Concepts of Symbiogenesis

A Historical and Critical Study of the Research of Russian Botanists

edited by
Lynn Margulis and
Mark McMenamin

Liya Nikolaevna Khakhina

translated by
[illegible] Merkel and
[illegible]son

with an appendix
on Ivan E. Wallin by
Donna C. Mehos

CONCEPTS OF SYMBIOGENESIS

A Historical and Critical Study of the Research of Russian Botanists

LIYA NIKOLAEVNA KHAKHINA

Edited by

Lynn Margulis and Mark McMenamin

Translated by

Stephanie Merkel and Robert Coalson

With an appendix on Ivan E. Wallin by
Donna C. Mehos

A Russian and Western History of

Symbiosis as an Evolutionary Mechanism

Yale University Press

New Haven and London

Originally published in Russian as *Problema simbiogeneza: istoriko-kritichesky ocherk issledovany otechestvennykh botanikov* by L. N. Khakhina. Copyright by the Institute of the History of Natural Science and Technology, The Academy of Sciences of the USSR, Leningrad, Nauka, 1979.

Designed by Jill Breitbarth and set in Sabon and Bodoni types by Keystone Typesetting, Inc., Orwigsburg, Pennsylvania.
Printed in the United States of America by BookCrafters, Chelsea, Michigan.

Library of Congress Cataloging-in-Publication Data

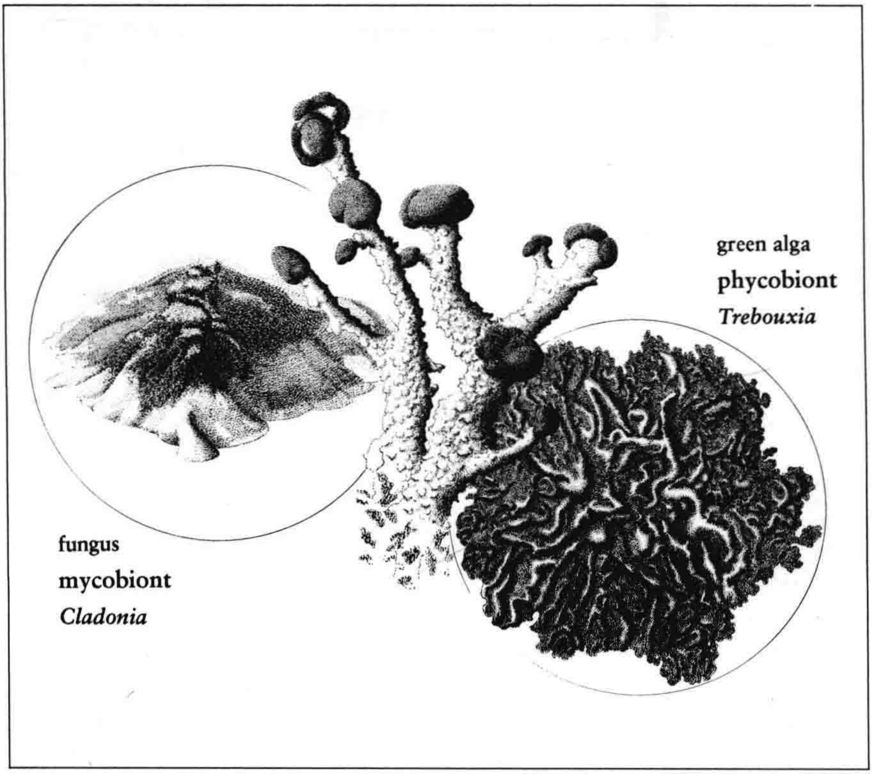
Khakhina, Liîa Nikolaevna.
[Problema simbiogeneza. English]
Concepts of symbiogenesis : historical and critical study of the research of Russian botanists / Liya Nikolaevna Khakhina ; edited by Lynn Margulis and Mark McMenamin ; translated by Stephanie Merkel and Robert Coalson.
p. cm. — (Bio-origins series)
Translation of: Problema simbiogeneza.
Includes bibliographical references and index.
ISBN 0-300-04816-5 (alk. paper)
1. Symbiogenesis. 2. Biotic communities—Evolution.
I. Margulis, Lynn, 1938–
II. McMenamin, Mark A. III. Title.
IV. Series.
QH378.K4313 1992
575.01'6—dc20 92-14466 CIP

A catalogue record for this book is available from the British Library.

