

DIATOMS: BIOLOGY AND APPLICATIONS SERIES

# DIATOMS

FUNDAMENTALS AND APPLICATIONS

EDITED BY

Joseph Seckbach  
Richard Gordon



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# Diatoms: Fundamentals and Applications

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# **Diatoms: Fundamentals and Applications**

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**Joseph Seckbach and Richard Gordon**



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## Dedication to Lawrence Bogorad



Lawrence Bogorad, born on August 21, 1921 in Tashkent, Uzbekistan, came to the USA at the age of two and passed away on December 28, 2003. He served as a professor in the Botany Department at the University of Chicago for 14 years (from 1953 to 1967) and in the Biology Department at Harvard University for 34 years.

At the University of Chicago he pioneered the molecular biology of chloroplast biogenesis, and investigated the photosynthetic pigments. He studied (after the discovery and publication of DNA in chloroplasts), the endosymbiotic ancestor from cyanobacteria as the contributors of the chloroplast DNA. At Harvard, he continued his investigation on the molecular biology of the photosynthetic apparatus.

Laurie (his nickname among his colleagues, although I preferred to always approach him by his University title,) was involved in many scientific societies, among them the American Academy of Arts and Sciences (where he served a term as President) and the National Academy of Sciences (Merchant, 2009), and served on the editorial board of *Proceedings of the National Academy of Sciences*. Bogorad received many awards for his studies.

In the personal sphere, he was warm and friendly, full of optimism. His lab was home to five decades of graduate students, postdoctoral fellows, and visiting scientists—all benefiting from his training of them.

Here are some recollections of the four years I spent under the ‘wings’ of Professor Lawrence Bogorad at the University of Chicago. He was my mentor for my MSc and PhD (Seckbach, Bogorad and McIlrath, 1966; Rodermel, Viret and Krebbers, 2005). He welcomed me to the Botany Department at the end of 1961 when I first appeared at the gates of the University. During that interview, we planned my first-year program as a graduate student. Later on, he organized a research assistantship for me so I could continue with my graduate work. As a supportive professor close to his students, he shared with me the latest news on scientific updates in botany and even astrobiology.

Later on, when I was involved in a project on the possibilities of “Life on Venus” at UCLA in 1968 with Professor W. F. Libby (Seckbach and Libby, 1970), I approached him, among others, for advice on growing algae under high CO<sub>2</sub> and elevated temperatures. Bogorad suggested that I try the red alga *Cyanidium caldarium* (his “favorite alga”) for my Venus project, and his advice worked very well. Therefore, I have to give him great credit for his guidance and for my finally changing my focus from plant physiology to the new field of astrobiology, and asked him to write the foreword for a book on *Cyanidium* (Bogorad, 1994).

During the subsequent years, I visited him at his lab in Harvard and he hosted evenings in his home in Lexington, Massachusetts. Sometimes he even waited for my arrival at the train station and took me to his home. When he visited Israel and presented a seminar at The Hebrew University of Jerusalem, he introduced me to his mother, and I drove his wife Rosalyn on a tour of Jerusalem. I had warm feelings toward Bogorad and his family, considered him a colleague and a dear friend and dedicate this volume to his memory.

**Joseph Seckbach**, PhD University of Chicago, 1965; currently retired from The Hebrew University of Jerusalem; home address: P.O.B. 1132, Efrat, 90435, Israel [seckbach@huji.ac.il].

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## Foreword

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Already seven years have passed since the publication of *The Diatom World*, a review of progress in the field of diatom research, edited by Joseph Seckbach and John P. Kocielek (Seckbach & Kocielek 2011). Needless to say, this period was marked further with significant progress in studies on diatoms. In all certainty, the wealth of data acquired over this justifies the publication of this new book, “Diatoms: Fundamentals and Applications”. In addition to fundamental issues of diatom biology including valve morphogenesis, sexual reproduction and cell cycle, ecology and biodiversity, it includes numerous contributions on applied aspects of diatom research.

