I know that you have done considerable work on this issues, and if I recall correctly, you even tried to cultivate grains in isolated form. I would appreciate it if you would mail me offprints of your papers about this (Merezhkowsky 1903).

[9] Khakhina and Margulis have suggested that symbiogenesis was at the forefront of Russian evolutionary thought during the early 20th Century. (Khakhina et al 1992; Margulis 1991). However, Famintsyn and Merezhkowsky themselves made statements actually lamenting that symbiosis as a means for synthesizing new organisms was not taken into consideration in discussions of evolutionary theory in Russia as elsewhere. (Sapp 1994). Indeed, symbiosis in evolution is completely absent from Daniel Todes and Alexander Vucinich mentions symbiosis only in passing when discussing Famintsyn's attitudes toward Darwinism that he advocated a 'mental' factor as a key evolutionary element even among 'the lowest forms of life.' However, Todes does argue that mutual aid was a common feature of Russian evolutionary thought in the late nineteenth and early twentieth centuries (Todes 1989; Vucinich 1988).

[10] Merezhkowsky mentioned Famintsyn only once, in a footnote in his paper of 1905, p.559, to state that in 1889 Famintsyn had studied the independent nature of chromatophores and believed it was possible that one might be able to cultivate them outside of the cell.

Famintsyn did not reply. In 1906, a year after Merezhkowsky's first paper on the subject appeared, Famintsyn published a paper on chloroplasts as symbionts, in *Mémoire de l'Académie des sciences de St Peterburg* (and in 1907 in *Biologische Zentralblatt*) suggesting again that it might be possible to cultivate plastids outside the cell. He also ridiculed Merezhkowsky's paper of 1905 for being ill-informed: 'I could not help suspecting that the author knows little about this question, and moreover, that he possesses only a vague knowledge of the literature that deal with the subject' (Famintsyn 1907, 261).

Despite Famintsyn's denunciations of his young 'rival', Merezhkowsky's name became so associated with the idea that chloroplasts were symbionts during the first decades of the century that he was often credited as its originator. And no one did more to transform the idea into a full-blown theory than Merezhkowsky, first, in his now famous paper of 1905, written in Russian and German 'On the Nature and Origin of Chromatophores in the Plant Kingdom' (Merezhkowsky 1905) and finally in his most extensive paper, '*La plant considérée comme un complexe symbiotique*,' which he completed in Geneva a few weeks before the end of the First World War (Mérejkovsky 1920c, 17).

Merezhkowsky laid out carefully what he regarded as proof that chloroplasts represented organisms introduced into the cell from outside. His theory contained four main components: 1) the independent reproduction of chloroplasts, 2) their physiological and morphological similarities with Cyanobacteria, 3) their functional analogy with examples of algal symbiosis in animals, and 4) the polyphyletic origin of life. We examine each in turn.

1) The general opinion expressed in botanical treatises was that chloroplasts arise inside plant cells as a result of the gradual differentiation of the protoplasm of the cytoplasm. However, Merezhkowsky argued that chloroplasts do not arise *de novo*; they reproduce by division, and are not included in the hereditary substance of the nucleus. He claimed that he had shown this to be true for diatoms, and that Schimper and his successors had demonstrated that plastids of plants exist in the egg in the form of colourless leucoplasts, and exist in the spores of a plant in the form of chloroplasts. When the eggs or spores of a plant divide to form tissues of the new plant, the chloroplasts also divide and distribute themselves in the new cells. Thus, there was an uninterrupted continuity of chloroplasts. They were never formed anew (Mérejkovsky 1920c, 26).

In Merezhkowsky's view, the physical continuity of chloroplasts provided one of the important proofs that they had been independent organisms which entered a primitive cell at the beginning of the vegetable kingdom. The assumption that chloroplasts originated by differentiation, he argued, concealed 'a gross mistake in logic and lacked any comprehension of the essence of heredity' -because if chloroplasts had first emerged by differentiation within a protist in the remote past, one would have to explain why the cell had lost the ability to make them (Mérejkovsky 1920c, 27). Therefore, 'The continuity of chromatophores proves that they are organisms which came from outside and by consequence that the plant is a symbiosis' (Merezhkowsky 1920c, 28).

2) There was no consensus in regard to the structure of cyanophytes. Generally, they were understood to be a group of plants which resembled algae in some respects, but possessed some very marked structural differences. Observations of these extremely small organisms with microscopes of the day were far from straightforward. There were diverse interpretations of their structure and phylogenetic relationships. The central question concerned the presence or absence of a nucleus and/or chloroplasts. Some German cytologists maintained that cyanophytes contained numerous chloroplasts surrounding a *nucleus* with chromosomes. Others asserted that they were contained one chloroplast with cytoplasm at its core, and they lacked a nucleus. Merezhkowsky asserted that both views were incorrect: cyanophytes possessed neither nucleus nor chloroplast. The cyanophyte as a whole was a single chloroplast. The central body was neither a nucleus, nor cytoplasm; it was a pyrenoid, the starch forming centre of a chloroplast (Mérejkovsky 1920c, 39). The only difference between the cyanophyte and the chloroplast, he argued, was that the former had a membrane composed of a nitrogenous substance whereas the chloroplasts lacked a membrane. Cyanophytes and chloroplasts also shared two remarkable physiological properties. Both were able to transform inorganic substances into carbohydrates, and to produce the synthesis of albumous substances (proteins) out of inorganic substances.

Other cytologists of the early twentieth century had proposed that chloroplasts were derived from mitochondria. Merezhkowsky rejected that notion, as well as the proposition that mitochondria were symbionts. In fact, he considered such ideas to be wholly antagonistic to his theory of the symbiotic nature of plants but also his 'theory of the two plasmas' which will be discussed momentarily. If mitochondria were actually symbionts, he declared all of his 'theory of symbiogenesis would fall in ruin'.[11]

[11] (Mérejkovsky 1920c, 84). That mitochondria were symbiotic bacteria was developed into a comprehensive theory by the French biologist Paul Portier whose experiments and theorizing on *Les Symbiotes* caused great controversy in France in the years following the First World War. (Portier 1918; Sapp 1994).