The paper in this book meets the guidelines for permanence and durability of the Committee on Production Guidelines for Book Longevity of the Council on Library Resources.

10 9 8 7 6 5 4 3 2 1

CONCEPTS OF SYMBIOGENESIS



Drawing of British soldier lichen, *Cladonia Cristatella*, by Christie Lyons, used by permission of Lynn Margulis

THE BIO-ORIGINS SERIES

Genesis on Planet Earth: The Search for Life's Beginning, 2d edition, William Day, 1984

Origins of Sex: Three Billion Years of Genetic Recombination, Lynn Margulis and Dorion Sagan, 1986

Beginnings of Cellular Life: Metabolism Recapitulates Biogenesis, Harold J. Morowitz, 1992

FOREWORD

Although it faced challenges of harsh and penetrating criticism from many quarters, Russian evolutionary biology entered the twentieth century in robust health. Darwinian ideas had more supporters in the academic community than ever before, and Darwinian scholars dominated the university courses in general biology. University textbooks in biology, almost without exception, were built upon the ideas presented in the *Origin of Species* and the *Descent of Man.* The evolutionary approach formulated by the great English naturalist carried its authority to new domains of biological research. Russian biologists, led by A. N. Severtsov, were interested in building a bridge to connect Darwin's theoretical structures with the avalanches of new empirical data. The country had just received the first publication of Darwin's complete works, and preparations were under way for a second edition offering a larger share of Darwin's scientific legacy and fewer translation errors. In 1909, the universities and learned societies, led by the St. Petersburg Academy of Sciences, commemorated and celebrated the one-hundredth anniversary of Darwin's birth and the fiftieth anniversary of the publication of the *Origin of Species.* Overflowing crowds at numerous celebrations heard more than 150 papers that provided a magnificent display not only of the deep roots Darwin's theory had taken in Russian biology but also the triumphs of rationality over the forces of mysticism and superstition.

On entering the twentieth century, Darwinism encountered formidable challenges that originated mainly in various theoretical orientations in biology. In a state of intense fermentation, biology fed on new theoretical thought and methodological achievements, sometimes threatening to uproot the very foundations on which Darwin had built his evolutionary principles. Modern genetics, built on the resurrected theory of Gregor Mendel, made an auspicious entrance soon after 1900, and in 1909 the Institute of Applied Botany, a research component of the Ministry of Agriculture, showed strong signs of harnessing the tools of the new science in efforts to improve the existing species of cultivated plants. Neo-Lamarckism appeared in several forms, all emphasizing the environment as the primary factor of evolution and the hereditary transmission of acquired characteristics. Several variations of psychological theories considered the behavioral aspect of biological evolution. Influential authorities, led by I. P. Borodin, supported an integration of the selective principles of vitalism into general evolutionary theory. Vitalism, at this time, was undergoing a strong revival in western Europe in both idealistic metaphysics and in its opposition to mechanistic philosophy. As a branch of evolutionary biology, *vitalism* (asserting the uniqueness of living matter) was engaged in a bitter war with *mechanism,* as shown by the growing dependence of experimental biology on Newtonian physics and chemistry.

In Russia, more than in Western countries, it was eminently clear that the emergence of a critical attitude toward classical Darwinism was much stronger in botany than in zoology. Sergei I. Korzhinsky, a leading expert in plant geography, heralded the rebirth of Mendelian genetics and the triumph of mutation theory in 1899. The first Russian designs for experimental work in the genetics of cultivated cereals were prepared by R. E. Regel. A biologist turned philosopher, V. P. Karpov, advanced a brand of holistic organicism, which injected elements of vitalism into classical Darwinism. Andrei S. Famintsyn worked diligently to add a psychological dimension to Darwin's theory and deserved to be counted among the pioneers of ethology. Vladimir L. Komarov, a leading botanist, saw no reason why Darwin's and Lamarck's theories should not be brought into closer alliance.

