

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.

Bibliography of Jeremy D. Pickett-Heaps

- [1.1] Ackland, J.C., West, J.A., Pickett-Heaps, J., Actin and myosin regulate pseudopodia of *Porphyra pulchella* (Rhodophyta) archeospores. *J. Phycol.*, 43, 1, 129–138, 2007.
- [1.2] Beech, P.L., Wetherbee, R., Pickett-Heaps, J.D., Transformation of the flagella and associated flagellar components during cell division in the coccolithophorid *Pleurochrysis carterae*. *Protoplasma*, 145, 1, 37–46, 1988.
- [1.3] Beech, P.L., Wetherbee, R., Pickett-Heaps, J.D., Secretion and deployment of bristles in *Mallomonas splendens* (Synurophyceae). *J. Phycol.*, 26, 1, 112–122, 1990.
- [1.4] Boyle, J.A., Pickett-Heaps, J.D., Czarnecki, D.B., Valve morphogenesis in the pennate diatom *Achnanthes coarctata*. *J. Phycol.*, 20, 563–573, 1984.
- [1.5] Callow, M.E., Callow, J.A., Pickett-Heaps, J.D., Wetherbee, R., Primary adhesion of *Enteromorpha* (Chlorophyta, Ulvales) propagules: Quantitative settlement studies and video microscopy. *J. Phycol.*, 33, 6, 938–947, 1997.
- [1.6] Callow, M.E., Callow, J.A., Pickett-Heaps, J.D., Wetherbee, R., Primary adhesion of enteromorpha propagules. *Phycologia*, 36, 4, 15, 1997.
- [1.7] Cohn, S.A., Nash, J., Pickett-Heaps, J.D., The effect of drugs on diatom valve morphogenesis. *Protoplasma*, 149, 130–143, 1989.
- [1.8] Cohn, S.A. and Pickett-Heaps, J.D., The effects of colchicine and dinitrophenol on the *in vivo* rates of anaphase A and B in the diatom *Surirella*. *Eur. J. Cell Biol.*, 46, 3, 523–530, 1988.
- [1.9] Cohn, S.A., Schoeller, A., Spurck, T.P., Pickett-Heaps, J.D., Edgar, L.E., Sexual reproduction in the pennate diatom *Navicula cuspidata*. II. Auxo spore development and initial cell formation. *J. Phycol.*, 20, Suppl, 27, 1984.
- [1.10] Cohn, S.A., Spurck, T.P., Pickett-Heaps, J.D., High energy irradiation at the leading tip of moving diatoms causes a rapid change of cell direction. *Diatom Res.*, 14, 2, 193–206, 1999.
- [1.11] Cohn, S.A., Spurck, T.P., Pickett-Heaps, J.D., Edgar, L.A., Perizonium and initial valve formation in the diatom *Navicula cuspidata* (Bacillariophyceae). *J. Phycol.*, 25, 15–26, 1989.
- [1.12] Cohn, S.A., Weitzell, R.E., Spurck, T.P., Pickett-Heaps, J.D., Characterization of motility and adhesion in pennate diatoms. *Mol. Biol. Cell*, 6, Suppl. S, 261a, 1995.
- [1.13] Coss, R.A., Bloodgood, R.A., Brower, D.L., Pickett-Heaps, J.D., MacIntosh, J.R., Studies on the mechanism of action of isopropyl N phenyl carbamate. *Exp. Cell Res.*, 92, 2, 394–398, 1975.

- [1.14] Coss, R.A. and Pickett-Heaps, J.D., Gametogenesis in the green alga *Oedogonium cardiacum*. I. The cell divisions leading to formation of spermatids and oogonia. *Protoplasma*, 78, 1, 21–39, 1973.
- [1.15] Coss, R.A. and Pickett-Heaps, J.D., The effects of isopropyl N phenyl carbamate on the green alga *Oedogonium cardiacum*. I. Cell division. *J. Cell Biol.*, 63, 1, 84–98, 1974.
- [1.16] Crawford, R., Round, F., Pickett-Heaps, J., Johnson, A., Obituary: Lesley Ann Edgar (1955–2006). *Diatom Res.*, 22, 1, 237–240, 2007.
- [1.17] Crawford, S., Chiovitti, T., Pickett-Heaps, J., Wetherbee, R., Micromorphogenesis during diatom wall formation produces siliceous nanostructures with different properties. *J. Phycol.*, 45, 6, 1353–1362, 2009.
- [1.18] Crawford, S.A., Chiovitti, A., Pickett-Heaps, J., Wetherbee, R., Micromorphogenesis during diatom wall formation produces siliceous nanostructures with different properties. *J. Phycol.*, 45, 6, 1353–1362, 2009.
- [1.19] Edgar, L.A. and Pickett-Heaps, J.D., Ultrastructural localisation of polysaccharides in the motile diatom *Navicula cuspidata*. *Protoplasma*, 113, 10–22, 1982.
- [1.20] Edgar, L.A. and Pickett-Heaps, J.D., The mechanism of diatom locomotion. I. An ultrastructural study of the motility apparatus. *Proc. R. Soc. B: Biol. Sci.*, 218, 331–343, 1983.
- [1.21] Edgar, L.A. and Pickett-Heaps, J.D., Diatom locomotion. *Prog. Phycol. Res.*, 3, 47–88, 1984.
- [1.22] Edgar, L.A. and Pickett-Heaps, J.D., Valve morphogenesis in the pennate diatom *Navicula cuspidata*. *J. Phycol.*, 20, 47–61, 1984.
- [1.23] Forer, A. and Pickett-Heaps, J., Fibrin clots keep non adhering living cells in place on glass for perfusion or fixation. *Cell Biol. Int.*, 29, 9, 721–730, 2005.
- [1.24] Forer, A. and Pickett-Heaps, J., Precocious (pre anaphase) cleavage furrows in *Mesostoma* spermatocytes. *Eur. J. Cell Biol.*, 89, 8, 607–618, 2010.
- [1.25] Forer, A. and Pickett-Heaps, J.D., Checkpoint control in crane fly spermatocytes: Unattached chromosomes induced by cytochalasin D or latrunculin treatment do not prevent or delay the start of anaphase. *Protoplasma*, 203, 100–111, 1998.
- [1.26] Forer, A. and Pickett-Heaps, J.D., Cytochalasin D and latrunculin affect chromosome behaviour during meiosis in crane fly spermatocytes. *Chromosome Res.*, 6, 7, 533–549, 1998.
- [1.27] Forer, A., Pickett-Heaps, J.D., Spurck, T., What generates flux of tubulin in kinetochore microtubules? *Protoplasma*, 232, 3–4, 137–141, 2008.
- [1.28] Forer, A., Spurck, T., Pickett-Heaps, J.D., Ultraviolet microbeam irradiations of spindle fibres in crane fly spermatocytes and newt epithelial cells: resolution of previously conflicting observations. *Protoplasma*, 197, 230–240, 1997.
- [1.29] Forer, A., Spurck, T., Pickett-Heaps, J.D., Actin and myosin inhibitors block elongation of kinetochore fibre stubs in metaphase crane fly spermatocytes. *Protoplasma*, 232, 1–2, 79–85, 2007.
- [1.30] Forer, A., Spurck, T., Pickett-Heaps, J.D., Wilson, P.J., Structure of kinetochore fibres in crane fly spermatocytes after irradiation with an ultraviolet microbeam: Neither microtubules nor actin filaments remain in the irradiated region. *Cell Motil. Cytoskeleton*, 56, 3, 173–192, 2003.
- [1.31] Fowke, L.C. and Pickett-Heaps, J.D., Electron microscope study of vegetative cell division in two species of *Marchantia*. *Can. J. Bot.-Revue Can. Botanique*, 56, 5, 467–475, 1978.
- [1.32] Hepler, P.K., Pickett-Heaps, J.D., Gunning, B.E.S., Some retrospectives on early studies of plant microtubules. *Plant J.*, 75, 2, 189–201, 2013.
- [1.33] Hinz, I., Spurck, T.P., Pickett-Heaps, J.D., Metabolic inhibitors and mitosis. III. Effects of dinitrophenol on spindle disassembly in *Pinnularia*. *Protoplasma*, 132, 1–2, 85–89, 1986.
- [1.34] Hoffman, L.R., Vesik, M., Pickett-Heaps, J.D., The cytology and ultrastructure of zoospores of *Hydrurus foetidus* (Chrysophyceae). *Nord. J. Bot.*, 6, 1, 105–122, 1986.