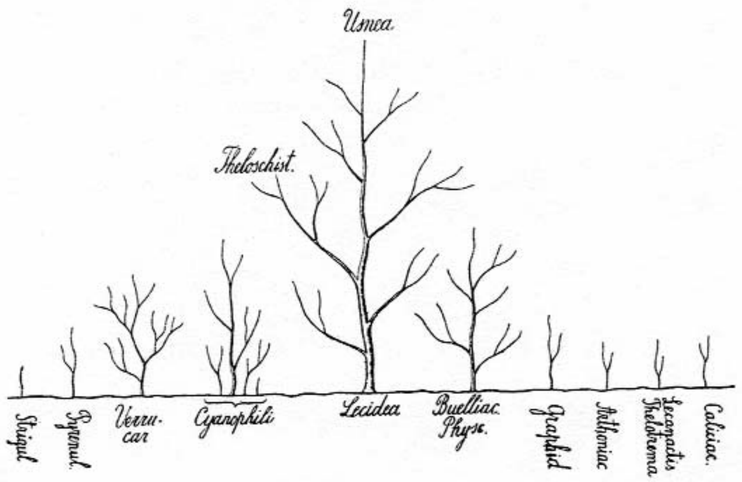

FIG. 7. — **Phylogénie des lichens.**

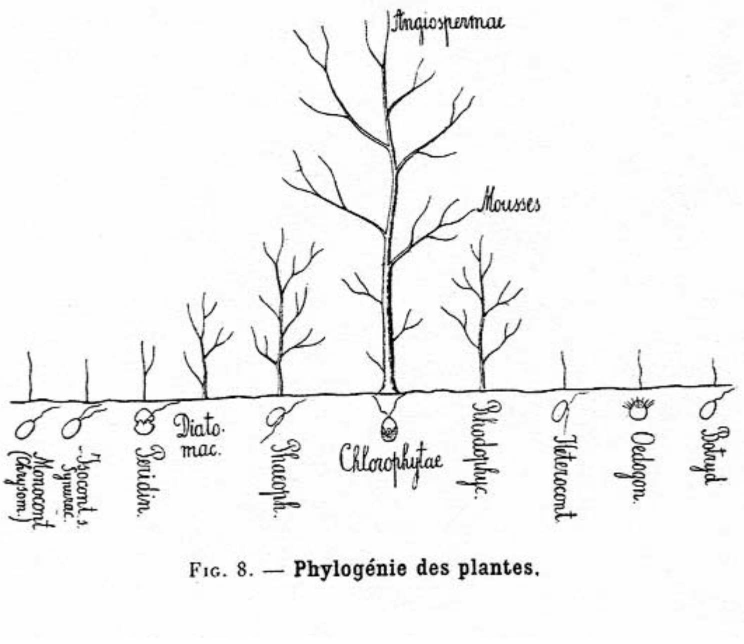

FIG. 8. — **Phylogénie des plantes.**

Fig. 2 – C. Merezhkowsky, 'La plante considérée comme un complexe symbiotique', *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France*, 6 (1920): 17-98, fig. 7, 8.

3) The well-established cases of symbiosis also lent support to his claim that chloroplasts were in reality cyanophytes. *Anabaena cycadeae*, living in the intercellular spaces of the roots of cycads, investigated by British Botanist Ethel Rose Spratt, merited special attention because this showed the great tendency of cyanophytes to enter into symbiotic relations with various kinds of organisms (Spratt 1911; Mérejkovsky 1920c, 81). Merezhkovsky further pointed to cases of algae (Zoochlorellae and Zooxanthellae) living symbiotically in protozoa, freshwater sponges, hydra and certain Turbellarians. By 1918, he could argue that symbiotic algae had been found in almost every class of 'lower invertebrates'. The various cases of protozoa containing Cyanophyceae were actual examples of 'animals on the way to becoming plants.' 'In creating these strange beings,' these 'plant-animals', he argued, 'nature seems to have wanted to give us a demonstration *ad oculos* of the symbiotic nature of the plant and teach us how the vegetable world had taken birth' (Mérejkovsky 1920c, 82).

4) The phylogeny of lichens offered Merezhkowsky a model for the phylogeny of all plants. Lichens had a polyphyletic origin: each of the (at least ten) phylogenetic lines of this order had a completely independent origin from the others, and each had originated by a combination of different fungi with different algae, and diverse *Cyanophyceae* (Mérejkovsky 1920c, 56-59). Similarly, he argued that plants originated several times - due to symbiosis: all algae were due to symbiotic combinations of diverse flagellates with diverse cyanophytes. Brown algae originated from the combination of a flagellate and a brown cyanophyte; red algae from a combination of a flagellate with a red cyanophyte; green algae from ciliated and flagellated Infusoria (Mérejkovsky 1920c, 60-62). As Merezhkowsky remarked, 'I believe it would be no exaggeration to say that the vegetable kingdom had originated at least fifteen times' (Mérejkovsky 1920c, 62).

In the phylogenetic landscape he imagined, both lichens and plants 'represented a grove of immense oak trees isolated on a meadow'. The animal kingdom was represented mainly by one single branching tree of Metazoa stood in stark contrast to these groves. But the animal world was also the result of a symbiosis - that of different Monera (cytoplasm) with different bacteria (nucleus). Growing around the large tree of Metazoa were small groups of 'Sporozoa' of independent origin which had acquired the dimensions of phylogenetic 'shrubs'. In addition to these, there were very small groups of Infusoria of independent origin which represented 'the grass of the lawn on which the great tree of animals grows' (Mérejkovsky 1920c, 62). (See figure 2).

Mycoplasm and Ameoboplasm, Nucleus and Cytoplasm

Merezhkowsky supported his views about chloroplasts as Cyanophytes with a brief comment from Haeckel who, when discussing the phylogeny of plants, remarked that one could 'suppose that Cyanophyceae are only individual chloroplasts of real plants.' But Merezhkowsky commented: 'As one can see, it is only a simple assertion, a pure supposition that Haeckel has not even tried to support with any fact, or argument. As a theory, I was the first to establish it in 1905' (Mérejkovsky 1920c, 19).

Haeckel was one of the first biologists to seriously consider the bacteria in a phylogenetic context (Haeckel 1866). He placed them in the order Moneres (later Monera) at 'the lowest stage of the protist kingdom'. Bacteria were unique, he argued, because unlike other protists, they possessed no nucleus. They were as different from nucleated cells as 'a hydra was from a vertebrate', or 'a simple algae from a palm' (Haeckel 1904, 205). Haeckel had postulated the existence of such non-nucleated primitive life as part of his 'monist philosophy', of life in terms of physical laws which break down the explanatory barrier between life and non-life. In his *Wonders of Life* of 1904, he included the Cyanophyceae or 'Chromacea' (blue green algae) among the Moneras with the bacteria. Though they were usually classified as a class of algae, Haeckel asserted that they lacked a nucleus and that the only real comparison between them and plants was with the chromatophores (chromatella) (chloroplasts). Thus, he suggested that the plant cell evolved as 'a symbiosis between a plasmodomonous green and plasmophagus not-green companions' (Haeckel 1904,195-196). Despite Haeckel's modern vision, bacteriologists continued to refer to the colorless bacteria as plants, and to cyanophycae as algae. The debate over the structure of bacteria was not resolved until the deployment of the electron microscope after the Second World War (Sapp 2003).

Haeckel's ideas were also at the basis of Merezhkowsky's proposal of an earlier symbiosis of nucleus and cytoplasm. Haeckel imagined that the simplest elementary organisms, entities he called 'cytodes,' consisted entirely of an albuminous substance, not yet differentiated into nucleus and cytoplasm.[12] Organisms supposed to be of the nature of cytodes constituted his systematic division Monera, comprised of the Phytomonera and the Zoomonera. The Phytomonera had their formative substance coloured green and to live in a plant-like manner (cyanophytes). The Zoomonera were colourless amoeboid masses which nourished themselves in the manner of animals.

