ALGAE AND CYANOBACTERIA IN EXTREME ENVIRONMENTS

Cellular Origin, Life in Extreme Habitats and Astrobiology

Volume 11

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The Hebrew University of Jerusalem, Israel

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Algae and Cyanobacteria in Extreme Environments

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LEGENDS FOR THE COVER PICTURE

An arrangement of 44 diatoms surrounded by images of cyanobacteria and chlorophyte algae. The diatoms include species from the genera *Actinoptychus, Amphitetras, Aulacodiscus, Caloneis, Cocconeis, Cymatopleura, Cymbella, Didymosphenia, Diploneis, Gyrosigma, Hemiaulus, Mastogloia, Melosira, Navicula, Neidium, Paralia, Pleurosigma, Rhabdonema, Stauroneis, Stictodiscus, Surirella, Synedra, Tetracyclus, Triceratium,* and *Trinacria*. The algae bordering the diatoms include (from top left corner): the desmid *Staurastrum artiscon*, the cyanobacterium *Anabaena*, the desmid *Micrasterias hardyii,* the coiled filaments of *Spirogyra*, the tapered cork screw-like filaments of the cyanobacterium *Spirulina,* and the coiled filaments of *Zygnema*. Border algae images are contributed by **Dr. Gordon W. Beakes**, Newcastle University, UK. The diatom arrangement and photomicrograph, and the composite image of all algae, are by **Dr. Stephen S. Nagy** (MD), Montana Diatoms, USA.

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FOREWORD

This volume encompasses a great diversity of subjects as well as authors, most of whom are well recognized and established in their fields and others who are younger, upcoming scientists of whom we will hear more in the future. The subject is extremophiles, and is almost entirely focused on photosynthetic microbes. It is a complementary and updated version of a volume of similar subject matter published in 2001 (*Algae and Extreme Environments: Ecology and Physiology*, eds. J. Elster, J. Seckbach, W.F. Vincent and O. Lhotsky, Nova Hedwigia, Beiheft 123: 1–602. Schweizerbart'sche Verlagsbuchhandlung, D-70176 Stuttgart. http://www.schweizerbart.de/pubs/books/bo/novahedwig-051012300-desc.ht, Berlin/Stuttgart, 602 pp.). Few of the authors of the present volume were involved in the earlier publication, and many of the subjects are quite different.

The studies of extremophiles have increased almost exponentially in the last several years, mainly because of the interest in early life on this planet and possible life (past or present) on others. This has necessitated the creation of a new and well-received journal, *Extremophiles* (Volume 1, 1997 to present). Unfortunately, few of the papers published in this journal to date have focused on phototrophs. Papers on tolerance to environmental extremes by phototrophic microorganisms are also frequently found in a number of journals, including *Journal of Phycology*, *Applied and Environmental Microbiology*, *Environmental Microbiology*, *Microbial Ecology*, *Archives of Microbiology*, and several others, and, of course, in the series of volumes entitled "*Cellular Origin, Life in Extreme Habitats and Astrobiology*" (www.springer.com/series/5775) edited by Joseph Seckbach.

The current volume is divided into nine subject areas in addition to an opening section: General introductory chapter (1), (2) Phototrophs at high and low light, (3) Phototrophs in the marine environment, (4) Phototrophs in cold environments, (5) Phototrophs in hot alkaline and acidic environments and non-thermal acidic habitats, (6) Phototrophs under water stress: dry and hypersaline environments, (7) Adaptability to changing environments, (8) Other microorganisms and extreme habitats, and (9) Outlook.