- [1.35] Jarman, M. and Pickett-Heaps, J., Cell division and nuclear movement in the saccoderm desmid *Netrium interruptus*. *Protoplasma*, 157, 1-3, 136–143, 1990.
- [1.36] Leslie, R.J. and Pickett-Heaps, J.D., Ultraviolet microbeam studies of diatom mitosis. *J. Cell Biol.*, 91, 2, A311, 1981.
- [1.37] Leslie, R.J. and Pickett-Heaps, J.D., Ultraviolet microbeam irradiations of mitotic diatoms: Investigation of spindle elongation. *J. Cell Biol.*, 96, 2, 548–561, 1983.
- [1.38] Leslie, R.J. and Pickett-Heaps, J.D., Spindle microtubule dynamics following ultraviolet microbeam irradiations of mitotic diatoms. *Cell*, 36, 3, 717–727, 1984.
- [1.39] Marchant, H.J. and Pickett-Heaps, J.D., Ultrastructure and differentiation of *Hydrodictyon reticulatum*. I. Mitosis in the coenobium. *Aust. J. Biol. Sci.*, 23, 6, 1173–1186, 1970.
- [1.40] Marchant, H.J. and Pickett-Heaps, J.D., Ultrastructure and differentiation of *Hydrodictyon reticulatum*. II. Formation of zooids within the coenobium. *Aust. J. Biol. Sci.*, 24, 3, 471–486, 1971.
- [1.41] Marchant, H.J. and Pickett-Heaps, J.D., Ultrastructure and differentiation of *Hydrodictyon reticulatum*. III. Formation of vegetative daughter net. *Aust. J. Biol. Sci.*, 25, 2, 265–278, 1972.
- [1.42] Marchant, H.J. and Pickett-Heaps, J.D., Ultrastructure and differentiation of *Hydrodictyon reticulatum*. IV. Conjugation of gametes and development of zygospores and azygospores. *Aust. J. Biol. Sci.*, 25, 2, 279–292, 1972.
- [1.43] Marchant, H.J. and Pickett-Heaps, J.D., Ultrastructure and differentiation of *Hydrodictyon reticulatum*. V. Development of polyhedra. *Aust. J. Biol. Sci.*, 25, 6, 1187–1197, 1972.
- [1.44] Marchant, H.J. and Pickett-Heaps, J.D., Ultrastructure and differentiation of *Hydrodictyon reticulatum*. VI. Formation of germ net. *Aust. J. Biol. Sci.*, 25, 6, 1199–1213, 1972.
- [1.45] Marchant, H.J., Pickett-Heaps, J.D., Jacobs, K., An ultrastructural study of zoosporogenesis and the mature zoospore of *Klebsormidium flaccidum*. *Cytobios*, 8, 29, 95–107, 1973.
- [1.46] McDonald, K., Pickett-Heaps, J.D., McIntosh, J.R., Tippit, D.H., On the mechanism of anaphase spindle elongation in *Diatoma vulgare*. *J. Cell Biol.*, 74, 2, 377–388, 1977.
- [1.47] McDonald, K.L. and Pickett-Heaps, J.D., Mitosis and cytokinesis in *Cladophora glomerata*. *J. Phycol.*, 11, 8–9, 1975.
- [1.48] McDonald, K.L. and Pickett-Heaps, J.D., Ultrastructure and differentiation in *Cladophora glomerata*. I. Cell division. *Am. J. Bot.*, 63, 5, 592–601, 1976.
- [1.49] McIntosh, K., Pickett-Heaps, J.D., Gunning, B.E.S., Cytokinesis in *Spirogyra*: Integration of cleavage and cell plate formation. *Int. J. Plant Sci.*, 156, 1, 1–8, 1995.
- [1.50] McIntosh, K.J., Pickett-Heaps, J.D., Gunning, B.E.S., Cytokinesis in *Spirogyra*: Integration of cleavage and cell plate formation. *Phycologia*, 36, 4, Suppl. 5, 71, 1997.
- [1.51] Northcote, D.H. and Pickett-Heaps, J.D., A function of the Golgi apparatus in polysaccharide synthesis and transport in the root cap cells of wheat. *Biochem. J.*, 98, 1, 159–167, 1966.
- [1.52] Ott, D.W. and Pickett-Heaps, J.D., Mitosis in *Sphaeroplea*. *J. Phycol.*, 11, 8, 1975.
- [1.53] Pickett-Heaps, J., Reproduction by zoospores in *Oedogonium*. I. Zoosporogenesis. *Protoplasma*, 72, 2-3, 275–314, 1971.
- [1.54] Pickett-Heaps, J., Cell division in *Cosmarium botrytis*. *J. Phycol.*, 8, 4, 343–360, 1972.
- [1.55] Pickett-Heaps, J., Cell division in *Cyanophora paradoxa*. *New Phytol.*, 71, 4, 561–567, 1972.
- [1.56] Pickett-Heaps, J., Cell division in *Klebsormidium subtilissimum* (formerly *Ulothrix subtilissima*), and its possible phylogenetic significance. *Cytobios*, 6, 23, 167–183, 1972.
- [1.57] Pickett-Heaps, J., Cell division and wall structure in *Microspora*. *New Phytol.*, 72, 2, 347–355, 1973.
- [1.58] Pickett-Heaps, J., The evolution of mitosis and eukaryotic condition. *BioSystems*, 6, 1, 37–48, 1974.
- [1.59] Pickett-Heaps, J., Cell division in eukaryotic algae. *Bioscience*, 26, 7, 445–450, 1976.