The section on applied aspects begins with a review of diatomite applications, including commercial use and future trends (Ghobara 2019). A related chapter discusses photonic properties of biogenic silica brought into the intricate patterns of diatom valves, an inspiration for numerous generations of professional and self-taught diatomists, but also chemists and physicists (Ghobara et al. 2019). Progress in biomedical applications research is presented in chapters on drug delivery with diatomaceous silica as a potentially biodegradable drug carrier, for tissue engineering and hemorrhage control on the one hand (Maher, Aw & Losic 2019), and on the use of molecular methods in forensic science on the other (Vinayak & Gautama 2019). The latter chapter is a leap forward as it may spare the diatomists performing forensic examinations the burden of processing drowning victims’ internal organs. The application of metabarcoding will not solve the problem of the physical presence of diatoms, e.g., in lungs, but will support the identification of diatoms and thus facilitate the identification of the habitat where the victim drowned. This may be another sign of metabarcoding outcompeting the classic light microscope (LM) examination and counting of processed diatom valves on slides. To remind the reader, the United Kingdom gave up the use of LM-based diatom valve counting in water quality assessment in 2017 (Mann et al. 2017). Metabarcoding became the preferred alternative, let us hope, successfully. This hope is expressed on behalf of all skeptical practitioners of classic diatom indices in river and lake monitoring.

Although diatom lipids are considered a very good source of biodiesel, and some species are even named as oleaginous forms (see *Fistulifera solaris* for an example), other microalgae

are still preferred in large scale biomass growth and oil production. The present book introduces a new term, and a corresponding trade mark, of Diafuel with *Fistulifera saprophila* valve graphics playing a central part (Vinayak, Joshi & Sharma 2019). Unlike other microalgae, diatom organelles and lipid drops are encased in a siliceous box-like frustule. Unlike the “soft bodied” microalgae, diatoms go undamaged unless the pressure applied to squeeze oil exceeds a critical strength. Shall this allow the process of milking diatoms? Let us wait and see. So far, however, a splendid field of research on nanoindentation is seeking to obtain a milking pressure that will not kill diatoms, and allow them to restore their lipid droplets. Considering human energy use forecasts, this shall be required within the time span of several human generations. A unique opportunity presented by the “diafuel” project is that the secondary product or “waste” of the technological process is the biogenic silica that - owing to its photonic properties - can be “recycled” in further production of energy, for instance in solar panels or as a component of new valuable materials with unique photonic properties (Ghobara et al. 2019). One drawback of using diatom mass cultures for biofuel production purposes is the necessity of choosing between open race ponds which can be contaminated with airborne mineral and microbial waste, and closed photobioreactors which are more expensive to maintain. Culturing diatoms in bubble wrap, proposed in the chapter by Gordon et al. (2019), could be an alternative to these two solutions. If successfully implemented, upon certain conditions, with “bubble farming” biofuel production costs could be lower than those of mineral fuels.

In line with this is the review of the enormous scale of applied ongoing research on diatoms in China (Zhang 2019). Discussed in this latter chapter are examples of applied research involving diatoms in materials and biomaterials science, energy production and storage, waste water treatment, composites, diatom-based ceramics, etc. Given that numerous laboratories in China also work on fundamental aspects in diatom research including ecology, biology, taxonomy and phylogeny, the overall impression is tremendous.

Framed prints of beautiful diatoms can generate substantial sums of money. However, it seems that the beauty of diatoms unspoiled with any commercial issues is a value in itself. It is quite common that professional diatomists maintain friendly relations with diatom enthusiasts who are experts in light microscopy, often using very sophisticated systems. Perhaps surprisingly, with the changing technologies there is also an increase in the number of non-professional diatomists who own scanning electron microscopes. I know at least a few in Europe. The diatom beauty chapter definitely hosts images that should rank within fine arts (Tiffany & Nagy 2019). Morphogenesis of the diatom frustule is the subject of another chapter (Bedoshvili & Likhoshway 2019). Despite the progress in our understanding of the cellular mechanism of valve formation, its genetic controls remain largely unknown.