We need to remember that phototrophs, except for a few, do not generally extend as far into some extreme environments as do the non-photosynthetic Bacteria and Archaea. With respect to upper temperature limits, a few Cyanobacteria and Chloroflexi extend to the lower 70°Cs which demarks the upper boundary for a few unique organisms of each of these phyla, and consequently the upper temperature limit for chlorophyll- or bacteriochlorophyll-based photosynthesis (a limit known and not disputed for many decades). With respect to upper salinity limits, there too the non-photosynthetic Bacteria and Archaea dominate the picture, but there are exceptions. Some phototrophic purple bacteria (e.g., *Halorhodospira* spp.) nearly equal the upper salinity limits of some of the non-phototrophs, and a few cyanobacteria (e.g., *Halothece* spp.) and diatoms come close, as does the green alga, *Dunaliella salina*. The non-phototrophs do not have the monopoly on cold or freezing tolerance, although they may have with respect to true psychrophily, since most of the cyanobacteria isolated from cold habitats are psychrotolerant rather than psychrophilic. Cyanobacteria appear to have an edge over eukaryotic microalgae with ability to withstand freezing in nature.

Acidophily or acidotolerance are well represented by the non-phototrophic Bacteria and Archaea. The Cyanobacteria and anoxygenic phototrophic Bacteria are almost excluded from acidic environments below pH 4–4.5 [with the exception of *Acidophilium* spp. (α-Proteobacteria) that use Zn in the center of the porphyrin ring of bacteriochlorophyll instead of Mg].

Periodic and long-term desiccation is another extreme that is well represented by phototrophs, particularly cyanobacteria – these to a greater extent than microalgae. It is not clear that non-phototrophic Bacteria or Archaea have the edge with desiccation as the stressor.

The chapters vary in subject matter from algae and cyanobacteria in subaerial urban environments, in environments that are exposed to freeze–thaw cycles and permanent coldness, as well as speculations as to the versatility and evolution of cyanobacteria in extremes and the role of reduced iron as a reductant in early photosynthesis. Some papers are more focused on individual species or natural groups of species and their responses to various extremes. Many habitats or natural groups of organisms included here have barely been described or discussed before in the context of extreme environments. There is extensive speculation in some of the chapters, particularly those that constitute brief reviews of the subjects. From a scan of abstracts and concluding remarks, I also believe that portions or conclusions of some of the chapters may be somewhat or highly controversial, and therefore should stimulate discussion.

With respect to the Eukarya (algae, except for a couple of chapters on "other" protists or fungi), there is a chapter that emphasizes the uniqueness of the dinoflagellates as a distinct group, and another, their probable propensity to acquire endosymbionts in crowded benthic environments. Diatoms are also discussed, particularly with respect to the mysteries of their intricate and rigidly controlled wall patterns, and in another chapter, their remarkable ability to thrive in cold seawater and even to endure freeze–thaw episodes.

Acidic environments are involved in a few chapters. The acidic Rio Tinto of southwestern Spain drains ancient mine pits. There are descriptions of other acid mine drainways that are also very rich in heavy metals that would be toxic for most algae, but these habitats nevertheless sustain a mixed assemblage of a few specialized species of algae, including diatoms, euglenoids, and green algae. The biomineral deposits of the extreme Rio Tinto are suggested as possible analogs in the search for remnants of possible microbial life in ancient deposits on Mars. Primitive photosynthetic, unicellular red algae of the order Cyanidiales inhabit acid environments from pH 0.0 to 4.0 with temperatures from about 40 to 56°C. A few species of acidophilic eukaryotic algae also inhabit waters of this pH range, but at lower temperature. Thermoacidic environments such as the sulfurous vents near Naples, Italy, are discussed with respect to the Cyanidiales that reside and thrive there. Another chapter delves into understanding the biology of these algae based on knowledge of their genomes.

Other chapters describe the distribution of various algae and cyanobacteria in varied habitats (e.g., under UV stress, in dim light, on man-made substrates, high diversity in urban environments, soils, and in other periodically xeric or aero-terrestrial environments).

About half of the chapters focus on prokaryotes (namely cyanobacteria or mixed communities). Some are reviews, such as that on the diversity, versatility, and specialization of cyanobacteria that may help to explain their extraordinary ability to inhabit various extreme environments. Three other chapters examine the tolerances of cyanobacteria in polar and other cold environments. Some authors have focused on specific cyanobacteria, such as *Acaryochloris*, the only cyanobacterium utilizing chlorophyll *d* instead of chlorophyll *a*, the extreme desiccation-tolerant cyanobacterium, *Chroococ-cidiopsis*, that may represent a type close to a form that may have inhabited a terrain like that of Mars in happier times past, and *Mastigocladus* cf. *laminosus*, a common global, thermophilic cyanobacterium that exhibits somewhat dissimilar genotypes in different portions of the thermal gradient of the same alkaline, geothermal stream as well as in near and distant geographic locations.