There were obvious reasons for the stronger growth of heterodox thought in the botanical sciences than in the branches of zoology. First, from the very beginning of Darwinian biology, botanists, much more than zoologists, felt uncomfortable with natural selection—which translated into the struggle for existence—as the primary moving force of evolution. Predatory drive as a reality and motor of evolution was much more visible in the animal world than in plant communities. Second, Russia had developed an especially strong tradition in plant physiology as an experimental science. Among biological laboratories, those in plant physiology were the most modern and elaborate; they brought the advanced methods of physics and chemistry to the experimental domain of biological studies. Laboratory research generated myriad questions that did not fall within the framework of Darwinian concerns.

Symbiogenesis became a legitimate and systematic part of biology in the age of rising theoretical uneasiness in evolutionary studies at the beginning of the twentieth century. The awareness of symbiosis as a unique mode of "cooperation" on the interspecific level had a long past but a short history of intensive and methodical study. In Russia, many pioneers in these studies were, not surprisingly, botanists who found Darwinian perspectives narrow and outdated. But not all Russian botanists were in the camp of Darwin's enemies. Fine botanists—for example, K. A. Timiryazev, N. V. Tsinger, and

V. I. Taliev—were among the leading Russian Darwinists.

The specific national concern that stimulated research in symbiosis as a general biological theme was the Russian involvement in the study of lichens, an abundant life form and one that covers large stretches of land in the regions of the Siberian tundra and parts of the northern taiga, as well as in many other parts of the world. Lichens occupy a pivotal position in the ecology of the northern reaches of Siberia. Numerous lichen species make the difference in the survival potential of much of Siberia's vegetative cover and many animal species. In winter, reindeer, both wild and domestic, feed exclusively on a species known as reindeer lichen. Lichens became a particularly attractive subject for scientific study after 1879 when A. de Bary, introducing symbiosis as a biological concept, established that they represented an evolutionary product of the symbiotic association of a fungal species and an algal species that normally exist as entirely different taxa. Lichen study constituted only the beginning of investigations of symbiosis as a mechanism of evolution. Other forms of symbiotic association, some newly discovered, came under intensive scrutiny and only gradually became research concerns of a promising branch of biology.

Three Russian scientists deserve credit for establishing symbiogenesis as a full-fledged and legitimate field of inquiry: Famintsyn (1835–1918), an expert in photosynthesis and a distinguished member of the St. Petersburg Academy of Sciences; K. S. Merezhkovsky (1855–1921), professor of botany at Kazan University; and B. M. Kozo-Polyansky (1890–1957), a professor at Voronezh State University.

Although Famintsyn preferred experimental research and observational data and held theoretical ventures to a minimum, Merezhkovsky displayed a strong flair for abstract thought, intuitive insights, and elaborate logical structures, as described in Khakhina's book. He was the first to rely on symbiogenesis, a term he coined, as a basis for major revisions in the classification of the smaller organisms and as a springboard for a major revision of the theory of biological evolution.

Deep involvement in the experimental study of cell membranes, their inner structures and adaptive functions, led Merezhkovsky to formulate an elaborate evolutionary theory: first, that all cells are symbiotic combinations of living units that originally lived independent lives, and second, that the entire living nature is made up of two plasms: mycoplasm (peculiar first to bacteria and then to the more elaborate cyanophyta and fungi) and amoeboplasm, which, emerging later, appeared in the form of minute "noncellular monera." Behind the somewhat antiquated terminological codification of Merezhkovsky's symbiogenetic theory stood a potent idea that invited a novel approach to the evolutionary process in the universe of living nature. Merezhkovsky's idea on symbiogenesis belonged to the future, not to the time in which he lived. As Lynn Margulis and Dorion Sagan put it: "It has taken the biological world over seventy years to catch up with him."[1]

Merezhkovsky accepted the Darwinian view of the growing complexity of internal structures and physiological processes as the most reliable index of evolutionary "progress," but he did not accept Darwin's thoughts on natural selection as the main factor of evolution. He preferred the cooperation of symbiotic associations to the "conflict" of Darwin's natural selection. The Russian community of biologists was involved in a major confrontation between the champions of new genetics and classical Darwinism. Despite fundamental differences in their general views, it found little use for Merezhkovsky's symbiosis as a mechanism of evolution.