[12] (Haeckel 1866). For a detailed review of Haeckel's concept of Monera, see Minchin 1915, 437-464.

The idea of structureless amoeboid organisms, without nuclei, filling the gap between the living and the nonliving, caught the imagination of biologists. T.H. Huxley claimed to verify the Monera hypothesis in sticky mud dredged in 1857 from the North Atlantic depths during the *Challenger* expedition (Rehbock 1976). He baptized the new species and genus *Baythibius haeckellii* and suggested that it covered large swaths of the ocean floor with a layer of primordial protoplasm. Unhappily this creature, or rather creation, was denounced during the 1870s, and Huxley conceded in 1879 that *Bathybius*, far from being Monera, was actually a precipitate induced by the application of chemical preservatives (alcohol) to organic substances (gypsum) in the seawater. Although many of the organisms Haeckel had classified as Monera were subsequently found to contain a nucleus, leading cell biologists insisted that simple cells made up of protoplasm lacking a nucleus may well have existed in the remote past, if not today.[13]

The existence of Monera was central to Merezhkowsky's theory of the origin of nucleus and cytoplasm. In 1909, he published his paper, 'The Theory of the Two Plasms as the Foundation of Symbiogenesis: New Doctrine on the Origin of Organisms', first in Russian, the next year in German. In it he elaborated his argument, proposed in 1905, that the nucleus of the cells of plants and animals represented a colony of bacteria living in symbiosis with another organism made up of simple protoplasm (Merezhkowsky 1910). He offered the term *symbiogenesis* for 'the origin of organisms by the combination or by the association of two or several beings which enter into symbiosis' (Merezhkowsky 1920c, 65). But again, he was not the first to suggest such a symbiosis. That the nucleus and cytoplasm represented symbiosis between two kinds of organisms had been argued at Woods Hole in 1893 by C. O. Whitman's student Shôsaburô Watasē, well known among American embryologists and cytologists. The idea was also suggested by famed German cytologist Theodor Boveri, who in 1904 suggested that the nucleated cell arose from a 'symbiosis of two kinds of simple plasma-structures – Monera, if we may so call them – in a fashion that a number of smaller forms, the chromosomes, established themselves within a larger one which we now call the cytosome' (Boveri 1904, 90; quoted in Wilson 1925, 1108). However, neither Boveri nor Watasē developed this idea.

[13] As microscopic methods improved, Haeckel recognized that many of the organisms he had assigned to Monera were either non-existent, or turned out to have a nucleus. Among his original examples, only *Vibrio* was true to the definition.(Haeckel 1904, 195-196; Geison 1969).

Merezhkowsky did develop it. He not only speculated on the physiological properties of the organisms involved, he also offered a reconstruction of the conditions for the origin of plant and animal cells from two sorts of protoplasm, which he called *mycoplasm* and *amoeboplasm*. Each was supposed to differ fundamentally in nature and to have historically distinct origins in different epochs of the earth's history. Bacteria, the chromatin grains of the nucleus, and chloroplasts were supposed to be of the nature of *mycoplasm*, the cytoplasm of nucleated cells was to be of *ameoboplasm*. Merezhkowsky also included observations about extremophile cyanophytes he studied in California, and startling deductions about the cyanophytes and the development of the first organisms on earth. He noted that cyanophytes could live and produce in temperatures approaching the boiling point, and that some spores of *Bacillus anthracis* could survive in temperatures of about 140° C. His conclusion was that these organisms made of mycoplasma were the first organisms on earth. Thus, he divided organisms into the Mycoidei and the amoeboidei.

He divided the history of the earth into four epochs. In the *first* epoch, the earth was an incandescent mass of vapour; in the *second*, it had a firm crust. Mycoplasm was the first type of protoplasm which came into existence during what he called the *third* epoch, at a time when the crust of the earth had cooled sufficiently for water to be condensed upon it, but when the temperature of the water was still near the boiling point. Consequently, the waters of the globe were free from oxygen, while saturated with all kinds of mineral substances. The origin of the second type of protoplasm, amoeboplasm was supposed to have taken place during a *fourth* terrestrial epoch when the waters covering the globe were cooled down to below 50° C, and contained dissolved oxygen but few mineral substances. The different nature and constitution of these two types of protoplasm corresponded to the differences of the epochs and the conditions under which they arose.

He called the earliest forms of life 'Biococci'. These were minute, ultramicroscopic particles of mycoplasm, without organization, capable of existing in temperatures close to the boiling point and in the absence of oxygen. Biococci possessed the power of building up proteins and carbohydrates from inorganic materials and were very resistant to strong mineral salts and acids and to various poisons. The bacteria arose from Biococci, and were for a long time the only living inhabitants of the earth. Later, when the temperature of the terrestrial waters had been lowered below 50° C, and contained abundant organic food (bacteria), amoeboplasm emerged in small masses as non-nucleated Monera. They crept in an amoeboid manner on the floor of the ocean, devouring bacteria. The next step in evolution occurred when, in some cases, bacteria ingested by the non-nucleated Monera, resisted digestion and maintained a symbiotic existence in the amoeboplasm. At first, the symbiotic bacteria were scattered in the Moneran body, but later, they became concentrated at one spot, surrounded by a membrane, and gave rise to the cell nucleus. This was an immense step forward in evolution because the locomotor powers of the simple and delicate Monera were now supplemented with the great capability of the bacteria to produce the most diverse kinds of ferments (enzymes).

Meanwhile, the free bacteria continued to evolve, giving rise to the cyanophytes, and to the whole group of fungi. The plant cell came into existence by a further process of symbiogenesis, in that some of the cyanophytes, red, brown or green in colour, became symbiotic in nucleated cells, for the most part flagellates, in which they established themselves as the chromatophores or chlorophyll corpuscles. The evolution of the vegetable kingdom started as a double symbiosis. Those amoeboid or flagellated organisms which formed no symbiotic union with cyanophytes, continued to live as animals and started the evolution of the animal kingdom. Thus, Merezhkowsky classified all organisms into three groups or kingdoms: The Mycoidea, comprising bacteria, cyanophytes, and fungi, and in which no symbiosis had taken place; the Animal Kingdom, in which true cells have arisen by a simple symbiosis of mycoplasm (chromatin) and amoeboplasm (cytoplasm); and the Vegetable Kingdom, in which nucleated cells had entered upon an additional symbiosis with cyanophytes.

In retrospect these ideas seem remarkable today because many of them – that chloroplasts had evolved from symbionts, that the nucleus had evolved from some sort of symbiosis, that protist motility had evolved from symbiosis, that life originated in extreme environments, – all have been reconsidered in recent years (Sapp 2003b). Indeed, it is easy to see why some scientists today see Merezhkowsky as a visionary. But there is still another side of Merezhkowsky's life that is less than heroic.