There are, of course, other topics that I have not mentioned. However, this compilation has such a remarkable variety of subject matter that I believe that it should not be treated simply as a reference volume for specialists who would concentrate on one habitat or on a few species, but should be read in full by every biologist interested in extreme or unusual environments and their organisms.

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December 2006

Biodata of **Richard Castenholz,** author of the ***Foreword***.

Dr. Richard W. Castenholz is professor emeritus in the Center for Ecology and Evolutionary Biology at the University of Oregon. He received his B.S. in Botany at the University of Michigan (1952) and his Ph.D. in Botany at Washington State University (1957). He has been a faculty member at the University of Oregon since 1957. His early research was focused on the ecology of both freshwater and marine epilithic diatoms, but in the late 1960s he switched almost entirely to the study of cyanobacteria and anoxygenic phototrophic bacteria of hot spring ecosystems. During this period, the anoxygenic phototrophs, *Chloroflexus* and *Heliothrix*, were first described by Pierson and Castenholz (1974) and Pierson et al. (1985), respectively. These unique new genera (with the later addition of others) have formed the base of a new phylum, the Chloroflexi. Later, this expanded into ecological and physiological studies of phototrophic prokaryotes from microbial mats in nonthermal freshwater, marine, and hypersaline habitats, including mats of Antarctic melt ponds dominated by cyanobacteria. The research questions that were asked include: how do various microorganisms adapt to environmental extremes (e.g., high and low temperatures, low pH, high salinity, desiccation, normally toxic sulfide concentrations, and high solar irradiance, especially UV radiation)?

In these studies, he and his students have characterized scytonemin, a UV-shielding compound in the extracellular sheaths of many highly exposed cyanobacteria, and have demonstrated its role in increasing fitness under UV exposure, even when cells are metabolically inactive. We have also shown that some motile cyanobacteria have a lifesaving escape response to UV exposure by moving downward into soft mats or sediments in geothermal, temperate, and polar environments. Currently, his main interest is in the ecology and diversity of the unicellular algae of the rhodophytan order Cyanidiales, a group of a few genera and species that inhabit hot (40–56°C) acid waters (pH 0.5–4.0) in Yellowstone Park and other volcanic regions of the earth.

Throughout the last 25 years, Castenholz has also been trying (with others) to unravel the extremely disordered and complex taxonomy of cyanobacteria and was heavily involved in writing and editing the cyanobacterial sections in two editions of ***Bergey's Manual of Systematic Bacteriology*** (1989 and 2001).

He has also been honored several times (e.g., J.S. Guggenheim Fellow, 1970–71; Fulbright Scholar, 1977–78; Fellow, AAAS; Trustee, Bergey's Manual Trust, 1991–2001; Fellow, American Academy of Microbiology, 1996; Bergey Medal for Distinguished Achievement in Bacterial Taxonomy, 2005).

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PREFACE

This volume, number 11 in the series of "COLE" (***C****ellular* ***O****rigins,* ***L****ife in* ***E****xtreme Habitats and Astrobiology,* see: www.springer.com/series/5775), deals with algae growing at the edge of life under extreme conditions. It contains over 40 chapters contributed by 50 authors from 17 countries.

Photosynthetic microorganisms such algae (including cyanobacteria) occupy most environments on Earth that are illuminated with visible light. Among these habitats are several places which are, from the anthropocentric view, inhospitable and different from the "normal" places. The microbes occurring in those environments are referred to as "extremophiles." We could assume that those extremophiles regard their harsh habitats as an oasis or a paradise. Not only bacteria and Archaea, which are known to be flexible and may occupy almost every niche and cope with severe habitats, but also algae are among the extremophiles. Extremophiles are classified into various categories according to the "extreme" character of their environments, such as very high or very low temperatures limit, pH values, salinity, dryness, high concentration of heavy metals, very high or low levels of radiation, especially ultraviolet radiation, and to a certain extent anaerobic environments.