- [1.60] Pickett-Heaps, J., Cell division and evolution of branching in *Oedocladium* (Chlorophyceae). *Cytobiologie*, 14, 3, 319–337, 1977.
- [1.61] Pickett-Heaps, J., The diatom spindle: A useful model for studying mitosis. *Proceedings of the International Botanical Congress*, vol. 13, p. 29, 1981.
- [1.62] Pickett-Heaps, J., Mitotic mechanisms: An alternative view. *Trends Biochem. Sci.*, 11, 12, 504–507, 1986.
- [1.63] Pickett-Heaps, J., Morphogenesis of the labiate process in the araphid pennate diatom *Diatoma vulgare*. *J. Phycol.*, 25, 1, 79–85, 1989.
- [1.64] Pickett-Heaps, J., Hidden Worlds: Pond Life. <https://www.youtube.com/watch?v=xXaTyYp-GkTU>, 1990.
- [1.65] Pickett-Heaps, J., Cell division in diatoms, in: *International Review of Cytology-A Survey of Cell Biology*, vol. 128, pp. 63–108, 1991.
- [1.66] Pickett-Heaps, J., The cytoskeleton in diatom valve morphogenesis. *Phycologia*, 40, 4 Supplement, 18, 2001.
- [1.67] Pickett-Heaps, J., Bush Stone-Curlew. https://www.youtube.com/watch?v=SY_fMZDplrc, 2013.
- [1.68] Pickett-Heaps, J., *Dictyostelium* - a cellular slime mold. <https://www.youtube.com/watch?v=5h8WOWEqP6o>, 2013.
- [1.69] Pickett-Heaps, J., Grey Fantail. <https://www.youtube.com/watch?v=Q6nQYbVoIpI>, 2013.
- [1.70] Pickett-Heaps, J., Rainbow Lorikeets. https://www.youtube.com/watch?v=ZBnI_ObpJyY, 2013.
- [1.71] Pickett-Heaps, J., Rufous Fantail. <https://www.youtube.com/watch?v=gG7qsrFQ9vk>, 2013.
- [1.72] Pickett-Heaps, J., Spurwing Plovers at their Nest. <https://www.youtube.com/watch?v=-uU-jXf0M2xE>, 2013.
- [1.73] Pickett-Heaps, J., Spurwinged Plover hatching chicks. <https://www.youtube.com/watch?v=DSx-PbWQpas>, 2013.
- [1.73] Pickett-Heaps, J., Superb Lyrebird. <https://www.youtube.com/watch?v=Iju8yIEycqU>, 2013.
- [1.75] Pickett-Heaps, J., Euglenoid Flagellates. <https://www.youtube.com/watch?v=WDWbId-0MAMu>, 2014.
- [1.76] Pickett-Heaps, J. and Carpenter, J., Spine formation in diatoms. *J. Phycol.*, 31, 3 SUPPL., 21, 1995.
- [1.77] Pickett-Heaps, J., Carpenter, J., Koutoulis, A., Spine morphogenesis in the diatom *Chaetoceros peruvianum*. *Mol. Biol. Cell*, 4, SUPPL., 403A, 1993.
- [1.78] Pickett-Heaps, J. and Forer, A., Mitosis: Spindle evolution and the matrix model. *Protoplasma*, 235, 1-4, 91–99, 2009.
- [1.79] Pickett-Heaps, J. and Kowalski, S.E., Valve morphogenesis and the microtubule center of the diatom *Hantzschia amphioxys*. *Eur. J. Cell Biol.*, 25, 1, 150–170, 1981.
- [1.80] Pickett-Heaps, J., McNiven, M., Porter, K., Translocation of pigment in erythrophares: Cine analysis of responses to various drugs. *J. Cell Biol.*, 99, 4, A122, 1984.
- [1.81] Pickett-Heaps, J., Spurck, T., Tippit, D., Chromosome motion and the spindle matrix. *J. Cell Biol.*, 99, 1 Pt 2, 137s–143s, 1984.
- [1.82] Pickett-Heaps, J. and Tippit, D., Time lapse cine analysis of mitosis in two diatoms. *J. Cell Biol.*, 79, 2, A286, 1978.
- [1.83] Pickett-Heaps, J.D., Effects of colchicine on ultrastructure of dividing plant cells xylem wall differentiation and distribution of cytoplasmic microtubules. *Dev. Biol.*, 15, 3, 206–236, 1967.
- [1.84] Pickett-Heaps, J.D., Further observations on the Golgi apparatus and its functions in cells of the wheat seedling. *J. Ultrastruct. Res.*, 18, 3, 287–303, 1967.

- [1.85] Pickett-Heaps, J.D., Preliminary attempts at ultrastructural polysaccharide localization in root tip cells. *J. Histochem. Cytochem.*, 15, 8, 442–455, 1967.
- [1.86] Pickett-Heaps, J.D., Ultrastructure and differentiation in *Chara* sp. I, 1967.
- [1.87] Pickett-Heaps, J.D., Ultrastructure and differentiation in *Chara* sp. II, 1967.
- [1.88] Pickett-Heaps, J.D., The use of adioautography for investigating wall secretion in plant cells. *Protoplasma*, 64, 1, 49–66, 1967.
- [1.89] Pickett-Heaps, J.D., Further ultrastructural observations on polysaccharide localization in plant cells. *J. Cell Sci.*, 3, 1, 55–64, 1968.
- [1.90] Pickett-Heaps, J.D., Microtubule like structures in growing plastids or chloroplasts of two algae. *Planta*, 81, 2, 193–200, 1968.
- [1.91] Pickett-Heaps, J.D., Ultrastructure and differentiation in *Chara (fibrosa)*. IV. Spermatogenesis. *Aust. J. Biol. Sci.*, 21, 4, 655–690, 1968.
- [1.92] Pickett-Heaps, J.D., Ultrastructure and differentiation in *Chara* sp. III, 1968.
- [1.93] Pickett-Heaps, J.D., The evolution of the mitotic apparatus: An attempt at comparative ultrastructural cytology in dividing plant cells. *Cytobios*, 1, 3, 257–280, 1969.
- [1.94] Pickett-Heaps, J.D., Preprophase microtubule bands in some abnormal mitotic cells of wheat. *J. Cell Sci.*, 4, 2, 397–420, 1969.
- [1.95] Pickett-Heaps, J.D., Preprophase microtubules and stomatal differentiation in *Commelina cyanea*. *Aust. J. Biol. Sci.*, 22, 2, 375–392, 1969.
- [1.96] Pickett-Heaps, J.D., Preprophase microtubules and stomatal differentiation; some effects of centrifugation on symmetrical and asymmetrical cell division. *J. Ultrastruct. Res.*, 27, 1, 24–44, 1969.
- [1.97] Pickett-Heaps, J.D., Mitosis and autospore formation in green alga *Kirchneriella lunaris*. *Protoplasma*, 70, 3-4, 325–347, 1970.
- [1.98] Pickett-Heaps, J.D., Some ultrastructural features of *Volvox*, with particular reference to phenomenon of inversion. *Planta*, 90, 2, 174–190, 1970.
- [1.99] Pickett-Heaps, J.D., Autonomy of centrioles: fact or fallacy? *Cytobios*, 3, 12, 205–214, 1971.
- [1.100] Pickett-Heaps, J.D., Bristly cristae in algal mitochondria. *Planta*, 100, 4, 357–359, 1971.
- [1.101] Pickett-Heaps, J.D., Cell division in *Tetraedron*. *Ann. Bot.*, 36, 693–701, 1972.
- [1.102] Pickett-Heaps, J.D., Possible virus infection in green alga *Oedogonium*. *J. Phycol.*, 8, 1, 44–47, 1972.
- [1.103] Pickett-Heaps, J.D., Reproduction by zoospores in *Oedogonium*. II. Emergence of zoospore and motile phase. *Protoplasma*, 74, 1-2, 149–167, 1972.
- [1.104] Pickett-Heaps, J.D., Reproduction by zoospores in *Oedogonium*. III. Differentiation of germling. *Protoplasma*, 74, 1-2, 169–193, 1972.
- [1.105] Pickett-Heaps, J.D., Reproduction by zoospores in *Oedogonium*. IV. Cell division in germling and evidence concerning possible evolution of wall rings. *Protoplasma*, 74, 1-2, 195–212, 1972.
- [1.106] Pickett-Heaps, J.D., Variation in mitosis and cytokinesis in plant cells: Its significance in phylogeny and evolution of ultrastructural systems. *Cytobios*, 5, 17, 59–77, 1972.
- [1.107] Pickett-Heaps, J.D., Cell division in *Bulbochaete* .1. Divisions utilizing wall ring. *J. Phycol.*, 9, 4, 408–420, 1973.
- [1.108] Pickett-Heaps, J.D., Cell division in *Tetraspora*. *Ann. Bot.*, 37, 153, 1017–1026, 1973.
- [1.109] Pickett-Heaps, J.D., Stereo scanning electron microscopy of desmids. *J. Microsc.*, 99, SEP, 109–116, 1973.
- [1.110] Pickett-Heaps, J.D., Scanning electron microscopy of some cultured desmids. *Trans. Am. Microsc. Soc.*, 93, 1, 1–23, 1974.
- [1.111] Pickett-Heaps, J.D., Aspects of spindle evolution. *Ann. N. Y. Acad. Sci.*, 253, 352–361, 1975.
- [1.112] Pickett-Heaps, J.D., Cell division and evolution in *Bulbochaete* .3. Sexual reproduction and evolution of branched habit. *Cytobiologie*, 12, 1, 28–51, 1975.