In his attitude toward Darwin's evolutionary legacy, Kozo-Polyansky differed from Famintsyn and Merezhkovsky.[2] Although Famintsyn professed that his theory complemented Darwin's ideas and Merezhkovsky acknowledged that Darwin's and his theories were basically incompatible, Kozo-Polyansky was particularly anxious to present his theory of symbiogenesis as an integral part of the theory of evolution as presented by Darwin. He identified himself as a consistent and thorough Darwinist and waged a relentless war against all kinds of anti-Darwinian stirrings in biology. The acceptance of the ideas of symbiosis and symbiogenesis depended on the acceptance of the concepts built into natural selection and the struggle for existence. He was convinced that the reality of evolution rested to a large extent on symbiotic associations selected for in the struggle for existence. A corresponding member of the Academy of Sciences of the USSR, V. L. Ryzhkov was ready to cite concrete examples to illustrate the work of symbiosis as a factor of evolution.[3]

Kozo-Polyansky's effort to merge the idea of new biology with dialectical materialism attracted little attention, even in Marxist circles. Perhaps Marxist scholars found it much easier to drop the issue of symbiogenesis altogether than to become involved in the arduous task of reconciling the species cooperation emphasized by Kozo-Polyansky with the species conflict built into Darwin's theory. A typical biologist of this time was inclined not to tamper with Darwin's theory. During the 1920s, Russian biologists played a vital role in the development of population genetics in an effort to effect a synthesis of mutation theory with Darwin's principle of natural selection.

1. Margulis, L., and Sagan, D. 1986. *Microcosmos.* Summit Books, New York, 119.

2. Khakhina, L. N. 1983. Problema simbiogeneza: Osnovnye etapy razrabotki problemy. In *Razvitie evoliutsionnoi teorii v SSSR (1917–70–e gody),* ed. Mikulinsky, S. R., and Polyansky, Iu.I. Leningrad, 426.

3. Ryzhkov, V. L. 1966. Vnutrikletochnyi simbioz. *Priroda* 3:9–17.

In *A New Principle of Biology* (1924), Kozo-Polyansky presented examples of the wide occurrence of symbiosis in the world of living nature. He made it clear, however, that he did not consider symbiogenesis to be the exclusive factor of evolution. It was obvious that he wanted to recognize the power of the struggle for existence beyond the limits of symbiosis.

The studies of Famintsyn, Merezhkovsky, and Kozo-Polyansky laid the foundation for a burgeoning interest in symbiosis, which in the following decades helped to illuminate the key biological problems related to the inner dynamics of species and to the mechanisms of evolution and which employed many methods, including those of physiology, cell biology, and molecular biology. Despite the originality of their theoretical constructions and the breadth of their knowledge and experimental skills, the three scientists fared poorly. They received much more national recognition for the contributions they made to other fields in biology—Famintsyn for the study of photosynthesis, Merezhkovsky for the systematics and morphology of "lower" plants, and Kozo-Polyansky for the defense of classical Darwinism and the application of Haeckel's biogenetic law to the world of plants. Their ideas were exceedingly slow in reaching the West, where the interest in symbiotic processes occupied a somewhat broader but more diffuse front.