Thermophiles, organisms that love elevated temperature levels, grow in hot environments such as hot springs. The highest temperature for algae is in the upper 50°Cs and for the cyanobacteria close to 70°Cs. At the lower temperature scale are the cold lovers (psychrophiles) growing in geographical regions such as in the Arctic, Antarctica, and the permafrost of Siberia. They tolerate low temperatures as long as the internal cytosol is not damaged from freezing ice inside the cells. Their cellular membranes protect their internal content by selective permeability, and in some cases the cells produce compounds to provide an "antifreeze" effect. Among the eukaryotic algae are the ice *Chlorophytes* (green algae) which "paint" ice in various colors.

Algae also grow in alkaline or acidic media. The alkaliphiles occur at higher ranges of pH as in the soda lake in Africa, while the acidophiles thrive in acidic media at the lower ranges of pH scale. They occur, for example, in acidic hot springs and abandoned coal mines. Among the acidophiles are eukaryotic algae such as *Cyanidium caldarium*, *Galdiera sulfuraria*, and certain diatoms. Other algae, the halophiles, may be found in high salinity, which include the eukaryotic alga *Dunaliella salina*, some diatoms, and to a certain extent also *Galdiera sulphuraria* could be regarded as halotolerant. Extensive research has been carried out with the halophiles, growing in media of high salt solution (up to saturation). Some halophilic algae synthesize and accumulate organic compounds in their cytosol, such as glycerol. These compounds balance internal–external osmotic pressure and prevent plasmolysis from occurring. Fewer algae have been observed growing at depths where hydrostatic pressure could be a factor, but where there is still minimal light availability.

Some environments are characterized by more than one extreme factor. The microbes dwelling in those habitats are referred to as poly-extremophiles. Higher temperature may go together with acidic media (which is the habitat of thermoacidophilic microorganisms); hot or cold environments are often exposed to UV irradiation (occurring in such places are xerophilic algae and cyanobacteria; observed in the deserts or near the polar regions), likewise, high temperatures and high pH levels occur in salinity areas.

These extremophiles can provide important answers to the ecology and biochemistry and lead to biotechnological applications and industrial aspects. Furthermore, understanding of the diversity of algal life in various environments is vital also for the study of the origin and evolution of life on Earth. They thrived in conditions which are probably similar to the current extreme habitats, and it is well possible that similar phototrophs also live elsewhere in the universe.

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December 2006

Biodata of **Joseph Seckbach**, author of ***Preface***, "Oxygenic Photosynthetic Microorganisms in Extreme Environments: Possibilities and Limitations" (with co-author Aharon Oren), and "Algae and Cyanobacteria under Environmental Extremes: Final Comments" (with co-authors David J. Chapman, David J. Garbary, Aharon Oren, and Werner Reisser).

Professor Joseph Seckbach is the initiator and chief editor of ***Cellular Origins, Life in Extreme Habitats and Astrobiology*** **(COLE)** book series (see www.springer.com/sereis/5775). He is the author of several chapters in this series. Dr. Seckbach earned his Ph.D. from the University of Chicago, Chicago, IL (1965) and spent his postdoctoral years in the Division of Biology at Caltech (Pasadena, CA). Then he headed a team for searching for extraterrestrial life at the University of California at Los Angeles (UCLA). He has been appointed to the faculty of the Hebrew University (Jerusalem, Israel), where he performs algal research and teaches biological courses. He spent his sabbatical periods in Tübingen (Germany), UCLA, and Harvard University, and served at Louisiana State University (LSU) (1997/1998) as the first selected occupant of the John P. Laborde endowed Chair for the Louisiana Sea Grant and Technology transfer, and as a visiting Professor in the Department of Life Sciences at LSU (Baton Rouge, LA). Recently, he spent 3 months in Ludwig Maximilians University in Munich with a DAAD fellowship from the German service of exchange academicians, where several forward steps of this volume have been performed.