Fundamental aspects of diatom research are represented by such highlights as a review of sexual reproduction and life cycle, with the latest perspective on these issues (Pouličková & Mann 2019). This research, which involves experiments for scientists of Benedictine patience, is crucial for understanding numerous aspects in diatom taxonomy and systematics. However, despite its splendid reputation and importance, few young scholars are willing to learn the techniques and spend days, months and years at an inverted microscope isolating clonal cultures of similar strains to discover their sexual compatibility and perform successful crossing experiments. Certainly the use of molecular tools makes the search for potentially compatible clones easier, but does not guarantee offspring. Research on diatom symbiosis is less common. Fortunately, a chapter on endosymbionts in diatom cells

(cyanobacteria), and on diatoms as endosymbionts (in dinoflagellates) is published in this book (Stancheva & Lowe 2019). Any attempt to define a diatom usually involves a phrase like: diatoms are unicellular, photosynthetic organisms present in all habitats providing enough ambient light and a minimum of moisture. Diatom life and valve morphogenesis are intertwined with photosynthesis. Despite the fact that diatoms play such an important role in aquatic and terrestrial ecosystems, their photosynthesis at the organellar level, as emphasized by the authors of the chapter on diatom photosynthesis diatoms, is rather poorly known (Scarsini et al., 2019).

A series of chapters presents reviews on biodiversity and comparisons of diatoms living in freshwater habitats including rivers and freshwater mountainous habitats on one hand and potentially toxic marine diatoms on the other. Research on inland diatom assemblages of the Russian Far East (Nikulina & Medvedeva 2019) and on those from hot springs in Kamchatka (Nikulina et al. 2019) is presented in two chapters. Included are also chapters on freshwater diatoms of the South and Central European Mountain Ranges, including Tatra (Poland) and Rila (Bulgaria) (Ognjanova-Rumenova et al. 2019). The review of freshwater diatom ecology provides a link between fundamental and applied aspects of diatom research (Pouličková & Manoylov, 2019). Covered in this review are the most recent aspects of freshwater diatom ecology, dispersal, biodiversity and biogeography, with an emphasis on practical aspects of using freshwater diatoms, i.e., in biomonitoring of freshwater habitats. As in the chapter on Kamchatka hot springs, another extreme habitat is presented in a review on ecophysiology of the Arctic fjord diatom strain *Navicula directa* (Karsten & Holzinger, 2019). The adaptation of this species to harsh environmental conditions related to low temperatures and lack of light during the long polar night has been proven in a series of experiments. The role of iron (Fe) in diatom physiology is reviewed by (Raven 2019). Despite the importance of iron, the existing knowledge is scarce and mostly limited to marine planktonic taxa. This book is crowned with the most up to date review on diatoms as potential producers of toxins dangerous to humans and other living organisms (not only domoic acid). Aside from fairly numerous representatives of *Pseudo-nitzschia*, only two marine *Nitzschia* species have been detected as toxin producers. However, we should expect the list of toxins and their producers to increase. It is not always the case that bloom forming toxin producers appear in strongly human impacted environments (e.g. shrimp aquaculture). Some inhabit Arctic and Antarctic marine waters or cold oceanic currents. The chapter by Bates et al. (2019) presents the complex biology of toxic diatoms, their distribution, and detection methods.

The present book is unique as it provides also an emotional component: it includes several chapters that commemorate those of our diatomist colleagues who recently passed away. Joseph Seckbach commemorates his friend Lawrence Bogorad, a late professor at the University of Chicago and dedicates the whole volume to his memory (Seckbach 2019). This is a tribute to Joseph Seckbach's MSc and PhD mentor at the University of Chicago. They remained in very friendly contact after Joseph's graduation. Lawrence Bogorad's research on photosynthetic pigments made a considerable impact on our understanding of chloroplast origin and photosynthesis. Further, Wladyslaw Altermann summarizes the life and scientific career of Alex Altenbach, a renowned palaeontologist and protistologist (Altermann 2019). The third, touching text by Janice Pappas is dedicated to Frithjof Sterrenburg, a diatom enthusiast with whom many of us had collaborated in the past (Pappas 2019). Personally, I met Frithjof in Frankfurt am Main during his visit to Horst Lange-Bertalot. We spent a memorable few days with Frithjof. I cherish the memory of countless phone calls I made

