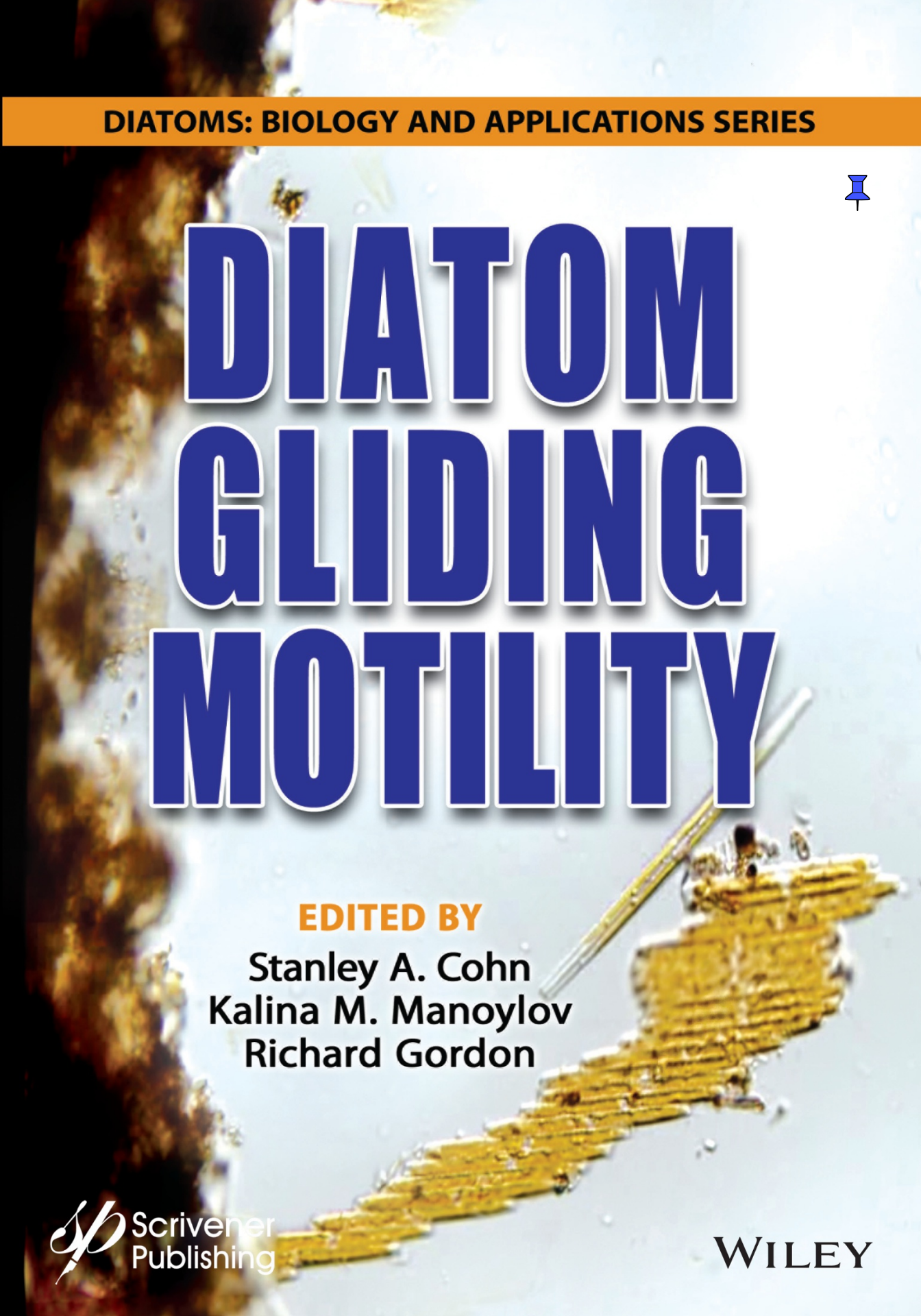
DIATOMS: BIOLOGY AND APPLICATIONS SERIES
DIATOM GLIDING MOTILITY
EDITED BY
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Diatom Gliding Motility

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Diatoms: Biology and Applications