Among his publications are books, scientific articles concerning plant ferritin (phytoferritin), cellular evolution, acidothermophilic algae, and life in extreme environments. He also edited and translated several popular books. Dr. Seckbach is the co-author (with R. Ikan) of the ***Chemistry Lexicon*** (1991, 1999) and other volumes, such as the Proceeding of ***Endocytobiology VII Conference*** (Freiburg, Germany, 1998) and the Proceedings of ***Algae and Extreme Environments*** meeting (Trebon, Czech Republic, 2000) (see http://www.schweizer-bart.de/pubs/books/bo/novahedwig-051012300-desc.ht). His recent interest is in the field of enigmatic microorganisms and life in extreme environments.

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INTRODUCTION TO THE ALGAL WORLD

If you leave a glass of water near the window, after a while you may notice changes in color and clarity of the water. If you then examine a sample of the water under a light microscope you will see a beautiful, marvelous microscopic world unfold. Microalgae are everywhere! They occupy virtually every habitat including those with extreme conditions. Many microalgae live in extremely hot environments (>70°C) such as deserts and the outflow of geothermal springs. They can live in the Dead Sea, where salt concentrations are seven times that of the oceans, and in highly acidic or extremely alkaline conditions. They can even live in snow!

Such extreme environments may be either their optimum niche, or be "limiting" to their growth. A sudden change in environment parameters generally induces two kinds of response in microalgae: changes in their metabolism and biochemical composition, and/or changes in their morphological structure. In addition, some taxa may change the stage in their life cycle (a common seasonal variation for many phytoplankton species). For instance, the alga *Haematococcus* forms green vegetative cells with two flagella that grow autotrophically in the light and heterotrophically in the dark. Environmental stressors, including high light, increased salinity, or shortage of nutrients such as nitrogen, induce encystment. The cells change their morphology and life stage. They lose their flagella and become spherical. Their protoplast is enveloped within a closely adherent palmellar membrane; cells increase their volume and start to produce the secondary carotenoid astaxanthin. This is a naturally occurring carotenoid, which provides a wide range of antioxidant benefits protecting cell membranes and other sensitive structures against free radical attack.

Microalgae can produce more than 100 different carotenoids, with comparable structural diversity. Primary carotenoids are generally synthesized under optimal growth conditions whilst the production of secondary (keto) carotenoids, located outside the chloroplasts, is often enhanced under stress conditions. The composition and content of ketocarotenoids vary depending on the alga.

Haematococcus and *Dunaliella* are the two main organisms employed in the commercial manufacture of algal carotenoids, producing astaxanthin and β-carotene, respectively. Like *Haematococcus*, *Dunaliella* produces carotenoids when subjected to stress conditions. Under elevated salt concentrations, cells lose their flagella, become surrounded by mucus, and form resistant cysts. *Dunaliella* is the most halotolerant eukaryotic organism, and is capable of living under salt concentrations ranging from 0.1 to 4 M NaCl. To cope with this wide range of osmotic potentials it employs a unique osmoregulatory mechanism changing its cellular glycerol concentration. It naturally grows in hypersaline lakes or lagoons with low nitrogen concentration exposed to high solar irradiation. In these stressful conditions, *Dunaliella* may produce more than 12% of its dry weight as β-carotene. β-Carotene is a pro-vitamin A carotenoid and a natural antioxidant, which has been used as food and animal feed additive and cosmetic ingredient.

In addition, microalgae are also a source of a wide range of fats, oils, hydrocarbons, and sterols. Many of these metabolites have the potential to be used either for biodiesel production or pharmaceutical applications. The lipid synthesis pathways in algae are similar to those found in higher plants. However, there are some differences. Thus, exposure to stress conditions causes variations in the fatty-acid composition of the oils in algae, and lipid synthesis by algae continues, in spite of the reduction in photosynthetic activity observed under stress conditions. Nitrogen limitation stress has the greatest influence on lipid storage of algae. Limitation of other key nutrients, for instance silica starvation in diatoms, may also result in increased lipid content. In contrast, some microalgae such as *Dunaliella* and *Tetraselmis* respond to stress conditions by decreasing their lipid content and producing carbohydrates. Thus, as for commercial carotenoid production, knowledge on the fundamental responses of individual taxa to extreme stresses is the key to the success of any future commercial production processes.