that were answered by Frithjof, when an answer to an urgent taxonomic issue was past due. It is a pity that our two joint efforts to get the Kinker collection project funded failed. One special recollection that I have is Frithjof's pride when he published a joint paper with his father (Sterrenburg & Sterrenburg 1990). Probably few diatomists know that *Nitzschia nienhuisii* Sterrenburg F.A.S. & Sterrenburg F.J.G. 1990 from the coast of Mauritania was described by son and father Sterrenburgs. This distinctive and beautiful diatom, common around African coasts of Atlantic and Indian Oceans, seems to require a transfer to a new (as yet unnamed) genus. Years after witnessing Frithjof's pride, I found myself moved by similar feelings when publishing a joint paper with my son (Dabek et al. 2015).

This book will definitely be a connection between the fundamental and applied research on diatoms, and a connection between two scientific communities. Personally, I consider my professional contacts with materials science community and use of their tools, i.e. Focused Ion Beam (FIB, Witkowski (2019)) as very inspiring and fruitful in my own, principally fundamental, diatom research.

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# Introduction to Diatoms: Fundamentals and Applications

Joseph Seckbach

*Diatoms: Fundamentals and Applications* is the first volume in the series *Diatoms: Biology and Applications*, published by Wiley-Scrivener and edited by Richard Gordon and Joseph Seckbach.

*Diatoms: Fundamentals and Applications* complements adds further to the knowledge presented in our first volume (*The Diatom World*, Joseph Seckbach and J. Patrick Kocielek, eds., Springer, 2011). Moreover, the current volume includes some topics not covered in the previous volume.

What are the diatoms? They are fascinating microscopic unicellular or colonial, microscopic eukaryotic algae. They are ubiquitously distributed in aqueous habitats, considered a major part of phytoplankton. They are present in fresh water, saline environments, brackish water and marine areas, and they are a source of biofuel. They live in high and low temperatures, and at different pH values. Their cells are divided into 2 halves. Their cell wall is silicified.

This volume presents many facets of diatoms that you have never encountered and had no inkling of their existence. Diatoms utilize 20% of the atmospheric CO<sub>2</sub> and release (via their photosynthesis process) our atmospheric O<sub>2</sub> vital to all life. (See chapter by Matteo et al.). Their chloroplasts are uniquely composed and differ from other green algae and from higher plants by not possessing chlorophyll **b** as is present in other green plants.

Our contributors are from quite a few countries, including Canada, China, Egypt, France, Germany, India, Israel, Poland, Russia, South Africa, UK and USA.

## The Topics Covered in This Volume are Varied

Ecology; cell biology; biodiversity, distribution in nature; photosynthesis, light and diatoms; iron and ferritin; toxic diatoms, sexual reproduction, biofuel; ion beams; diatom uses; external uses; forensic use; medical silica; and diatom research in China.

It is assumed that an endosymbiotic event (see Stancheva and Lowe), took place in the past during the evolution of diatoms. According to this theory, a host eukaryotic primitive cell absorbed a cyanobacteria type of cell and used this guest (or penetrator) as part of its eukaryotic plastid entity with some exchange of genetic material with the host nucleus. For full photosynthetic activity **iron** is required (chapter by Raven). Otherwise, with a lack of iron in its nutrition, the green algae and higher plants turn pale and chlorotic - green-less). Algal-ferritin presents as a storehouse of iron for the photosynthetic reaction and for other requirements for cellular iron.

Cytological studies of the silicon diatomic cell wall, exhibiting the most beautiful diatoms appearance, are presented by Karsten and Holzinger, by Witkowski, and by others. Furthermore, the “ideal beauty” of the diatomic walls is admired specifically in the chapter by Tiffany and Nagy.

From among the ecological environments, diatoms are ubiquitous, living in fresh water, cold Polar water, hot spring water, and mountain lakes (see Poulickova and Mann, Nikulina et al., Ognjanova-Rumenova et al.)

This book is dedicated to the memory of three close colleagues; Lawrence Bogorad, -who was my mentor for my MSc and PhD at the University of Chicago.