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Scope: The diatoms are a single-cell algal group, with each cell surrounded by a silica shell. The shells have beautiful attractive shapes with multiscalar structure at 8 orders of magnitude, and have several uses. 20% of the oxygen we breathe is produced by diatom photosynthesis, and they feed most of the aquatic food chain in freshwaters and the oceans. Diatoms serve as sources of biofuel and electrical solar energy production and are impacting on nanotechnology and photonics. They are important ecological and paleoclimate indicators. Some of them are extremophiles, living at high temperatures or in ice, at extremes of pH, at high or low light levels, and surviving desiccation. There are about 100,000 species and as many papers written about them since their discovery over three hundred years ago. The literature on diatoms is currently doubling every ten years, with 50,000 papers during the last decade (2006-2016). In this context, it is timely to review the progress to date, highlight cutting-edge discoveries, and discuss exciting future perspectives. To fulfill this objective, this new Diatom Series is being launched under the leadership of two experts in diatoms and related disciplines. The aim is to provide a comprehensive and reliable source of information on diatom biology and applications and enhance interdisciplinary collaborations required to advance knowledge and applications of diatoms.

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Dedication to Jeremy D. Pickett-Heaps
In Memoriam 1940–2021

The editors of this volume would like to dedicate this collection to Dr. Jeremy D. Pickett-Heaps, with thanks and gratitude for his leadership and stalwart advocacy in advancing studies of diatoms and diatom motility. Sadly, Jeremy passed away just prior to this volume's publication. One of the editors (SAC) had the pleasure and honor of studying and working with Jeremy and is proud to write this dedication. In addition, another editor (RG) visited Jeremy in Colorado where he was greatly influenced on his work in diatom morphogenesis.

Jeremy was truly an international scholar. Born in Mumbai, India, he received his B.A. and Ph.D. in Cambridge, England, and did his postdoctoral work back in his home of Australia. He then worked for almost 20 years as a professor at the University of Colorado Boulder, after which he went back to Melbourne to the University of Melbourne until his retirement. His work on algae was prodigious, as witnessed by the large number of excellent publications listed at the end of this dedication.

Jeremy was always a strong advocate for live observation of cell behaviors. While Jeremy always understood the value and use of theoretical and *in vitro* biochemical studies (in fact, early in my career I published a theoretical model of cell division along with him [1.180]), Jeremy would always tell everyone in the lab to let the *in vivo* living cells tell you what is really going on. While the *in vitro* studies and electron microscope structural studies could provide direction and constraints, Jeremy always relied on live cell observations to drive his understandings.

His love of microscopy led Jeremy to not only record cells for research purposes, but to start a new company, Cytographics, in which he used 16 mm and video recordings to make educational materials displaying cellular processes (e.g., [1.128] [1.129] [1.161]). In Jeremy's own words from his Cytographics site, "As this [electron microscope] work progressed, I became increasingly frustrated at trying to recreate dynamic cellular events solely from static images. A turning point in my career came when I first saw the extraordinary sight of a live diatom undergoing mitosis at high magnification. After borrowing a 16 mm time-lapse camera, I was soon filming algae doing all the things I had studied with the electron microscope. Since then, I have built up a laboratory devoted to the high-resolution video imaging and recording of all sorts of cells and microscopic organisms going about their complex and extraordinary lives. It's the best peep show around!"

Jeremy was a true trailblazer in the study of algae. Discovering the passage of cell wall material from the Golgi [1.51], the role of microtubules and microtubule organizing centers

(e.g., [1.90] [1.94] [1.119] [1.123]), and evolutionary relationships among algae (e.g., [1.93] [1.106] [1.111] [1.113]) Jeremy always tried to look at algae in new ways. His work, and that of his students and colleagues, was instrumental in using the highly organized mitotic spindle in diatoms to understand microtubule organization during cell division [1.61] [1.79] [1.218] [1.224] [1.228]. But among the algae, diatoms have always been special to Jeremy.