The Secret Lives of Merezhkowsky

Post-Darwinian biologists in Russia and elsewhere who emphasized mutualisms have often been juxtaposed to those 'social-Darwinists' who emphasized a ruthless Hobbesian struggle of all against all among individuals, or among groups for 'racial superiority' (Todes

1989). One thinks of the anarchist Prince Peter Kropotkin whose well-known book *Mutual Aid* aimed to put the case for kindness and cooperation among humans on a biological basis (Kropotkin 1915, 62). However, there is no inherent logical correlation between studies of symbiosis and ideas about a more tolerant or gentler view of human social relations. Nothing underscores this point more dramatically than Merezhkowsky's socio-political views and activities.

During the pre-revolutionary period in Russia, around the time he turned to symbiosis, Merezhkowsky shed his youthful pro-revolutionary ideology, and emerged as a collaborator of the Czar's secret police. He was also one of the organizers of a nationalistic, anti-Semitic organization of Kazan: 'The Kazan Department of the Union of Russian People' – an organization supported by the Czar, and he was a secret mediator for the ministry of internal affairs. As a 'right-wing professor' as they were called, his job was to seek out and report about all dangerous and suspicious circumstances and root out Jews and other 'traitors'. Several of his colleagues were discharged after his secret and even public denunciations in the Kazan newspaper. In fact, famed biologist, ichthyologist and physical geographer, Lev Simonovich Berg (1876-1950) a founder of limnology in Russia was prevented from obtaining a Chair at Kazan University after Merezhkowky's public denunciations. Berg was a Jew, and Merezhkowsky hated him. Between 1908-1909 there was a conflict between those who wanted to make Berg Professor of Geography of Kazan University and those who, like Merezhkowsky protested against Berg because he was a Jew.[14]

A Mid-Winter Night's Dream

Merezhkowsky was eventually forced to leave Russia in March 1914, not for his 'secret' politics, but for sex scandals: for paedophilic activities between 1905 and 1914 with some twenty-six young girls, including, Kaleeria Korshunova, who was six years-old when he became her tutor. The public scandal was nation-wide. It began in March 26, 1914 when the first news appeared in the left-wing St. Petersburg newspaper *Den'* (Day). Newspapers reported that he had raped 26 girls. He was referred to as the 'Marquis de Sade of Kazan'.[15] That Merezhkowsky was a paedophile, as well as extreme

[14] Subsequently, Berg was Professor of Ichthyology at the Moscow Agricultural Institute between 1914 and 1916 when he became Professor of physical Geography at the University of Petrograd.

[15] See, *'Kazanets*. Marquis de Sade of Kazan', *Den'* March 26 1914. The best accounts of the paedophilic sandal are: (Anonymous 1914, March 29; 1914, April 3).

right-wing, secret-police informer was raised in the Russian parliament by zoologist Mikhail Novikov (1876-1965). The Russian Parliament discussed the case for several days in May 1914. The scandal continued to the beginning of the First World War.[16]

But the trouble started earlier. In 1886 Merezhkowsky suddenly left St. Petersburg and went to the Crimea after unknown circumstances, perhaps connected with his paedophilia and scandal.[17] In 1898, he suddenly left the Crimea for the United States, after paedophilic scandal, leaving his wife, Olga Petrovna with their son Boris. They lived in poverty. During his four years in the United States, he travelled under the false name, 'William Adler'.[18] There he wrote a novel entitled *The Earthly Paradise, or a Winter Night's Dream. A Fairytale of the Twenty-seventh Century: A Utopia*, published in 1903 (Merezhkowsky 1903b).

Merezhkowsky's *Earthly Paradise* was essentially a fascist-eugenics utopia, with the breeding of a new race of humans in accordance with his paedophilic ideal form. The novel consists of a narrative and philosophical supplement. The narrator is asleep and dreams of a paradise on Earth in the twenty-seventh century. The population of the earth has been purposefully decreased and everyone now lives in the tropics where no clothes are needed. The population consists of three groups: *Patrons*, *Friends* and *Slaves*. *Friends* are modified people who look like children, twelve to fourteen years old. It is a fantasy on the theme of neotenisation. *Friends* are always naked and can make love in natural conditions, and play games, especially sexual ones. The narrator makes love with Lorelej, a woman, but who looks like a 12 year-old girl, naked, sweet and caressing. *Friends* are happy: the single purpose of life. *Slaves* (some kind of primate) do all the labour. *Patrons* rule both *slaves* and *friends* and keep friends in an infantile condition, because mind and knowledge are incompatible with happiness. But when *friends* become 35 years old, *Patrons* kill them (they drink *nirvana* and die), because old age is also incompatible

[16] See Zolotonosov (2003), where the scandal is described in detail based on information from 70 Russian newspapers and secret materials from the Ministry of Public Education and Ministry of Internal Affairs (Department of Police).

[17] Merezhkowsky was discharged from the University of St. Petersburg in September 1886. In 1886 he published a lengthy paper, titled 'On problems and methods of investigation of physical development of children', in which he describes in detail how to measure a child's body (Merezhkowsky 1886).

[18] In a search of Merezhkowsky's apartment in Kazan in 1914, a few false passports were found for the names: 'William Adler' and 'Bruno Adler' and other false passports which he used after returning to Russia for making orders for 'girls' and in corresponding with 'suppliers' of 'live goods' as they were called in Russia. His paedophilic activities also continued in the United States. Not feeling safe in New York and the Eastern States generally, where there were many Russians, he fled to California where he settled on a farm, and with his microscope he examined Diatoms. After an attempted rape of a farmer's 14 year-old daughter it is said that Merezhkowsky moved to Los Angeles. (Zolotonosov 2003).

with happiness. Merezhkowsky considered the separation of mind, happiness and labour as the ideal way to structure life.

The novel also includes a detailed description of the horrors of civilization which had led to the movement of *renovators* who aimed to end war, suffering, and relentless labour, the eternal curses of mankind. They created a drink which made men sterile (an oral male contraceptive) which had put an end to the earlier population. Six-hundred and fifty women and twenty-five men had been selected as the basis of the future of humankind. The Supplement of the book describes how progress is the principal enemy of the mankind. As a whole, the book describes a Utopia free from the harm of progress, and based on the importance of eugenics for the happiness of humankind.

In April 12, 1914, criminal case number 1303 was opened in the Department of Justice in St. Petersburg. (It was closed in February 22, 1917, and in 1931 the archive was destroyed by order of the Central Archives Department). A criminal case was also opened in Kazan, April 28 by an investigator of the city's district court. The Minister of Public Education (L.A. Kasso) discharged Merezhkowsky from the position of Ordinary Professor in Botany at Kazan University, and placed him as a member of his staff. Merezhkowsky remained officially in that position until February 1917.

Fig. 3 – Hôtel des Familles, Geneva, where Merezhkowsky put an end to his life on January 9, 1921. Collection François Martin.