My colleague Alex Altenbach, whom I met when I was a DAAD in the Department of Geology at Ludwig Maximilian University in Munich.

Frithjof Sterrenburg, a colleague who was an electron microscopist and an amateur diatomist from The Netherlands.

All three of the above were involved in algae and diatom research.

## **Acknowledgment**

We, the editors thank our authors for their contributions, specifically our Russian authors, and the reviewers of the chapters.

# A Memorial to Frithjof Sterrenburg: The Importance of the Amateur Diatomist

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## **Abstract**

Frithjof A.S. Sterrenburg was an amateur diatomist who became an expert in taxonomy, nomenclature, microscopy, and photomicrography. He is best known for his work on *Gyrosigma* Hassall and *Pleurosigma* W. Smith but contributed in many areas of diatom research. Because of who he was and the nature of his interactions with the diatom community, he has had and will continue to have a lasting impact. His contributions to diatom research have influenced our understanding and usage of diatom taxonomy and nomenclature and how taxonomy informs ecological, biostratigraphic and other biological studies. His affable yet incisive character enabled him to be a teacher and mentor to professionals and amateurs and to be respected and appreciated internationally.

**Keywords:** Diatoms, *Gyrosigma*, *Pleurosigma*, microscopy, amateur diatomists, photomicrography, museum collections, taxonomy, valve morphogenesis, constructal morphology

## **1.1 Introduction**

Throughout science, amateurs have contributed to the body of knowledge in many disciplines. Amateurs dedicate themselves to the pursuit of knowledge concerning their specific interests, and when it comes to diatoms, this is no exception. During the 1800s, diatom research was conducted by hobbyists who had occupations in very different fields (Bahls 2015; Gordon et al. 2009). For example, Friedrich Traugott Kützing was a pharmacist and school teacher who became a diatomist. He discovered that diatoms were composed of silica and had two parts to their shells, one was “primary” and the other “secondary,” and was aided in publishing his findings by C.G. Ehrenburg, the preeminent zoologist and diatomist of the time (Werner 1977). Some amateurs formed microscopical societies or clubs as enthusiasts pursuing their common interest in the microscopic world (e.g., The Quekett Microscopical Club). In the post-Victorian world, diatom research has become professionalized, and currently, individuals can find

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**Figure 1.1** Frithjof A. S. Sterrenburg at his microscope. (courtesy of H. van Dam)

professional mentors for formalized training to become a diatom researcher as one's occupation.

Having said this, modern amateur or citizen scientists are still making contributions to diatom research. Because so few individuals are formally trained, credentialed, paid, and have a career specifically in diatom research, and because diatom research is at a stage where the enormity of necessary work involves potentially hundreds of thousands of species, amateurs have a vital role to play. Amateurs who engage in this role seriously soon realize that contributing requires associating oneself with professionals, especially concerning technical matters in taxonomy, nomenclature, microscopy, and photomicrography.

The quintessential example of the modern amateur diatomist was Frithjof Sterrenburg (Figure 1.1). He died on March, 11, 2016 and left his mark on diatom research. He had passion and dedication to diatom research that earned him recognition and respect from professionals internationally. Frithjof's work in diatom taxonomy and nomenclature as well as microscopy and photomicrography has benefited professional and amateur diatomists alike, and his contributions have continued to be influential in the way diatom researchers engage in and pursue their studies. No matter how one perceives what it means to be an amateur, Frithjof transcended the notion because of who he was and how he lived his life.

Historically, amateur diatomists were unpaid and typically worked in various occupations (Bahls 2015; Werner 1977). A prime example was Astrid Cleve-Euler. She was the first female to be awarded a doctorate in science at Uppsala University, Sweden in the late 19<sup>th</sup> century. Yet, throughout her life, she was never employed as a scientist despite her contributions to chemistry, botany, geology, and diatom research (Swedish

Natural History Museum). Even van Leeuwenhoek (17<sup>th</sup> to 18<sup>th</sup> century) who was a tradesman and politician did not get paid to study the microscopic world (Pedrotti accessed on 2016; Sterrenburg 1982).