Many cyanobacteria have the ability to fix atmospheric nitrogen. Nitrogen fixation of cyanobacteria is catalyzed by the enzyme nitrogenase, which is sensitive to oxygen and is irreversibly inactivated in the presence of free oxygen. Some taxa have evolved heterocysts (special thick-walled cells that protect nitrogenase against damage from oxygen); however, there appears to be no universal system to protect the enzyme complex from both atmospheric and intracellular sources of oxygen in non-heterocystous cyanobacteria. During cyanobacterial evolution, it seems reasonable to assume that nitrogen fixation preceded oxygenic photosynthesis. After the evolution of this event, in the Precambrian period, the atmospheric oxygen level started to rise. It is clear that environmental perturbations and their associated stress induction have acted as a major stimulus to the evolution of stress.

This book highlights a number of examples of microalgae surviving, or even thriving, in extreme niches, and the mechanisms they have evolved that allow them to cope with the stresses to which they are subjected.

To paraphrase William Shakespeare:
To survive, or not to survive
To evolve, or not to evolve
To be, or not to be: These are the questions . . .

I congratulate the editor, Prof. Joseph Seckbach, and the authors of "*Algae and Cyanobacteria in Extreme Environments*." I'm sure this book will be a guide source in this exciting field.

Ege University Bioengineering Department **Meltem Conk Dalay**
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December 2006

Biodata of **Meltem Conk Dalay,** author of the chapter "***Introduction to the Algal World***."

Dr. Meltem Conk Dalay is an Associate Professor of Limnologic Sciences and Algal Biotechnology at Ege University, Engineering Faculty, Bioengineering Department, Izmir, Turkey. She obtained Ph.D. from the Faculty of Aquatic products at Ege University (1997). Dr. Conk Dalay's research over the past 15 years has emphasized the isolation, cultivation, and valuable chemical ingredients of algae, especially the effects of culture conditions on growth and biochemical composition of algal biomass. In addition, she has been working on photobioreactors and commercially important microalgae production facilities.

She coordinated the first commercial microalgae (*Spirulina*) production in Turkey with a private sector and her University cooperation project (2000) and she established the first microalgae culture collection (Ege-MACC) in Turkey. Dr. Conk Dalay has been coordinating many national and international scientific and industrial projects related to her scientific interests. Among her publications are over 30 scientific articles and the book entitled ***Aquatic Plants***, published by Ege University press (2001). She has also organized several educational meetings and symposia and has been awarded two prizes by the Ebiltem (Ege University Science and Technology Centre).

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ACKNOWLEDGEMENTS

First of all, let me select one colleague who was extremely active in all the aspects of this book and begin by thanking Professor **Aharon Oren** (Hebrew University of Jerusalem). Aharon did so much for this book from the re-coining of the title and sorting all the chapters into sections to reviewing almost half of the manuscripts of this book. He has actually been my "right hand" and an active advisor for this book as well for most of the other volumes of the ***Cellular Origin, Life in Extreme Habitats and Astrobiology*** series. He was always ready to review manuscripts for the series – which he did most efficiently – and to share authorship of chapters with the editor. His chapters have appeared in almost every volume of this series. He has contributed two books to the series; as an author he composed volume 5 [*Halophilic Microorganisms and Their Environments* (2002)] and co-edited volume 9 [*Adaptation to Life at High Salt Concentrations in Archaea, Bacteria and Eukarya* (2005)]. He performed all his tasks meticulously and promptly. This book has reached its high state of content and scientific quality due to him and the effort he invested in it. Thank you Aharon for all you did for this Alex project.

Secondly, I wish to thank my wife **Fern Seckbach** for her patience and understanding during the compilation of this volume. She assisted me in various channels during my assembling of this book. Fern was my general advisor, my English stylist, and the one who understood the importance of this project.

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