- [1.113] Pickett-Heaps, J.D., *Green Algae. Structure, Reproduction and Evolution in Selected Genera*, Oxford University Press, Oxford, UK, 1975.
- [1.114] Pickett-Heaps, J.D., Electron microscopy and the phylogeny of green algae and land plants. *Am. Zool.*, 19, 2, 545, 1979.
- [1.115] Pickett-Heaps, J.D., Cell division in *Surirella*, a tribute to Robert Lauterborn. *J. Cell Biol.*, 95, 2, A307, 1982.
- [1.116] Pickett-Heaps, J.D., New Light on the Green Algae, Carolina Biology Reader 115, Carolina Biological Supply Company, Burlington, North Carolina, 1982.
- [1.117] Pickett-Heaps, J.D., Cell division and morphogenetic movements in the diatom *Cymatopleura*. *J. Cell Biol.*, 97, 5, A248, 1983.
- [1.118] Pickett-Heaps, J.D., Morphogenesis in desmids: Our present state of ignorance, in: *Spatial Organization of Eukaryotic Cells: Proceedings of a Symposium Held in Honor of Keith R. Porter*, Boulder, Colorado, April 30-May 2, 1982, pp. 241–258, 1983.
- [1.119] Pickett-Heaps, J.D., Valve morphogenesis and the microtubule center in three species of the diatom *Nitzschia*. *J. Phycol.*, 19, 3, 269–281, 1983.
- [1.120] Pickett-Heaps, J.D., Diatom mitosis: implications of a model system, in: *Cell Walls and Surfaces, Reproduction, Photosynthesis*, W. Wiessner, R.C. Starr, D. Robinson (Eds.), pp. 28–33, Springer Verlag, Berlin, 1987.
- [1.121] Pickett-Heaps, J.D., Morphogenesis of the labiate process in the centric diatom *Ditylum brightwellii*. *Protoplasma*, 143, 139–149, 1989.
- [1.122] Pickett-Heaps, J.D., Microtubule cytoskeletons in cellular reorganization of the diatom *Cymatopleura*. *J. Phycol.*, 26, 2 SUPPL, 12, 1990.
- [1.123] Pickett-Heaps, J.D., Post mitotic cellular reorganization in the diatom *Cymatopleura solea*: The role of microtubules and the microtubule center. *Cell Motil. Cytoskeleton*, 18, 4, 279–292, 1991.
- [1.124] Pickett-Heaps, J.D., The kinetochore fiber in *Oedogonium*: An extended component visible when microtubules are removed. *Mol. Biol. Cell*, 3, A345, 1992.
- [1.125] Pickett-Heaps, J.D., Cell division and morphogenesis of the centric diatom *Chaetoceros decipiens* (Bacillariophyceae) I. Living cells. *J. Phycol.*, 34, 6, 989–994, 1998.
- [1.126] Pickett-Heaps, J.D., Cell division and morphogenesis of the centric diatom *Chaetoceros decipiens* (Bacillariophyceae) II. Electron microscopy and a new paradigm for tip growth. *J. Phycol.*, 34, 6, 995–1004, 1998.
- [1.127] Pickett-Heaps, J.D., Rapid, highly efficient method for collecting, fixing, and embedding planktonic and other small cells for electron microscopy. *J. Phycol.*, 34, 6, 1088–1089, 1998.
- [1.128] Pickett-Heaps, J.D., *Remarkable Plants: The Oedogoniales [DVD]*, Cytographics, <http://cytographics.com>, 2004.
- [1.129] Pickett-Heaps, J.D., *The Kingdom Protista: The Dazzling World of Living Cells [DVD]*, Cytographics, <http://cytographics.com>, 2006.
- [1.130] Pickett-Heaps, J.D., Foreword: The enigma of morphogenesis - a personal view, in: *Handbook of Biomineralization*, vol. 1, E. Bäuerlein (Ed.), pp. vii–ix, Wiley-VCH, 2009.
- [1.131] Pickett-Heaps, J.D., *Volvox carterii*, 2014, <https://www.youtube.com/watch?v=n7RggKhWD8g>.
- [1.132] Pickett-Heaps, J.D., 2020. Jeremy D. Pickett Heaps. https://www.researchgate.net/profile/Jeremy_Pickett-Heaps.
- [1.133] Pickett-Heaps, J.D., 2020. Prof Jeremy Pickett-Heaps Honorary. <https://findanexpert.unimelb.edu.au/profile/13098-jeremy-pickett-heaps>.
- [1.134] Pickett-Heaps, J.D. and Bajer, A.S., Mitosis: An argument for multiple mechanisms achieving chromosomal movement. *Cytobios*, 19, 75-76, 171–180, 1977.