In the Soviet Union, the recognition of the scientific merit of the theory of symbiogenesis was slow and painful. A quick way to identify attitudes of Russian biologists is to compare entries on the subject in the three editions of the *Great Soviet Encyclopedia*. The 1945 volume of the first edition in which symbiogenesis is an entry refers to the contributions of Famintsyn, Merezhkovsky, and Kozo-Polyansky but expresses a thoroughly negative attitude toward symbiogenesis as a mechanism of evolution. The author of the article, L. Kursanov, states that the theory of symbiogenesis was not confirmed by a single experiment and could not be recommended even as a "working hypothesis."[4] The second edition—most volumes of which were published in the heyday of Lysenkoism (the 1950s)—solved the problem of symbiogenesis by omitting it from even the general article on symbiosis. The third edition of the encyclopedia (in the 1970s), signaled a strong reversal: It carried an article on symbiogenesis, presenting it as the theory that "many eukaryotic cell structures . . . originate as a result of the prolonged symbiosis between eukaryotes and prokaryotes, for example, bacteria and blue-green algae."[5]

The article considered Merezhkovsky, Famintsyn, and Kozo-Polyansky to be the founders of the theory of symbiogenesis, and named A. L. Takhtad-

4. Kursanov, L. 1945. Simbiogenez. *Bol'shaia sovetskaia entsiklopediia*, 51:126.

5. *Great Soviet Encyclopedia*, 3d ed. 1979, s.v. "symbiogenesis."

zhyan, a leading Russian botanist, Margulis (USA) and J. D. Bernal (Great Britain) as its most eminent modern champions. Takhtadzhyan helped to improve the status of symbiogenetic studies in the Soviet Union by putting his great reputation and authority behind it. In "Four Kingdoms of the Living World," published in *Priroda* [Nature] in 1973, he analyzed Western and Russian studies, which led him to conclude that "it has become perfectly obvious that the symbiotic theory of the origin of the eukaryotic cell, previously received with suspicion or rejected, has acquired many supporters in recent years."[6] Modern science, particularly molecular biology, had rejected some of the classical explanations of the origin of eukaryotic cells but had generally accepted classical views on "the kinetic center, chloroplast and mitochondria."[7]

The place of the theory of symbiogenesis in modern biological thought extended even farther. Liya Khakhina (1973) published the first systematic historical survey of the development of this theory in czarist Russia and the Soviet Union, indicating not only its chief architects but also its critics.[8] The monumental *Development of Evolutionary Theory in the USSR*, published in 1983, was the first book-length survey of the history of a leading branch of Soviet biology to include an entry on symbiogenesis, which states that modern advances have led to the recognition of symbiosis as a "probable factor" in the evolution of eukaryotes.[9] A modern college textbook on Darwinism states that there was a possibility that the emergence of the first animals with a distinct cell nucleus and mitochondria was connected to symbiotic activities.[10] The *Biological Encyclopedic Dictionary* (1986) is both positive and cautious. It acknowledges both the rising importance of the theory of symbiogenesis and its continued controversial nature.[11]

Two books have played an important role in helping to consolidate and strengthen the interest of Soviet biologists in the theory of symbiogenesis: Khakhina's *Concepts of Symbiogenesis* (1979), presented here in an English translation, and Margulis's *Symbiosis in Cell Evolution* (1981), published in a Russian translation in 1983.[12] While Khakhina's book presents a historical analysis of the gradual maturation of the idea of symbiosis as a factor of evolution, Margulis's volume provides a systematic analysis of the full spectrum of scientific arguments in favor of accepting symbiogenesis not as a

6. Takhtadzhyan, A. L. 1973. Chetyre tsarstva organicheskogo mira. *Piroda* 2:27.

7. Ibid., 23.

8. Khakhina, L. N. 1973. K istorii ucheniia o simbiogeneze. *Iz istorii biologii* 4:63–75.

9. Khakhina, L. N. Problema simbiogeneza. op. cit. 421–35.

10. Paramonov, A. A. 1978. *Darvinizm*. Moscow, 148–49.

11. 1986. Symbiogenez. *Biologichesky entsiklopedichesky slovar*. Moscow, 574.

12. Margulis, L. 1983. *Rol' simbioza v evoliutsii kletki*. Moscow.

mere probability but as an established and fertile fact of modern scientific thought.