Merezhkowsky had fled to France in 1914 where he remained for most of the war: Nice, Menton and Paris. In February 1918, he took refuge in Switzerland where he remained for the rest of his life. He lived very modestly off saved income, in a room at *Hôtel des Familles* in Geneva. It was there, two weeks before the end of the war, on October 25, 1918, that he gave his last paper on what he considered to be 'the work of his life'. This presentation was the basis of his lengthy paper, '*La plante considérée comme un complexe symbiotique*', published two years later in *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France.* Merezhkowsky was bitter, sick and tired. As he lamented, since announcing his theory on the symbiotic nature of chloroplasts in 1905, 'it had made little headway'; it was often 'completely ignored'. He had the intention of writing a book on the subject, but other work got in the way, and then, he had become too weak, during the political struggle in Russia before the war, to write it; 'finally the war, the revolution...' Thus, he remarked, 'It is only today, on the eve of leaving this sad world, that I have decided to develop my ideas in a little more detail in consolidating and enlarging the basis on which they rest' (Mérejkovsky 1920c, 19-20). Merezhkowsky reported that he had written

> to more that fifty scientists, publishers and institutions (including the Carnegie Institution) asking them to publish the work, and explaining to them that being deprived of all resources (the reader will understand why, the moment they know that I am Russian) that there was not much time left to live and that after my death the manuscript will infallibly perish be it in the furnace of the hotel or where I live or be it in the archives of an academy. Everyone has refused without even having read the manuscript.[19]

While in Geneva, he had approached several French botanists for help in providing a forum for him to speak on symbiogenesis. But R. Chodat, Professor of Botany at the University of Geneva, went out of his way to prevent him from speaking (Mérejkovsky 1920c, 20). Two zoologists, Yves Delage, Professor of Zoology, Anatomy and Comparative Physiology at the Sorbonne and director of the marine biological station at Roscoff, and A. Labbé, president of the *Société des Sciences naturelles de l'ouest de la France*, came to his aid. Merezhkowsky declared, 'One day the history of botany will thank them' (Merezhkowsky 1920c, 20-21).

Delage was one of the old savants of French biology. He had written one of the great texts reviewing and criticising nineteenth

[19] C. de Mereschkovsky, 'La Plante comme Symbiose,' mss. Jardin Botanique de Genève, Suisse.

century theories on the cell, heredity and variation: *La Structure du Protoplasma et les Théories sur L'Hérédité et les Grandes Problèmes de la Biologie Générale* (1895). His book with E. Hérouard, *La Cellule et les Protozoaires* (1896) was one of the few protozoology texts of its time (Delage and Herouard 1896). Together with the anarchist neo-Lamarckian biologist, Marie Goldsmith, Delage edited the journal *L'Année Biologique* which kept biologists abreast of recent contributions, reviewing them with their own commentary. One of the early neo-Lamarckians in France, Delage was always on the lookout for alternative theories to neo-Darwinism; and he maintained a longstanding interest in symbiotic theories of the cell. In fact, a great deal of controversy about the role of symbiosis in heredity, development and evolution was brewing in France at the very time Merezhkowsky was in Geneva (Portier 1918; Sapp 1994).

Spiritualism

Constantin's famous brother Dimitri Sergeevich, ten years his junior, a famous poet, novelist, and religious philosopher had, with his wife, Zinaida Hippius, organized a religious-philosophical society in St. Petersburg in 1901. But Constantin remained an atheist all of his life; he had little contact with his brother. His metaphysics were based on a spiritualism expressed in his novel *The Earthly Paradise*, and in another novel he published in French *, Outline of a new philosophy of the universe* (Merezhkowsky 1920b). Based on applying evolutionary theory to the universe, this book describes a seven-dimension oscillating universe. The inhabitants of the highest dimensions may be compared with gods, ruling our three-dimensional world. But this is not a theistic image, but rather a quasi-physical one, difficult to imagine. This aspect of Merezhkowsky's ideas was part of a Russian tradition, connected with the writings of Petr Uspensky on the fourth dimension.[20] It was not related to the Judeo-Christian concept of God; it was para-scientific and atheist: the 'spirits' were considered as inhabitants of the 4-dimension space, the mediums between our world and 4-dimension. Merezhkowsky's spiritualist ideas also evolved from his student years in the 1880s when his professor Nicolas Wagner involved him in spiritualist activity.

[20] Merezhkowsky was especially influenced by Uspensky (1914), (= Chetvertoe izmerenie: Obzor glavnejshih teorij i popytok >issledovanija oblasti neizmerimogo), and (1916), (=Tertium organum: Kljuch k zagadkam mira).

Fragments of his spiritualist thinking penetrated into the conclusion of his longest and most elaborate paper on symbiosis, 'La Plante considérée comme une complexe symbiotique' and generated there a mixture of biology and cosmological fantasies. The ultimate goal of the universe, he argued was its 'complete spiritualization, that is, the gradual transformation of all the mechanical energy of the Universe into psychic energy'. 'In creating the vegetable world, Nature has followed the principle of the division of labour':

> The vegetable world seizes solar energy and transforms it into potential chemical energy in the form of albumous substances, so that the animal world, in nourishing itself on plants, can with so much more amplification transform it into psychic energy. The spiritualization of the Universe, far from losing by this division of labour which exists between the two organic worlds, only gains by it.[21]

In the shorter term, Merezhkowsky hoped that he himself was the saviour of humanity. In January 1920, he wrote a brief manuscript in French entitled, 'Instructions for my disciples, concerning my doctrine for the salvation of humanity' (Merezhkovsky 1920d). He called for the establishment of a society of twelve disciples to preserve his doctrine for the salvation of humanity for centuries. Each disciple, he declared, must feel a deep indignation before the evil and suffering of the universe which he expressed in his poem, 'The Tears of Brahma'. Each must believe in the ultimate establishment of *The Earthly Paradise* he had depicted. Each disciple was to have a copy of his *Outline of a New Philosophy of the Universe* in which he also expressed his view that the march of progress will lead humanity to ruin because of so much suffering. Merezhkowsky advocated a fierce eugenics program. His disciples were to establish societies to regenerate humanity with a battalion of sterilizers.[22]

Again he insisted that a peaceful society allowed no room for Jews. 'No Jew, nor anyone with Jewish blood in his veins (métis) can become a member, because it would lead to the dissolution in the work. This is my expressed wish'. (Merezhkovsky 1920d) Indeed, he had a pre-Nazi-like vision about what society ought to do to Jews:

[21] (Merezhkowsky 1920c, 98). The interpretation of symbiosis, based on a division of labour, exemplified by reciprocal relations between plants and animals, was developed by other biologists during the first two decades of the century. And when constructed in terms of cooperation for the common good, the concept of symbiosis opposed an amoral view of cosmic processes in which nonhuman organismic interaction was understood in terms of a multitude of selfish interests. (Sapp 1994).

[22] The disciples' immediate duties:1. Guard his three works, publish them and furnish libraries with them.2. Study the laws of heredity and especially their application to man.3. Collect facts confirming his theories. 4. Improve the sterilizer. 5 Accumulate means necessary for the struggle. (Merezhkovsky 1920d).