Jeremy was fascinated by the early microscopy work by the botanist Robert Lauterborn and his exquisitely detailed drawings of algal phenomena. In 1984 he published a work with some co-authors on a translation of Lauterborn's 1896 treatise, along with some modern microscopic observations of the same cells [1.167]. The publication displayed how modern optical and electron microscopy simply confirmed the excellent work of Lauterborn in understanding the dynamics of diatom mitosis. I had the great privilege of seeing a copy of the 1896 document when Jeremy had it briefly on loan to take copies of some of the original images for his publication, and the drawings truly were beautiful and amazingly detailed.

I was lucky enough to be working in Jeremy's lab in Boulder during an exciting time in diatom motility. Dr. Lesley Edgar was working in the lab, investigating the underlying ultrastructure of motile diatoms, leading her to develop a model of diatom gliding [1.20] [1.21], and where I had the honor of publishing with her on some aspects of diatom morphogenesis [1.11]. She searched through Boulder for some ponds containing the best diatoms for investigation, one of which I still use as my major source of cells for research. As a graduate student I began working with intracellular motility and the role of microtubules and microtubule organizing centers in forming the diatom valves used in motility. I, too, became enthralled with watching diatoms as they glided, and divided, and formed new cell walls. Using both video and film, under Jeremy's tutelage the lab analyzed the motile behavior and intracellular movements of the cells, and using scanning electron microscopy I studied the forming raphe and valve structures of diatoms during development and reproduction. Jeremy always wanted to know what cell phenomena members of the lab were watching and seeing, helping us to contemplate both their mystery and their beauty as well as their biological importance. After a short time in Jeremy's lab I was hooked on diatoms and their movement and have never looked back.

During my time in his lab, Jeremy always filled the lab with joy and enthusiasm for science and exploration. Any time someone would come up with an idea or suggested an experiment, Jeremy would always encourage us to try it out and see what happens. He was a firm believer in the idea that science is about using new techniques and new approaches to poke at the cells and see what they were trying to tell you. And at every point in the work we were doing, Jeremy would strive for excellence in the microscopy coming out of the lab. Whether it was light microscopy using the newest optical techniques, electron microscopy using the best approaches for serial sectioning, or scanning electron microscopy finding the best angles for imaging, he wanted the cleanest, clearest images possible. He had an innate sense of the images that would not only be the best to show the processes or structures we were trying to explain, but would also be the most beautiful. He was worried far less about dogma or current trends, and far more about trying to find the truth.

I also had the pleasure of working in his lab as a visiting colleague after he had gone back to the University of Melbourne. His enthusiasm was undiminished, and his love for microscopy and for developing educational materials had, if anything, only expanded. His encouragement to test and try new ideas led to investigations into some of the light-based

responses of diatoms that I continue to this day. As always, he encouraged everyone in the lab to use the latest techniques to tease the truth out of the cells.

His care for everyone who came into the lab, whether student, technician, visiting colleague, or postdoc, was always an inspiration. He constantly showed a love of life, a love of science, and a love for his lab personnel, all in equal measure. He helped us understand that science is a way to help organize and understand the world and the fabric of nature, and that the diatoms were a beautiful and glimmering thread in that fabric.

This dedication would also be remiss if it did not mention the incredible diatom researchers from the Pickett-Heaps Lab who were remarkable colleagues and mentors, but have also unfortunately passed away far too soon. I owe my deepest thanks to the late Drs. Lesley Edgar, Cindy Troxell, and Timothy Spurck. Their friendship, knowledge, humor, and dedication helped foster and guide my research into diatoms. It is to their love of science and diatoms, and to Jeremy's, that this book is dedicated.

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Contents

Preface

Anyone who has peered into a microscope and observed the movement of diatoms knows they have witnessed an intriguing example of cellular biology. Unlike most other of their sister algae, this movement involves neither swimming through solution (like *Euglena* or *Chlamydomonas*) or amoeboid crawling of membrane and cytoplasm (like *Synchroma*). Surrounded by a hardened silicified cell wall, motile diatoms are still able to glide gracefully along surfaces while the cell protoplast remains contained within these ornate cell walls. As such, the mysteries involving this curious form of movement have been of interest for well over a hundred years, and models of many sorts have been proposed to explain it (see [1.20]).