- [1.135] Pickett-Heaps, J.D. and Carpenter, J., An extended corona attached to metaphase kinetochores of the green alga *Oedogonium*. *Eur. J. Cell Biol.*, 60, 2, 300–307, 1993.
- [1.136] Pickett-Heaps, J.D., Carpenter, J., Koutoulis, A., Valve and seta (spine) morphogenesis in the centric diatom *Chaetoceros peruvianus* Brightwell. *Protoplasma*, 181, 1-4, 269–282, 1994.
- [1.137] Pickett-Heaps, J.D., Cohn, S., Schmid, A.M., Tippit, D.H., Valve morphogenesis in *Surirella* (Bacillariophyceae). *J. Phycol.*, 24, 35–49, 1988.
- [1.138] Pickett-Heaps, J.D. and Forer, A., Pac Man does not resolve the enduring problem of anaphase chromosome movement. *Protoplasma*, 215, 1-4, 16–20, 2001.
- [1.139] Pickett-Heaps, J.D., Forer, A., Spurck, T., Rethinking anaphase: Where “Pac Man” fails and why a role for the spindle matrix is likely. *Protoplasma*, 192, 1-2, 1–10, 1996.
- [1.140] Pickett-Heaps, J.D., Forer, A., Spurck, T., Traction fibre: Toward a “tensegral” model of the spindle. *Cell Motil. Cytoskeleton*, 37, 1, 1–6, 1997.
- [1.141] Pickett-Heaps, J.D. and Fowke, L.C., Cell division in *Oedogonium*. I. Mitosis, cytokinesis, and cell elongation. *Aust. J. Biol. Sci.*, 22, 4, 857–894, 1969.
- [1.142] Pickett-Heaps, J.D. and Fowke, L.C., Cell division in *Oedogonium*. II. Nuclear division in *O. cardiacum*. *Aust. J. Biol. Sci.*, 23, 1, 71–92, 1970.
- [1.143] Pickett-Heaps, J.D. and Fowke, L.C., Mitosis, cytokinesis, and cell elongation in desmid, *Closterium littorale*. *J. Phycol.*, 6, 2, 189–215, 1970.
- [1.144] Pickett-Heaps, J.D. and Fowke, L.C., Conjugation in the desmid *Closterium littorale*. *J. Phycol.*, 7, 1, 37–50, 1971.
- [1.145] Pickett-Heaps, J.D., Gunning, B.E.S., Brown, R.C., Lemmon, B.E., Cleary, A.L., The cytoplasm concept in dividing plant cells: cytoplasmic domains and the evolution of spatially organized cell division. *Am. J. Bot.*, 86, 2, 153–172, 1999.
- [1.146] Pickett-Heaps, J.D., Hill, D.R.A., Blaze, K., Active gliding motility in an araphid marine diatom, *Ardissonea* (formerly *Synedra*) *crystallina*. *J. Phycol.*, 27, 718–725, 1991.
- [1.147] Pickett-Heaps, J.D., Hill, D.R.A., Wetherbee, R., Cellular movement in the centric diatom *Odontella sinensis*. *J. Phycol.*, 22, 334–339, 1986.
- [1.148] Pickett-Heaps, J.D. and Klein, A.G., Tip growth in plant cells may be amoeboid and not generated by turgor pressure. *Proc. R. Soc. B-Biol. Sci.*, 265, 1404, 1453–1459, 1998.
- [1.149] Pickett-Heaps, J.D. and Marchant, H.J., Phylogeny of green algae: New proposal. *Cytobios*, 6, 24, 255–264, 1972.
- [1.150] Pickett-Heaps, J.D. and Martin, A., An early, neglected description of the fibers (microtubules) in the eukaryotic flagellum. *Protoplasma*, 176, 1-2, 14–16, 1993.
- [1.151] Pickett-Heaps, J.D. and McDonald, K.L., Cylindrocapsa: Cell division and phylogenetic affinities. *New Phytol.*, 74, 2, 235–241, 1975.
- [1.152] Pickett-Heaps, J.D., McDonald, K.L., Tippit, D.H., Cell division in pennate diatom *Diatoma vulgare*. *Protoplasma*, 86, 1-3, 205–242, 1975.
- [1.153] Pickett-Heaps, J.D., McDonald, K.L., Tippit, D.H., Cell division in the pennate diatom *Diatoma vulgare*. *Protoplasma*, 86, 1-3, 205–242, 1975.
- [1.154] Pickett-Heaps, J.D., McDonald, K.L., Tippit, D.H., Spindle structure and function in diatoms. *J. Cell Biol.*, 67, 2, A336, 1975.
- [1.155] Pickett-Heaps, J.D. and Northcote, D.H., Cell division in formation of stomatal complex of young leaves of wheat. *J. Cell Sci.*, 1, 1, 121–128, 1966.
- [1.156] Pickett-Heaps, J.D. and Northcote, D.H., Cell division in the formation of the stomatal complex of the young leaves of wheat. *J. Cell Sci.*, 1, 1, 121–128, 1966.
- [1.157] Pickett-Heaps, J.D. and Northcote, D.H., Organization of microtubules and endoplasmic reticulum during mitosis and cytokinesis in wheat meristems. *J. Cell Sci.*, 1, 1, 109–120, 1966.

- [1.158] Pickett-Heaps, J.D. and Northcote, D.H., Relationship of cellular organelles to formation and development of plant cell wall. *J. Exp. Bot.*, 17, 50, 19–?, 1966.
- [1.159] Pickett-Heaps, J.D. and Ott, D.W., Ultrastructural morphology and cell division in *Pedinomonas*. *Cytobios*, 11, 41, 41–58, 1974.
- [1.160] Pickett-Heaps, J.D. and Pickett-Heaps, J., *From Egg to Tadpole: Early Morphogenesis in Xenopus [VHS and DVD]*, Sinauer, 1999.
- [1.161] Pickett-Heaps, J.D. and Pickett-Heaps, J., *Diatoms: Life in Glass Houses [DVD]*, Cytographics, 2003.
- [1.162] Pickett-Heaps, J.D. and Pickett-Heaps, J., *Teacher's Guide, Diatoms: Life in Glass Houses [http://www.cytographics.com/resource/catalog/tapes/pg.dia.htm + video tape]*, Cytographics, Melbourne, 2003.
- [1.163] Pickett-Heaps, J.D. and Pickett-Heaps, J.F., 3' 21" *Bacillaria paradoxa*, a colonial marine diatom; 2X: Living Cells: Structure and Diversity. Instructor's Guide. <http://www.cytographics.com/resource/catalog/tapes/in-lc.htm>, 1996.
- [1.164] Pickett-Heaps, J.D. and Pickett-Heaps, J.F., Colonial diatom *Bacillaria paradoxa* (5X), Microscopic Life Instructor's Guide, Obtaining Living Micro Organisms for Light Microscopy. <http://www.cytographics.com/resource/catalog/tapes/in-ml.htm>, 2002.
- [1.165] Pickett-Heaps, J.D., Schmid, A.M.M., Edgar, L.A., The cell biology of diatom valve formation. *Prog. Phycol. Res.*, 7, 1–168, 1990.
- [1.166] Pickett-Heaps, J.D., Schmid, A.M.M., Tippit, D.H., Cell division in diatoms. *Protoplasma*, 120, 1-2, 132–154, 1984.
- [1.167] Pickett-Heaps, J.D., Schmid, A.M.M., Tippit, D.H., Cell division in diatoms: A translation of part of Robert Lauterborn's treatise of 1896 with some modern confirmatory observations. *Protoplasma*, 120, 1-2, 132–154, 1984.
- [1.168] Pickett-Heaps, J.D. and Spurck, T., Effects of drugs on the diatom spindle. *J. Cell Biol.*, 91, 2, A316, 1981.
- [1.169] Pickett-Heaps, J.D. and Spurck, T.P., Studies on kinetochore function in mitosis. I. The effects of colchicine and cytochalasin on mitosis in the diatom *Hantzschia amphioxys*. *Eur. J. Cell Biol.*, 28, 1, 77–82, 1982.
- [1.170] Pickett-Heaps, J.D. and Spurck, T.P., Studies on kinetochore function in mitosis. II. The effects of metabolic inhibitors on mitosis and cytokinesis in the diatom *Hantzschia amphioxys*. *Eur. J. Cell Biol.*, 28, 1, 83–91, 1982.
- [1.171] Pickett-Heaps, J.D. and Staehelin, L.A., Ultrastructure of *Scenedesmus* (Chlorophyceae). II. Cell division and colony formation. *J. Phycol.*, 11, 2, 186–202, 1975.
- [1.172] Pickett-Heaps, J.D. and Tippit, D.H., Desmid morphogenesis. *Brookhaven Symp. Biol.*, 25, 191–205, 1973.
- [1.173] Pickett-Heaps, J.D. and Tippit, D.H., The diatom spindle in perspective. *Cell*, 14, 3, 455–467, 1978.
- [1.174] Pickett-Heaps, J.D., Tippit, D.H., Andreozzi, J.A., Cell division in pennate diatom *Pinnularia*. I. Early stages in mitosis. *Biol. Cell.*, 33, 1, 71–78, 1978.
- [1.175] Pickett-Heaps, J.D., Tippit, D.H., Andreozzi, J.A., Cell division in the pennate diatom *Pinnularia* I. Early stages in mitosis. *Biol. Cell.*, 33, 1, 71–78, 1978.
- [1.176] Pickett-Heaps, J.D., Tippit, D.H., Andreozzi, J.A., Cell division in the pennate diatom *Pinnularia*. II. Later stages in mitosis. *Biol. Cell.*, 33, 1, 79–84, 1978.
- [1.177] Pickett-Heaps, J.D., Tippit, D.H., Andreozzi, J.A., Cell division in the pennate diatom *Pinnularia*. III. The valve and associated cytoplasmic organelles. *Biol. Cell.*, 35, 2, 195–198, 1979.
- [1.178] Pickett-Heaps, J.D., Tippit, D.H., Andreozzi, J.A., Cell division in the pennate diatom *Pinnularia*. IV. Valve morphogenesis. *Biol. Cell*, 35, 2, 199–203, 1979.