> The Jews in Russia, led by Zederblum-Lenin, have conducted a very interesting experiment. They cut throats of a million people, the best of the nation, to see what would happen. As nothing good came out of it, for the Russians at least, I would like to propose another experiment one day. Slit the throats of a million Jews and see what the result would be. But Russians being less ferocious than Jews, we will change the conditions of the experiment a little, and replace a massacre by castration of millions of Jews, that is, of all Jewish males, to see what the result will be. I believe the result will be peace on Earth.[23]

Thus, Merezhkowsky reflected whether he would be the saviour of humanity:

> Will this not be my mission? I am note sure, but it could be the case. Had not Tolstoy predicted that a slav would come to save humanity? And did not Dostoevsky sketch my doctrine, as did Jean (Baptiste) the precursor? But mission or not, what is not in doubt is that my Earthly Paradise is the unique salvation for humanity (Merezhkovsky 1920d, 14).

Suicide

In Paris in September 1917, Merezhkowsky contemplated ending his life sometime in 1919 or 1920. As he wrote to Ivan Borodin, director of the Botanical Museum in Petrograd: 'I thought that I would live for another 5-6 years, but now it has turned out that because of the War, I have means (money) only for two reliable years (not even 3), and after that I have to die' (Merezhkowsky 1917).

On Sunday January 9, 1921, having run out of money and after paying all his hotel bills, he finally committed suicide - and in a most elaborate manner (Anon 1921). The obituary note published in the Geneva newspaper *La Suisse* of January 11 read as follows:

> In room number 58, which he occupied at the hotel, and where he willingly shut himself in for long hours to work, he prepared a scientific mixture of his composition, which included chloroform and several acids. He tipped the mixture in a metal container fixed to the wall, above his head on the bed. To this recipient he attached a pipe which was attached at the other end to a mask surrounded with wire. Having made this, he carefully sealed off the room, stretched himself out on the bed after tying himself up with three strips of cloth. A rope which passed over his legs and his stomach was tied to the base of the

[23] (Merezhkovsky 1918-1920, 23). 'Les juifs en Russie, avec Zederblum-Lenine à la tête, ont fait une très intéressante expérience: ils ont égorgé un million par la fleur de la nation pour voir ce qui sortira. Comme il n'en est rien sorti de bon, pour les Russes du moins, j'aurais proposé de faire un jour une autre expérience: égorger un million de juifs, et voir ce qui en sortira. Mais les Russes étant moins féroces que les juifs, nous changerons un peu les conditions de l'expérience en remplaçant le massacre par la castration de plusieurs millions de juifs, c'est à dire de tous les juifs males pour voir ce qui en ressortira. Je crois qu'il en ressortira la paix sur Terre'.

> bed. He further attached his right arm underneath his head. Then with his left arm free, he opened the valve of the container with the asphyxiating mixture. He then had the time to put his hand under a strip and await his death… Yesterday at two o'clock, the hotel porter noticed a letter passed under the door of the professor. The missive, addressed to the hotel manager, contained the lines:
> 'Do not enter my room. The air in it is poisoned. It will be dangerous to enter for several hours'.
>
> …At 4: 14, despite the danger, M Vivert (the police commissioner) took off the mask that the deceased still had on his face and cut the ties. The magistrate seized one letter addressed to several professors at the university, as well as a long formula in Latin pinned to a cord. In a letter addressed to M. Vibert, Constantin de Merezhkowsky said that, possessing nothing more, too old to travel, and too poor to live, he took his own life.
> M. Vibert also seized some pills as well as a number of flasks and jars which contained poisons.

We speculate that Merezhkowsky's suicide was a 'ritual' suicide with some kind of scientific/mystical symbolism or message. Although it would be interesting to know the Latin words he wrote in his final message, the police file was destroyed. But consider the way he tied himself up in the bed and the complex apparatus he used to commit suicide (by gas). Perhaps, the 'message' was in regard to his 'Theory of the Two Plasms'. Perhaps he intended to recreate a primitive atmosphere (the production of methane for example) in the suicide room, like a rebirth of life. The association of different elements related to symbiogenesis in the 'message' is indeed plausible.

Concluding Remarks

When considered in isolation, it is easy to see Merezhkowsky's symbiogenetic views about early evolution as prescient. That chloroplasts are cyanobacterial symbionts is part of the conceptual consensus today, and the idea that the nucleus arose as some sort of symbiosis is well considered.[24] Usually we speak about A. I. Oparin's ideas published in the 1924 as the main source for the development of the modern thinking on the origins of life,[25] but in hindsight,

[24] Although Merezhkowsky is often cited today by those who argue that the nucleus and cytoplasm emerged as a symbiosis between two different kinds of bacteria, his theory differed in that for him, and for others who preceded him, the nucleus represented a colony of organisms. He is not a precursor of contemporary ideas. On the nucleus as emerging from symbiosis, see for example, (Lake and Rivera 1994; Hartman and Federov 2002).

[25] Oparin first proposed his theory in 1918, less than a year after the Bolshevicks seized power. The czarist censors had yet been cast aside. Prior to the Revolution, the Czar had ruled over both state and

Merezhkowsky may seem more 'visionary' when he writes in 1909 about the importance of extremophiles and extreme environments in the early stages of life on Earth.

The history of Merezhkowsky's writings about symbiosis is much more complex than a standard tale of 'neglect' and 'rediscovery' would betray. Although he is celebrated by biologists for his heroic single-handed achievement, his theories of symbiogenesis resulted from a synthesis of ideas, developed by others before him (and after him). Indeed, all the elements of his theories of symbiogenesis were in the scientific literature of day, scattered among several specialties in cytology, botany, and natural history. Merezhkowsky's sagacity was to select among them to see how the pieces could be fit together. When contemplating the fate of his ideas we have to consider more than his sordid, troubled life. We also have to understand that symbiosis did not fit with ever-increasing specialization in the life sciences.

A series of disciplinary aims and doctrines confronted the study of symbiosis in evolution (Sapp 1994). The emphasis on conflict and competition in nature, which many critics then and now argued is merely a reflection of dominant views of human social progress. The overwhelming interest in the disease-causing nature of some microbes meant that most microbiologists were concerned with killing them, or with using them as technologies for chemistry and later genetics, rather than with understanding their evolution and ecology. Studies of hereditary symbiosis conflicted with the doctrine that the chromosomes in the cell nucleus were the predominant if not exclusive carriers of heredity. A view which emphasized the prevalence of heredity symbiosis also confronted the evolutionary synthesis based on Mendelian gene mutations and recombination as the sources of evolutionary change, and therefore that the mechanisms of macroevolution were the same as those for microevolution.

Scientific revolutions are not made by theories alone. The postulated role of symbiosis in cell origins was highly speculative, and not the basis of a coherent research programme. It was not until new techniques were developed for investigating bacterial genealogies beginning in the 1970s, after the rise of molecular biology, that one could begin to systematically investigate the role of symbiosis in the origin of cells.

Merezhkowsky's theories about symbiogenesis were not unique to Russia nor to any other single nation. Nor were they unique to any

orthodox church. To Russian Orthodoxy, the origin of life was sacrosanct. Oparin's manuscript was rejected from publication. His ideas re-emerged in a more developed form in a small book in 1924, translated into English in 1938. (Oparin 1965).

one political ideology. Herein lies a salient issue. In the popular and the technical scientific literature, symbiosis is often correlated with mutualism. As such symbiosis has been associated with the more cooperative social ideals of Kropotkin in contradistinction to the fierce competition of so called 'social Darwinism'. The fuller story of Merezhkowky's symbiogenesis reinforces historians' assertions that there is no *universal* one-to-one correspondence between scientists' theories about nature and their prescriptions for a better society.