Our hope is that this volume will help to not only convey our excitement about research in diatoms, but also demonstrate a variety of techniques and approaches currently used to understand some of the aspects of diatom movement. We have included chapters centering on a number of areas: detailed observation of movements [1.23] [1.43], cellular aspects of motility [1.5] [1.8], ecology and environmental interactions [1.13] [1.40] [1.44], more passive and epiphitic movements [1.18] [1.42], new and novel methodologies [1.2] [1.51] and potential models of motility [1.7] [1.20] [1.47].

Our goal is not to vigorously promote and defend any one particular model, but rather to present the reader with the variety of experimental approaches that are currently being used to address the problem. In this way readers will be able to assess for themselves the areas of diatom motility that require further exploration, and the predictions of various models that still need to be tested. For example, the exact mechanism of force production for diatom motility is still unresolved. While models of force generation arising from motor proteins interacting with the cytoskeleton and coupled to secreted mucilage strands are favored by some, others currently favor models generating motile force generated by the explosive release and hydration of mucilage regulated by the localization of the secretory site directed by the underlying cytoskeleton.

There are certainly areas of diatom motility that were unfortunately not able to be included in this volume, and we encourage readers to explore these areas if they wish to be more fully aware of important work in the field. In particular, the editors want to note a number of areas of diatom motility that are not fully addressed in the current volume or are open areas and questions needing more research:

Chemotaxis: Understanding the chemical triggers that can stimulate and help regulate diatom movement, especially during cell pairing during reproduction, is crucial to a full understanding of the process. Important work on diatom chemoattractants and pheromones has been done in recent years (e.g., diatom pheromones [1.19] [1.39]), although

the mechanisms by which these chemical stimulants interact with and help to regulate the motility generating process are still poorly understood.

Tube-dwelling diatoms: A number of species have the ability to specialize their extracellular secretions to provide their own surfaces for movement [1.27] [1.48], generating types of stalks and tubes through which the diatoms can move, but providing three-dimensional structures important for attachment and ecology of other organisms [1.17] [1.28].

Centric diatoms: While centric diatoms have little or no direct substratum motility as seen with many of the pennate diatoms, they can modify their position in the water column [1.36] and there has been some great recent work demonstrating there is direct regulation of diatom buoyancy [1.16] [1.34]. We encourage readers to explore this topic as well if they wish to be further engaged in current approaches regarding functional regulation of centric movement.

Composition of diatom mucilage: Understanding the chemical and physical nature of diatom mucilages and secretions is important to understanding the way that diatoms can use mucilage for a variety of functions. It is likely that different materials are secreted for purposes such as protection of cells during reproduction, and holding the two halves of their frustule together, stalk production, as well as making connections that can move their position relative to the frustule. A number of prior investigations have begun to look into this (e.g., [1.26] [1.27]) and it seems like a great opportunity for continued future work. It has practical impact in the study of biofouling [1.50] and underwater adhesives.

Photoreception: A number of labs have begun to investigate the types of molecules responsible for photoreception in algae. While numerous types of promising candidates have been described (e.g. [1.12] [1.29] [1.31] [1.35] [1.37]), there have been no definitive studies pointing to specific molecules driving the diurnal, light aggregation, or light avoidance behaviors. Better knowledge of the specific light and chemical receptors in diatoms, and how they alter the processes of force generation and directional bias in cells will be needed too. Light piping in the colonial pennate diatom *Bacillaria* has been postulated [1.21], but not yet tested.

Effect of morphogenetic alterations on motility: Numerous diatom species have alternative morphologies based on the environmental conditions (e.g., [1.9] [1.30]). In addition, while numerous pennate diatoms are basically symmetric about the transapical plane dividing the two raphe branches (e.g., *Navicula* spp.), there are also numerous other species (e.g., *Gomphonema* spp.) in which the raphe runs down the apical axis, but the morphology at the two ends is decidedly different. There are also species where the raphe is displaced along valvar wings and the break between branches is at one end (e.g., *Surirella* spp.). The characterization of such species, correlating the valve morphology and raphe morphology with motility characteristics, seems like a productive line of research to better determine the relationship between wall structure and movement, and whether the motility associated with the ends of raphe branches can be regulated independently.

Cytoskeletal organization: The actin cables comprised of large bundles of actin filaments underlying the raphe in motile raphid diatoms appear essential to active,