- [1.179] Pickett-Heaps, J.D., Tippit, D.H., Andreozzi, J.A., Cell division in the pennate diatom *Pinnularia*. V. Observations on live cells. *Biol. Cell.*, 35, 3, 295–304, 1979.
- [1.180] Pickett-Heaps, J.D., Tippit, D.H., Cohn, S.A., Spurck, T.P., Microtubule dynamics in the spindle. Theoretical aspects of assembly/disassembly reactions *in vivo*. *J. Theor. Biol.*, 118, 2, 153–169, 1986.
- [1.181] Pickett-Heaps, J.D., Tippit, D.H., Leslie, R., Cell division in the diatom *Hantzschia amphioxys*. *J. Cell Biol.*, 87, 2, A234, 1980.
- [1.182] Pickett-Heaps, J.D., Tippit, D.H., Leslie, R., Light and electron microscopic observations on cell division in two large pennate diatoms, *Hantzschia* and *Nitzschia*. I. Mitosis *in vivo*. *Eur. J. Cell Biol.*, 21, 1, 1–11, 1980.
- [1.183] Pickett-Heaps, J.D., Tippit, D.H., Leslie, R., Light and electron microscopic observations on cell division in two large pennate diatoms. *Hantzschia* and *Nitzschia*. II. Ultrastructure. *Eur. J. Cell Biol.*, 21, 1, 12–27, 1980.
- [1.184] Pickett-Heaps, J.D., Tippit, D.H., Porter, K.R., Rethinking mitosis. *Cell*, 29, 3, 729–744, 1982.
- [1.185] Pickett-Heaps, J.D. and West, J., Time lapse video observations on sexual plasmogamy in the red alga *Bostrychia*. *Eur. J. Phycol.*, 33, 1, 43–56, 1998.
- [1.186] Pickett-Heaps, J.D., West, J.A., Wilson, S.M., McBride, D.L., Time lapse videomicroscopy of cell (spore) movement in red algae. *Eur. J. Phycol.*, 36, 1, 9–22, 2001.
- [1.187] Pickett-Heaps, J.D. and Wetherbee, R., Spindle function in the green alga *Mougeotia*. Absence of anaphase a correlates with postmitotic nuclear migration. *Cell Motil. Cytoskeleton*, 7, 1, 68–77, 1987.
- [1.188] Pickett-Heaps, J.D., Wetherbee, R., Hill, D.R.A., Cell division and morphogenesis of the labiate process in the centric diatom *Ditylum brightswellii*. *Protoplasma*, 143, 139–149, 1988.
- [1.189] Pickett-Heaps, J.D.P.-H.J., *Living Cells: Structure, Diversity, and Evolution* [12" NTSC video-disc], Sinauer Associates, Sunderland, MA, 1994.
- [1.190] Pollock, F., Pickett-Heaps, J., Schmid, A.M., Diatom protoplasts are amoeboid during recovery from osmotic shock. *J. Phycol.*, 34, 3 SUPPL., 48–48, 1998.
- [1.191] Pollock, F., Pickett-Heaps, J., Schmid, A.M., Diatom protoplasts are affected differently by cytochalasin D, latrunculin B and oryzalin. *J. Phycol.*, 35, 3 SUPPL., 24–25, 1999.
- [1.192] Pollock, F.M. and Pickett-Heaps, J.D., Spatial determinants in morphogenesis: Recovery from plasmolysis in the diatom *Ditylum*. *Cell Motil. Cytoskeleton*, 60, 2, 71–82, 2005.
- [1.193] Pollock, F.M. and Pickett-Heaps, J.D., Valve formation without mitosis in the diatom *Ditylum* recovering from plasmolysis. *Nova Hedwigia*, Suppl. 130, 119–125, 2006.
- [1.194] Reymond, O.L. and Pickett-Heaps, J.D., A routine flat embedding method for electron microscopy of microorganisms allowing selection and precisely orientated sectioning of single cells by light microscopy. *J. Microsc.*, 130, Pt 1, 79–84, 1983.
- [1.195] Sampson, K. and Pickett-Heaps, J.D., Phalloidin staining of the mitotic spindle in the green alga *Oedogonium*. *Mol. Biol. Cell*, 11, Suppl. 5, 370A, 2000.
- [1.196] Sampson, K. and Pickett-Heaps, J.D., Phalloidin stains the kinetochore region in the mitotic spindle of the green algae *Oedogonium* spp. *Protoplasma*, 217, 4, 166–176, 2001.
- [1.197] Sampson, K. and Pickett-Heaps, J.D., Phalloidin stains the kinetochore region in the mitotic spindle of the green algae *Oedogonium* spp. (vol 217, pg 166, 2001). *Protoplasma*, 218, 3-4, 237, 2001.
- [1.198] Sampson, K., Pickett-Heaps, J.D., Forer, A., Cytochalasin D blocks chromosomal attachment to the spindle in the green alga *Oedogonium*. *Protoplasma*, 192, 3-4, 130–144, 1996.
- [1.199] Schibler, M.J. and Pickett-Heaps, J.D., Mitosis in *Oedogonium*: spindle microfilaments and the origin of the kinetochore fiber. *Eur. J. Cell Biol.*, 22, 2, 687–698, 1980.