Alexander Vucinich
Professor of History and Sociology of Science, Emeritus, University of Pennsylvania, Philadelphia

EDITORS' INTRODUCTION TO THE ENGLISH TEXT

By now nearly every scientist involved in the life sciences acknowledges that eukaryotic cells (those of plants, animals, fungi, and protoctists) evolved from the symbiotic union of two or more types of once free-living prokaryotic microbes (bacteria). This simple idea with far-reaching implications languished for decades in the West, entirely apart from mainstream scientific thought.

The parallel between the prolonged rejection by important biologists of the idea of a symbiotic origin of the eukaryotic cell and the similar rejection by mainstream geologists of the idea of continental drift (revived as a consequence of plate tectonics) is notable. In the case of continental drift, the simple idea was the apparent fit between the adjacent coastlines of South America and Africa. The general assessment of both the idea of the symbiotic origin of the eukaryotic cell and continental drift began to change drastically at nearly the same time, during the late 1960s and early 1970s.

Why did these two paradigm shifts—both the geological and biological—occur so nearly simultaneously? Do these parallel developments have to do primarily with the historical-social and technological context of post–World War Europe and North America, in the same way that Darwin's work has been linked to the political, social, religious, and industrial history of Victorian Britain (Bynum 1991), or did Thomas Kuhn's "Structure of Scientific Revolutions" (1962) have a catalytic effect on both of these twentieth-century scientific revolutions, which followed only a few years after its publication?

At this moment, the Russian people are struggling with their second political revolution of the century. Liya Khakhina's book is a fascinating review of a Russian scientific breakthrough from an earlier age of political revolution. For reasons of language and isolation, the new scientific paradigm fabricated during the first Russian revolution failed to gain a wide audience in either the East or the West until new techniques in biology provided the tools to test Lynn Margulis's assertions that nucleated cells are complex unions of prokaryotes (Sagan 1967; Margulis 1970, 1981).

The illuminating concept of symbiogenesis compares with plate tectonics in making sense of a bewildering quantity of otherwise confusing facts. A book detailing the acceptance of the idea of the symbiotic origin of the eukaryotic cell and Margulis's role in this scientific revolution needs to be written. In lieu of that, the early days of her symbiosis research program are recalled below. The following pages also review the contemporary status of *serial endosymbiosis theory* (SET) detailed in the two articles we wrote together (1990a, 1990b).

Impressed with the frequency of cases of non-Mendelian heredity in a world of nuclear inheritance (for example, photosynthesis mutants of plants and algae, "petites" in yeast, cortical inheritance in *Paramecium*, and so on), as a genetics student at the universities of Wisconsin (1957–60) and California, Berkeley (1960–65), Lynn Margulis explored the early literature for clues to explain cytoplasmic heredity. That there were no "naked genes" outside of cells (or even in them) became clear, and evidence for the presence of bacterial genetic systems inside eukaryotic ones became equally obvious. Based on studies of cytoplasmic heredity and consequent predictions of organellar DNA, she wrote (under the name Lynn Sagan) the statement of the origin of nucleated (*mitosing*) cells from bacterial symbiotic associations in the year 1964–65. James Danielli, co-originator of the lipoprotein-bilayer-membrane theory, published Margulis's work in the *Journal of Theoretical Biology* after approximately fifteen rejections of various transformations of the manuscript (Sagan 1967). The expanded version of the theory of the origin of eukaryotic-cell organelles (mitochondria, plastids, and centrioles in nucleocytoplasm) was developed into a book originally under contract, and then rejected, by Academic Press. Eventually it was published by Yale University Press (Margulis 1970). The theory itself was supported scientifically (never financially) during the 1970s and 1980s by many new results from molecular biological, genetic, and ultrastructural studies. The revised version of the work became the monograph *Symbiosis in Cell Evolution* (Margulis 1981, 1992).