Acknowledgments

The authors are grateful for the kind cooperation of Barbara Prout, Bibliothèque Publique et Universitaire, Genève; Jacques Barrelet, Archives d'Etat de Genève Bibliothèque du Conservatoire et Jardin Botaniques de la Ville de Genève; Nicolas Exchaquet, Bibliothèque Publique et Universitaire, Genève; Marianne Dieterle, Service de Presse Police, Genève; Olga Gurbanova and Valerie Dvoretskova, National Library of Russia, St. Petersburg; Karin Olt and Pierre André Loizeau, Conservatoire et Jardin Botaniques de la Ville de Genève. We thank Lucie Comeau, Centre de documentation, Centre interuniversitaire de recherche sur la science et la technologie, UQAM, and the Canada Research Chairs Programme. We also thank François Martin for the photo of the Hôtel des Familles. A special thanks to Christiane Groeben for her editorial expertise.

References

Anonymous, 1921 (January 11), *La Suisse*.

Anonymous, 1914 (March 29), 'Delo Prof. Merezhkovskogo (Prof. Mereszhkowsky's case', *Kamsko-Volzhskaja rech'* (Kazan).

Anonymous, 1914 (April 3), 'Istorija, professora Merezhkowskogo (prof. Merezhkowsky's History)', *Birzhevye Vedomosti. Vechernij vypusk* (St. Petersburg).

Boveri T., 1904, *Ergebnisse über die Konstitution der chromatischen Sunstanz des Zellkerns*, Jena: Gustav Fischer.

Brackman C., 1974, *The Dream of Troy*, New York: Mason and Lipcomb Publishers.

Cleve P.R., Merezhkowsky C., 1902, 'Notes on Some Recent Publications Concerning Diatoms,' *The Annals and Magazine of Natural History,* vol. 10 Seventh Series, 27-38.

De Bary A., 1879, 'Die Erscheinung der Symbiose', Vortrag auf der Versammlung der Deutschen Naturforscher und Aertze zu Cassel, Strassburg: Verlag von Karl J. Trubner, 1-30.

Delage Y., Hérouard E., 1896, *La Cellule et les Protozoaires. Traité Zoologie Concrète*, vol. 1, Paris: Schleicher Frères.

Dyer B., Obar R., 1994, *Tracing the History of Eukaryotic Cells*, New York: Columbia University Press.

Famintsyn A., 1889, 'Die Symbiose einer *Chaetoceras*-Art mit einer Protozoe (*Tintinnus inquilinus*)', *Mémoires de l'Académie de St. Petersbourg, sér.* 7, 36.

Famintsyn A., 1889b, 'Beitrag zur Symbiose von Algen und Thieren', *Mémoires de l'Académie impériale des Sciences, St. Petersbourg* sér. 7, 26.

Famintsyn A., 1891, 'Beitrag zur Symbiose von Algen und Thieren', *Mémoires de l'Académie impériale des Sciences, St. Petersbourg* sér. 7, 38.

Famintsyn A., 1892, 'Nochmals die Zoochlorellen', *Biologisches Centralblatt,* 12: 51-54.

Famintsyn A., 1907, 'Die Symbiose als Mittel der Synthese von Organismen,' *Biologisches Centralblatt*, 27: 253-264.

Frank A.B., 1885, 'Ueber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze', *Berichte der Deutschen Botanischen Gesellschaft,* 3: 128-145.

Geison G.L., 1969, 'The Protoplasmic Theory of Life and the Vital-Mechanist Debate', *Isis,* 60: 273-292.

Haeckel E., 1866, *Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*, 2 vols, Berlin: Georg Reimer.

Haeckel E., 1904, *The Wonders of Life. A Popular Study of Biological Philosophy*, translated by Joseph McCabe, New York: Harper and Brothers.

Hartman H., Federov A., 2002, 'The Origin of the Eukaryotic Cell: A Genomic Investigation', *Proceedings of the National Academy of Sciences, USA*, 99: 1420-1425.

Hoextermann E., 1998, 'Konstantin S. Merezkovskij und die Symbiogenesetheorie der Zellevolution'. In: Geus A. (ed.), *Bacterienlicht und Wurzelpilz: Endosymbiosen in Forschung und Geschichte*, Marburg: Basiliken-Presse, 11-29.

Khakhina L.N., 1992, *Concepts of Symbiogenesis*, edited by L. Margulis and M. McMenamin, translated by S. Merkel and R. Coalson, Foreword by A. Vucinich, New Haven: Yale University Press.

Khakhina L.N., Margulis L., McMenamin M., 1993 (eds), *Concepts of Symbiogenesis: History of Symbiosis as an Evolutionary Mechanism*, New Haven: Yale University Press.

Kropotkin P., 1915, *Mutual Aid. A Factor of Evolution*, London: William Heinemann, popular edition.

Lake J., Rivera M., 1994, 'Was the Nucleus the First Symbiont?', *Proceedings of the National Academy of Science* (USA), 91: 2880-2881.

Margulis L., 1991, 'Symbiogenesis and Symbionticism'. In: Margulis L., Fester R. (eds), *Symbiosis as a Source of Evolutionary Innovation*, Cambridge: The MIT Press, 1-14.

Margulis L., 1993, *Symbiosis in Cell Evolution*, New York: W.H. Freeman, 2nd edition.

Martin W., Kowallik K.V., 1999, 'Annotated English Translation of Merezhkowsky's 1905 paper Über Natur und Ursprung der Chromatophoren im Pflanzenreiche', *European Journal of Phycology,* 34: 287-295.

Merezhkowsky C., 1877, 'On a New Genus of Hydroids from the White Sea, with a short Description of other new Hydroids', *Annals and Magazine of Natural History,* 4th series, 20: 220–229.

Merezhkowsky C., 1878, 'On Wagnerella, a new Genus of Sponge nearly allied to the Physemaria of Ernst Haeckel', *The Annals and Magazine of Natural History* vol. 1 fifth series, 71-77.

Merezhkowsky C., 1878b, 'New Hydroida from Ochotsk, Kamtschatka, and Other Parts of the North Pacific Ocean', *The Annals and Magazine of Natural History* 5th series, 2: 433-451.

Merezhkowsky C., 1878c, 'Studies on the Hydroida', *The Annals and Magazine of Natural History*, 5th series, 1: 322-339.

Mérejkovsky C., 1881, 'Les Crustacés inférieurs distinguent-ils les couleurs?' *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* (Paris), XCIII : 1160–1161.

Merezhkowsky C., 1881b, 'On Some New or Little-known Infusoria', *The Annals and Magazine of Natural History*, fifth series, 7: 209-219.

Mérejkovsky C., 1881c, 'Sur la tetronérythrine dans le règne animal et sur son rôle physiologique', *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* (Paris), XCIII: 1029–1032.