- [1.200] Schibler, M.J. and Pickett-Heaps, J.D., Kinetochore bundle structure in the green alga, *Oedogonium*. *J. Cell Biol.*, 91, 2, A316, 1981.
- [1.201] Schibler, M.J. and Pickett-Heaps, J.D., The kinetochore fiber structure in the acentric spindles of the green alga *Oedogonium*. *Protoplasma*, 137, 1, 29–44, 1987.
- [1.202] Schoeller, A., Cohn, S.A., Spurck, T.P., Pickett-Heaps, J.D., Edgar, L.E., Sexual reproduction in the pennate diatom *Navicula cuspidata*. I. Gametogenesis and zygote formation. *J. Phycol.*, 20, Suppl, 28, 1984.
- [1.203] Schoeller, A., Pickett-Heaps, J.D., Gilkey, J., The cytoplasm in algal cell structure. *J. Cell Biol.*, 99, 4, A196, 1984.
- [1.204] Snyder, J.A., Armstrong, L., Stonington, O.G., Spurck, T.P., Pickett-Heaps, J.D., UV microbeam irradiations of the mitotic spindle: Spindle forces and structural analysis of lesions. *Eur. J. Cell Biol.*, 55, 1, 122–132, 1991.
- [1.205] Soranno, T. and Pickett-Heaps, J., Directionally controlled spindle disassembly after mitosis in the diatom *Pinnularia*. *Eur. J. Cell Biol.*, 26, 2, 234–243, 1982.
- [1.206] Spurck, T., Forer, A., Pickett-Heaps, J., Ultraviolet microbeam irradiations of epithelial and spermatocyte spindles suggest that forces act on the kinetochore fibre and are not generated by its disassembly. *Cell Motil. Cytoskeleton*, 36, 2, 136–148, 1997.
- [1.207] Spurck, T., Pickett-Heaps, J., Klymkowsky, M., Metabolic inhibitors and mitosis .1. Effects of DNP DOG and nocodazole on live cells. *J. Cell Biol.*, 99, 4, A240, 1984.
- [1.208] Spurck, T., Pickett-Heaps, J., Klymkowsky, M., Metabolic inhibitors and mitosis .2. Effect of DNP DOG and nocodazole on microtubules. *J. Cell Biol.*, 99, 4, A443, 1984.
- [1.209] Spurck, T.P. and Pickett-Heaps, J.D., On the mechanism of anaphase A: evidence that ATP is needed for microtubule disassembly and not generation of polewards force. *J. Cell Biol.*, 105, 4, 1691–1705, 1987.
- [1.210] Spurck, T.P. and Pickett-Heaps, J.D., The effects of diazepam on mitosis and the microtubule cytoskeleton. I. Observations on the diatoms *Hantzschia amphioxys* and *Surirella robusta*. *J. Cell Sci.*, 107, 2643–2651, 1994.
- [1.211] Spurck, T.P., Pickett-Heaps, J.D., Klymkowsky, M.W., Metabolic inhibitors and mitosis. I. Effects of dinitrophenol deoxyglucose and nocodazole on the live spindle. *Protoplasma*, 131, 1, 47–59, 1986.
- [1.212] Spurck, T.P., Pickett-Heaps, J.D., Klymkowsky, M.W., Metabolic inhibitors and mitosis. II. Effects of dinitrophenol deoxyglucose and nocodazole on the microtubule cytoskeleton. *Protoplasma*, 131, 1, 60–74, 1986.
- [1.213] Spurck, T.P., Stonington, O.G., Snyder, J.A., Pickett-Heaps, J.D., Bajer, A., Molebajer, J., UV microbeam irradiations of the mitotic spindle. II. Spindle fiber dynamics and force production. *J. Cell Biol.*, 111, 4, 1505–1518, 1990.
- [1.214] Staehelin, L.A. and Pickett-Heaps, J.D., Ultrastructure of *Scenedesmus* (Chlorophyceae). I. Species with reticulate or warty type of ornamental layer. *J. Phycol.*, 11, 2, 163–185, 1975.
- [1.215] Stonington, O.G., Spurck, T.P., Snyder, J.A., Pickett-Heaps, J.D., UV microbeam irradiations of the mitotic spindle. I. The UV microbeam apparatus. *Protoplasma*, 153, 1-2, 62–70, 1989.
- [1.216] Storey, E., Spurck, T., Pickett-Heaps, J., Beyreuther, K., Masters, C.L., The amyloid precursor protein of Alzheimer's disease is found on the surface of static but not actively motile portions of neurites. *Brain Res.*, 735, 1, 59–66, 1996.
- [1.217] Storey, E., Spurck, T., Pickett-Heaps, J., Beyreuther, K., Masters, C.L., Surface app is not found on rapidly changing portions of neurites, including growth cones. *Neurobiol. Aging*, 15, S63, 1994.

- [1.218] Tippit, D.H., Fields, C.T., O'Donnell, K.L., Pickett-Heaps, J.D., McLaughlin, D.J., The organization of microtubules during anaphase and telophase spindle elongation in the rust fungus *Puccinia*. *Eur. J. Cell Biol.*, 34, 1, 34–44, 1984.
- [1.219] Tippit, D.H., McDonald, K.L., Pickett-Heaps, J.D., Cell division in the centric diatom *Melosira varians*. *Cytobiologie*, 12, 52–73, 1975.
- [1.220] Tippit, D.H. and Pickett-Heaps, J.D., Apparent amitosis in the binucleate dinoflagellate *^*. *J. Cell Sci.*, 21, 2, 273–289, 1976.
- [1.221] Tippit, D.H. and Pickett-Heaps, J.D., Mitosis in pennate diatom *Surirella ovalis*. *J. Cell Biol.*, 73, 3, 705–727, 1977.
- [1.222] Tippit, D.H. and Pickett-Heaps, J.D., Reconstruction of spindle microtubules during anaphase elongation in the rust fungus *Puccinia*. *J. Cell Biol.*, 97, 5, A187, 1983.
- [1.223] Tippit, D.H., Pickett-Heaps, J.D., Leslie, R., Cell division in two large pennate diatoms *Hantzschia* and *Nitzschia*. III. A new proposal for kinetochore function during prometaphase. *J. Cell Biol.*, 86, 2, 402–416, 1980.
- [1.224] Tippit, D.H., Pillus, L., Pickett-Heaps, J., Organization of spindle microtubules in *Ochromonas danica*. *J. Cell Biol.*, 87, 3, 531–545, 1980.
- [1.225] Tippit, D.H., Pillus, L., Pickett-Heaps, J.D., Interactions of spindle microtubules in *Ochromonas danica*. *Eur. J. Cell Biol.*, 22, 1, 309–309, 1980.
- [1.226] Tippit, D.H., Pillus, L., Pickett-Heaps, J.D., Near neighbor analysis of spindle microtubules in the alga *Ochromonas*. *Eur. J. Cell Biol.*, 30, 1, 9–17, 1983.
- [1.227] Tippit, D.H., Schulz, D., Pickett-Heaps, J.D., Changes in spindle structure during mitosis in *Fragilaria*. *J. Cell Biol.*, 75, 2, A279, 1977.
- [1.228] Tippit, D.H., Schulz, D., Pickett-Heaps, J.D., Analysis of the distribution of spindle microtubules in the diatom *Fragilaria*. *J. Cell Biol.*, 79, 3, 737–763, 1978.
- [1.229] Tippit, D.H., Smith, H., Pickett-Heaps, J.D., Cell form mutants in *Micrasterias*. *Protoplasma*, 113, 3, 234–236, 1982.
- [1.230] Troutt, L.L. and Pickett-Heaps, J.D., Reactivating prometaphase movement in permeabilized animal cells. *Protoplasma*, 170, 1-2, 22–33, 1992.
- [1.231] Troutt, L.L., Spurck, T.P., Pickett-Heaps, J.D., The effects of diazepam on mitosis and the microtubule cytoskeleton. II. Observations on newt epithelial and Ptk1 cells. *Protoplasma*, 189, 1-2, 101–112, 1995.
- [1.232] Troxell, C.L., Scheffey, C., Pickett-Heaps, J.D., Ionic currents during wall morphogenesis in *Micrasterias* and *Closterium*. *Prog. Clin. Biol. Res.*, 210, 105–112, 1986.
- [1.233] van de Meene, A.M.L. and Pickett-Heaps, J.D., Spine morphogenesis in three marine centric diatoms. *Phycologia*, 36, 4, 115, 1997.
- [1.234] van de Meene, A.M.L. and Pickett-Heaps, J.D., Cytoplasmic rotation during valve morphogenesis of the marine centric diatom *Rhizosolenia setigera*. *Phycologia*, 40, 4 Supplement, 40, 2001.
- [1.235] van de Meene, A.M.L. and Pickett-Heaps, J.D., Valve morphogenesis in the centric diatom *Proboscia alata* Sundstrom. *J. Phycol.*, 38, 2, 351–363, 2002.
- [1.236] van de Meene, A.M.L. and Pickett-Heaps, J.D., Valve morphogenesis in the centric diatom *Rhizosolenia setigera* (Bacillariophyceae, Centrales) and its taxonomic implications. *Eur. J. Phycol.*, 39, 1, 93–104, 2004.
- [1.237] Vesk, M., Hoffman, L.R., Pickett-Heaps, J.D., Mitosis and cell division in *Hydrurus foetidus* (Chrysophyceae). *J. Phycol.*, 20, 4, 461–470, 1984.
- [1.238] Weatherill, K., Lambiris, I., Pickett-Heaps, J.D., Deane, J.A., Beech, P.L., Plastid division in *Mallomonas* (Synurophyceae, Heterokonta). *J. Phycol.*, 43, 3, 535–541, 2007.
- [1.239] Weatherill, K.J., Lambiris, I., Pickett-Heaps, J., Beech, P.L., Chloroplast division in the chromophyte alga, *Mallomonas*. *Phycologia*, 36, 4, Suppl. 5, 121, 1997.