The theory of the evolution of nucleated cells from a series of bacterial symbioses was named serial endosymbiosis theory by F. J. R. (Max) Taylor (1974). A Canadian marine biologist and expert on dinomastigotes, Taylor attempted, with limited success, to develop the details of the contrasting nonsymbiotic origin of eukaryotes. As an intellectual exercise, he described the origin of organelles by "direct filiation" or autogenesis (Taylor 1976). He also distinguished different versions of cell symbiosis theory: the xenogenous view of organelle origin, that is, the serial endosymbiosis idea.

Taylor collected data on the possible origins of mitochondria (from respiring bacteria) and plastids (from cyanobacteria). The concept of the origin of plastids (but not mitochondria) or the origin of both plastids and mitochondria by symbiosis was labeled the "mild" version of the SET. Taylor called

Margulis's theory the "extreme" version because she had insisted that the cilia kinetosomes and related microtubule organelles (undulipodia and their generative structures) were, like mitochondria and plastids, also of symbiotic origin from motile bacteria.

As far as Margulis knew at the time, hers was an entirely original contribution. In the 1960s, cell-symbiosis ideas were still disreputable. Some scientists, like Hans Ris (Margulis's professor at the University of Wisconsin, Madison), knew well E. B. Wilson's 1928 masterpiece, *The Cell in Development and Heredity,* and saw to it that articles in the early 1970s on the discovery of DNA outside the cell nucleus mentioned earlier ideas of organellar origin by symbiosis. Although some authors cited historical views of cell symbiosis and presented ideas of the symbiotic origin of mitochondria and plastids originally brought forth by American (for example, Wallin 1927) and French (such as Portier 1918) authors, these extremely skeptical scientists of the 1960s and 1970s tended to discount hereditary endosymbiosis as a mechanism of evolution (Margulis 1992, chap. 3).

Indeed, Max Taylor and Lynn Margulis were conscious of both prejudice against and ignorance of cell symbiosis theories by most experimental biologists. Yet neither of them had knowledge of our eastern European predecessors: the "symbiogeneticists," such as the Russians Konstantin Sergeevich Merezhkovsky (1855–1921) and Boris M. Kozo-Polyansky (1890–1957), who from the late nineteenth century until the 1950s developed detailed proposals for the origin of evolutionary novelty, including cell organelles, by hereditary symbioses. Although she was superficially acquainted with some of the names of early Russian and German biologists, her knowledge of the history of the ideas she was espousing was woefully limited.

In a fellowship application to the Eastern European–Soviet Studies Program of the National Academy of Sciences (USA) (1987–88), Margulis was finally in a position to propose research into the origins of the obscure concept of symbiogenesis in pre–Soviet Russia. She planned the fellowship to coincide with the residence of her daughter, Jennifer Margulis, at Leningrad University. She fully expected to have to visit the stacks at Kazan University in search of the intellectual history of Merezhkovsky and his correspondence with the West. Because she neither reads nor speaks Russian, she brought Jennifer as translator so that she would be able to use the time to develop a plan to recover the original papers of Merezhkovsky, Kozo-Polyansky, and the other symbiogeneticists, such as Andrei Sergeevich Famintsyn (1835–1918).

During the visit, in April 1989, she lectured at Moscow State University and mentioned her interest in the concept of symbiogenesis in evolution. A talkative, busy crowd of the curious surrounded her afterward, enduring the usual problems of language incomprehensibility. She felt a pressure on her hand; a small paper-wrapped package was placed in it warmly but firmly by a young earnest woman with whom she had absolutely no words in common. She remains, alas, anonymous. On returning to the Hotel Russiya, to her delight she found in the package two slim volumes: the Russian version of the one you have in your hand now, *Concepts of Symbiogenesis* by Liya Nikolaevna Khakhina, and *History of Concepts in Evolutionary Theory* (1975), edited by K. M. Zavadsky, chapter 1 of which by Khakhina discusses Merezhkovsky's theory of symbiogenesis. To her surprise and relief, she found that Khakhina, employed by the History of Science section of the Academy of the USSR since the death of her colleague Zavadsky (1910–77), had been studying in a professional way what she planned to skim amateurishly. The second book, containing chapters on neo-Darwinism and developmental biology, has yet to be translated.