Other dedicated amateurs engaged in diatom research. *Pleurosigma angulatum*, originally named *Navicula angulata* by John Thomas Quekett (Sterrenburg 1990a), an amateur diatomist who was a microscopist and histologist, was typified by the Reverend William Smith, an amateur turned academic who was a prominent diatom researcher in the Victorian era (Werner 1977). As a common leisure activity, diatoms were mounted in various configurations, slides were either purchased or prepared by the individual, and mounts were viewed with microscopes situated in Victorian parlors (Lynk accessed on 2016). Diatom mounters such as Johann Diedrich Möller (originator of the art of diatom mounting) (Walker 2009) and dentist William Gatrell (Stevenson 2009) were much in demand to produce intricate arrangements for viewing. The advent of the microscope and its common usage paved the way for such activities and induced the proliferation of amateur diatomists interested in the natural history of these eye-catching, exquisite microorganisms.

Frithjof was a throwback, in a sense, to this ilk of diatom researcher. Yet, he developed his own style and went beyond amateurs such as surgeon and physician John Redmayne (Stevenson 2013) and teacher John Albert Long (Walker 2012). Like Quekett, Redmayne and Long plied their trade as amateur diatomists in the late 19<sup>th</sup> and early 20<sup>th</sup> century. They bought and sold diatom samples as well as made mounts and relied on popular publications such as Hardwicke's Science Gossip for the latest information on diatoms (e.g., Taylor 1885). In Hardwicke's volume XXI from 1885, an article on Jacques-Joseph Brun's publication, "The Diatoms of the Alps and the Jura," was presented in which Brun, a pharmacologist and diatomist (JStor Global Plants accessed on 2016), talked about the deposition of diatoms over time and the formation of Kieselgüühr (Taylor 1885). His taxonomic work like that of his contemporaries on fossil diatoms provided the impetus for the commencement of Adolph Schmidt's Atlas in 1874 (Schmidt et al. 1874–1959) that was continued with contributions from others until 1959—including Friedrich Hustedt, a teacher turned professional diatomist who has had a great influence on diatom research (Alfred Wegener Institute 2015). Frithjof's trajectory into diatom research was more along the lines of Smith, Brun, and Hustedt. Like these predecessors, Frithjof progressed from amateur to expert, garnering respect for his expertise. Frithjof elevated his contributions to the level of scientific peer-review rather than being only presentable in popular publications, and like many of his predecessors, he has had a lasting impact on diatom research.

## 1.2 Background and Interests

Frithjof A. S. Sterrenburg was born in 1934. Originally, he studied medicine at Amsterdam University. His autodidactic nature conflicted with a formalized education approach, and inevitably, he would venture out on his own. He was well-read and able to learn various subjects at many levels of difficulty and did so as a life-long endeavor. For Frithjof, life and learning was an adventure.



**Figure 1.2** Frithjof playing the trumpet with trombonist Bill Rank from the Paul Whiteman orchestra (1968). (permission from C.J.Sterrenburg)



**Figure 1.3** Frithjof in his backyard, extolling a friend to see into the night sky (circa 1980). She and her biologist husband were hosts of the Sterrenburgs in Sulawesi, Indonesia. (permission from C.J. Sterrenburg)

Frithjof showed a propensity for immersing himself in a wide range of learning experiences, and some of his emerging talents were expressed in such divergent fields as music (e.g., Sterrenburg 1967) and astronomy. In his youth, Frithjof played trumpet (Figure 1.2), saxophone, clarinet, and piano in big-band style orchestras, and he also arranged compositions for such orchestras. He was a jazz musician for many years (de Wolf, personal communication). He owned many telescopes (Figure 1.3). Some of Frithjof's first publications in the early 1980's described how to see the stars more clearly (Sterrenburg 1983a, b). He liked to share conversations about the stars with many people, including long-time friends Michael Stringer and Wulf Herwig, as he relished being able to see beyond our immediate world.

Frithjof was a tinkerer and had a knack for all things electronic, electrical and mechanical (e.g., Sterrenburg 1979). Frithjof shared an interest in electrical devices with