Merezhkowsky C., 1881d, '*Wagnerella borealis*, a Protozoan', *The Annals and Magazine of Natural History*, fifth series, 8: 288-290.

Mérejkovsky C., 1882, 'Structure et développement des nématophores chez les Hydroïdes', *Archives de Zoologie expérimentale et génerale*, 10: 583 – 610.

Mérejkovsky C., 1882b, 'Sur une série de crânes de la Sardaigne,' *Bulletin de la Société d'Anthropologie de Paris*, sér. 3, 5: 164–169.

Mérejkovsky C., 1882c, 'Sur quelques crânes américains', *Bulletin de la Société d'Anthropologie de Paris*, sér. 3, 5: 170–180.

Mérejkovsky C., 1882d, 'Sur un nouveau caractère anthropologique', *Bulletin de la Société d'Anthropologie de Paris, sér.* 3, 5: 293 – 304.

Mérejkovsky C., 1883a, 'The Materials for Understanding Animal Pigments', *Zapiski Imperatorskoj Academii Nauk*, 47, Supplement 3: 1–100.

Mérejkovsky C., 1883b, Recherches sur le développement du squelette humain', *Bulletin de la Société d'Anthropologie de Paris,* Ser. 3, 6: 152 - 164.

Mérejkovsky C., 1883c, 'Nouvelles recherches la Zoonérythrine et autres pigments animaux, (Note préliminaire)', *Bulletin de la Société Zoologique de France,* 8: 81-97.

Merezhkowsky C., 1886, 'O zadachah i metodah issledovanij fizicheskogo razvitija detej', *Medico-pedagogichesky vestnik*, 1: 63-97; 2: 53-76. [*'On problems and methods of investigation of physical development of children', Medical and Pedagogical Herald* (Petersburg)]

Merezhkowsky C., 1901, 'A List of California Diatoms', *The Annals and Magazine of Natural History*, 7th series, 7: 292-520.

Merezhkowsky C., 1901b, 'On Sellaphora, a new Genus of Diatoms', *The Annals and Magazine of Natural History*, 7th series, 9: 185-195.

Merezhkowsky C., 1902, 'On the Classification of Diatoms', *The Annals and Magazine of Natural History*, 7th series, 9: 65- 69.

Merezhkowsky C. to Famintsyn A., 1903 (May 7), Archives of Russian Science Academy. St.Petersburg branch. Fund 39. List 2. N 18. Pages 5 — 5 back.

Merezhkowsky C., 1903b, *Das irdische Paradies. Ein Märchen aus dem 27. Jahrhundert: Eine Utopie,* aus d. Russ. von Helene Mordaunt*,* Berlin: Friedrich Gottheiner.

Merezhkowsky C., 1905, 'Ueber Natur und Ursprung der Chromatophoren im Pflanzenreiche', *Biologisches Centralblatt* 25: 595-596.

Merezhkowsky C., 1910, 'Theorie der zwei Plasmaarten als Grundlage der Symbiogenese, einer neuen Lehre von der Entstehung der Organismen', *Biologisches Centralblatt*, 30: 277-303; 321-347; 353-367.

Merezhkowsky C. to Borodin I., 1917 (17 September), Manuscript Department of the Institute of Russian Literature of the Russian Academy of Science (St. Petersburg), N 14829, 3pp.

Merezhkowsky C., 1918-1920, 'Aphorismes et boutades' Texte a. 23pp. Bibliothèque Publique et Universitaire, Ville de Genève, Suisse, Ref. Ms.fr. 1550/11.

Merezhkovsky C., 1920b, *Fragments du 'Schéma d'une nouvelle philosophie de l'Univers'. I. Le rythme universel comme base d'une nouvelle conception de l'univers*, Genève et Lyon: Georg & Co.

Mérejkovsky C., 1920c, 'La plante considérée comme un complexe symbiotique', *Bulletin de la Société des Science Naturelles de l'Ouest de la France,* 6: 17-98.

Merezhkovsky C., 1920d (January 5), 'Instructions pour mes disciples concernant ma doctrine du salut de l'Humanité'. Texte a. Genève, 5 janv. 1920. Bibliothèque Publique et Universitaire, Ville de Genève, Suisse, Ref. Ms.fr. 1550/11.15.

Minchin E.A., 1915, 'The Evolution of the Cell', *Report of the Eighty-fifth Meeting of the British Association for the Advancement of Science*, 437-464.

Oparin A.I., 1965, *The Origin of Life*, translated by Sergius Morgulis, 2nd edition, New York: Dover publications.

Portier P., 1918, *Les symbiotes*, Paris: Mason.

Rehbock P.F., 1976, 'Huxley, Haeckel, and the Oceanographers: The Case of *Bathybius Haeckelii*', *Isis,* 66: 504-553.

Reinke J., 1873, 'Zur Kenntniss des Rhizoms von *Corallorhiza* und *Epipogon*,' *Flora,* 31: 145-209.

Sapp J., 1994, *Evolution by Association: A History of Symbiosis*, New York: Oxford University Press.

Sapp J., 2003, 'The Bacterium's Place in Nature'. In: Sapp J. (ed.), *Microbial Evolution. Conflict and Controversies,* New York: Oxford University Press.

Sapp J., 2003b, *Genesis: The Evolution of Biology*, New York: Oxford University Press.

Schimper A.F.W., 1883, 'Über die Entwicklung der Chlorophylkörner und Farbkörner', *Botanische Zeitung*, 41: 105-114.

Schimper A.F.W., 1885, 'Untersuchungen über die Chlorophyllkörner und die ihnen homologen Gebilde', *Jahrbücher für wissenschaftliche Botanik*, 16: 1-247.

Schwendener S., 1867, 'Über die wahre Natur der Flechten', *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft in Rheinfelden,* 51: 88-90.

Shumeiko, L., 2001, 'Konstantin Sergeevie Merezkovskij (1855-1921) als Begründer der Symbiogenesetheorie der Evolution', *Gesnerus,* 58: 40-52.

Spencer H., 1889, *Principles of Biology,* vol. 2, New York: Appleton.

Spratt E.R., 1911, 'Some Observations on the Life-history of *Anabeana cycadeae*,' *Annals of Botany:* 25: 369-380; 277-378.

Todes D., 1989, *Darwin without Malthus. The Struggle for Existence in Russian Evolutionary Thought,* New York: Oxford University Press.

Uspensky P.D., 1914, *The Fourth dimension: Review of the main theories and attempts of investigation of the field of the immensurable*, 2nd ed, St.Petersburg.

Uspensky P.D., 1916, *Tertium organum*: *The key to the puzzles of the world*. 2nd ed. Petrograd.

Vucinich A., 1988, *Darwin in Russian Thought,* Berkeley: The University of California Press.

Wilson E.B., 1925, *The Cell in Development and Heredity,* New York: The Macmillan Co. Ltd.

Zolotonosov M.N., 2003, *Brat'ja Merezhkovskie. Tom 1. Otschepenis Serebrjanogo veka*, *(The Merezhkowsky Brothers. Vol. I. Pariah of the Silver Age*) Moscou: Ladomir Publishing House.