With luck, Jennifer was able to locate Khakhina's telephone number in Leningrad and make a date to see her. The three women spent a blessed hour in the lobby of the Pribaltiskaya Hotel, some two hundred meters from the seven-story building in which Jennifer was housed in two small rooms with five other Soviet women students. From this frantic conversation about "big ideas in biology," came the decision to translate this book.

Khakhina's main point was fascinating. The early symbiogeneticists believed Darwinism and natural selection to be useless or irrelevant to the concept of evolutionary change. Mainly from botanical and marine biological studies, they deduced that increasingly intimate relations among symbiotic partners led to symbiogenesis: a living together in physical association of organisms of different species wherein the partner organisms become fully integrated. The ability to make these deductions was more or less a direct outcome of the Russian scientific reaction to the Darwinian revolution—particularly, as described by Alexander Vucinich (1988), the strong influence of Lamarckian thought and the rejection of social Darwinism.

For these early biologists, symbiogenesis was the main source of evolutionary novelty. The work of Famintsyn and Merezhkovsky, of the German scientist Richard Altmann, who spoke of theoretical "bioblasts" as elements of the cell, and of A. F. W. Schimper and A. Meyer, discoverers of the plastids of plant cells, was reviewed in a historical context by E. B. Wilson (1928). By introducing and then criticizing the concepts of symbiosis in evolution in the context of the bacterial origins of mitochondria and plastids, Wilson ensured that these concepts were at least mentioned in the West. The much younger associate of Famintsyn and Merezhkovsky, Kozo-Polyansky, however, was not known to Wilson or to anyone else in the English-speaking world interested in the role of symbiosis in evolution. Yet, according to Khakhina, it was Kozo-Polyansky who brought together the two essential lines of thought: he realized that symbiosis was the source of evolutionary novelty but that natural selection, in the ordinary Darwinian sense of the failure of any population to reach its biotic potential, acted on emerging and tightening symbiotic associations. In Khakhina's opinion, it was Kozo-Polyansky who developed the modern view of symbiogenesis, even though he received almost no credit for it, since his book *New Concepts of Organisms* (1924), was unknown outside of the Russian-literate world. This fact was made known to Margulis at the 1975 International Botanical Congress by the superb botanist Armen Takhtadzhyan, who told her that Kozo-Polyansky, not Margulis, first suggested the concept of the symbiotic origin of undulipodial motility! As you will see, Takhtadzhyan was correct.

Upon returning home Margulis contacted her colleague, geologist Mark McMenamin, about the Khakhina history book, since she knew of his familiarity with Russian and his interest in evolutionary discontinuities as recorded in the fossil record. Having just published a book with his wife, Dianna McMenamin, on the emergence of animals in the fossil record (McMenamin and McMenamin 1990), he was acutely aware of Russian and other relevant scientific literature that Americans and other English-only readers tend to ignore. With the help of Russian language expert Stephanie Merkel (Cornell University) and émigrée student of biology from the Soviet Union Maria Shteynberg (Hartford, Connecticut), McMenamin assisted in the translation and adaptation of the work for an English-speaking audience. We view this book as an essential aspect of the continuing international dialogue that attempts to evaluate the importance of symbiogenesis as an evolutionary mechanism (Margulis and Fester 1991).

Symbiogenesis, the evolution of novelty by the integration of partners belonging to different taxa—resulting from protracted physical association—had been a principle of evolution (at least in Russia) since the late nineteenth century. The term was coined by Merezhkovsky in part to explain the presence of very similar greenish photosynthetic units in heterotrophs as diverse as hydra, paramecia, and plant cells. Merezhkovsky, with his theory of two plasms, and his senior colleague from St. Petersburg, Famintsyn, were the most successful articulators of the theory of chloroplast origins as a specific example of the general symbiogenesis principle.

These keen Russian biologists suggested, in contemporary terms, that plastids originated as captive cyanobacterial symbionts in heterotrophic cells. Although dialogue, mutual criticism, and disagreement existed between these professional biologists,