- [1.240] West, J.A., Zuccarello, G.C., Scott, J., Pickett-Heaps, J., Kim, G.H., Observations on *Purpureofilum apyrenoidigerum* gen. et sp. nov. from Australia and *Bangiopsis subsimplex* from India (Stylonematales, Bangiophyceae, Rhodophyta). *Phycol. Res.*, 53, 1, 49–66, 2005.
- [1.241] Wetherbee, R., Andersen, R.A., Pickett-Heaps, J.D. (Eds.), *The Protistan Cell Surface ("Protoplasma")*, Springer, 1994.
- [1.242] Wetherbee, R., Andersen, R.A., Pickett-Heaps, J.D., Untitled. *Protoplasma*, 181, 1-4, R3, 1994.
- [1.243] Wetherbee, R., Platt, S.J., Beech, P.L., Pickett-Heaps, J.D., Flagellar transformation in the heterokont *Epipyxis pulchra* (Chrysophyceae): Direct observations using image enhanced light microscopy. *Protoplasma*, 145, 1, 47–54, 1988.
- [1.244] Wilson, S.M., Pickett-Heaps, J.D., West, J.A., Fertilization and the cytoskeleton in the red alga *Bostrychia moritziana* (Rhodomelaceae, Rhodophyta). *Eur. J. Phycol.*, 37, 4, 509–522, 2002.
- [1.245] Wilson, S.M., Pickett-Heaps, J.D., West, J.A., Vesicle transport and the cytoskeleton in the unicellular red alga *Glaucosphaera vacuolata*. *Phycol. Res.*, 54, 1, 15–20, 2006.
- [1.246] Wilson, S.M., West, J.A., Pickett-Heaps, J.D., Time lapse videomicroscopy of fertilization and the actin cytoskeleton in *Murrayella pericladus* (Rhodomelaceae, Rhodophyta). *Phycologia*, 42, 6, 638–645, 2003.

Contents

Preface	xxvii
1 Some Observations of Movements of Pennate Diatoms in Cultures and Their Possible Interpretation	1
<i>Thomas Harbich</i>	
1.1 Introduction	2
1.2 Kinematics and Analysis of Trajectories in Pennate Diatoms with Almost Straight Raphe along the Apical Axis	3
1.3 Curvature of the Trajectory at the Reversal Points	9
1.4 Movement of Diatoms in and on Biofilms	13
1.5 Movement on the Water Surface	16
1.6 Formation of Flat Colonies in <i>Cymbella lanceolata</i>	23
1.7 Conclusion	29
References	29
2 The Kinematics of Explosively Jerky Diatom Motility: A Natural Example of Active Nanofluidics	33
<i>Ahmet C. Sabuncu, Richard Gordon, Edmond Richer, Kalina M. Manoylov and Ali Beskok</i>	
2.1 Introduction	34
2.2 Material and Methods	35
2.2.1 Diatom Preparation	35
2.2.2 Imaging System	35
2.2.3 Sample Preparation	36
2.2.4 Image Processing	36
2.3 Results and Discussion	41
2.3.1 Comparison of Particle Tracking Algorithms	41
2.3.2 Stationary Particles	42
2.3.3 Diatom Centroid Measurements	43
2.3.4 Diatom Orientation Angle Measurements	46
2.3.5 Is Diatom Motion Characterized by a Sequence of Small Explosive Movements?	49
2.3.6 Future Work	50
2.4 Conclusions	51
Appendix	52
References	59

3	Cellular Mechanisms of Raphid Diatom Gliding	65
	<i>Yekaterina D. Bedoshvili and Yelena V. Likhoshway</i>	
3.1	Introduction	65
3.2	Gliding and Secretion of Mucilage	67
3.3	Cell Mechanisms of Mucilage Secretion	68
3.4	Mechanisms of Gliding Regulation	71
3.5	Conclusions	72
	Acknowledgments	72
	References	73
4	Motility of Biofilm-Forming Benthic Diatoms	77
	<i>Karen Grace Bondoc-Naumovitz and Stanley A. Cohn</i>	
4.1	Introduction	77
4.2	General Motility Models and Concepts	86
4.2.1	Adhesion	87
4.2.2	Gliding Motility	89
4.2.3	Motility and Environmental Responsiveness	91
4.3	Light-Directed Vertical Migration	93
4.4	Stimuli-Directed Movement	94
4.4.1	Nutrient Foraging	94
4.4.2	Pheromone-Based Mate-Finding Motility	97
4.4.3	Prioritization Between Co-Occurring Stimuli	99
4.5	Conclusion	99
	References	100
5	Photophobic Responses of Diatoms – Motility and Inter-Species Modulation	111
	<i>Stanley A. Cohn, Lee Warnick and Blake Timmerman</i>	
5.1	Introduction	112
5.2	Types of Observed Photoresponses	112
5.2.1	Light Spot Accumulation	112
5.2.2	High-Intensity Light Responses	114
5.3	Inter-Species Effects of Light Responses	118
5.3.1	Inter-Species Effects on High Irradiance Direction Change Response	119
5.3.2	Inter-Species Effects on Cell Accumulation into Light Spots	123
5.4	Summary	123
	References	131
6	Diatom Biofilms: Ecosystem Engineering and Niche Construction	135
	<i>David M. Paterson and Julie A. Hope</i>	
6.1	Introduction	135
6.1.1	Diatoms: A Brief Portfolio	135
6.1.2	Benthic Diatoms as a Research Challenge	136
6.2	The Microphytobenthos and Epipellic Diatoms	136
6.3	The Ecological Importance of Locomotion	137
6.4	Ecosystem Engineering and Functions	139
6.4.1	Ecosystem Engineering	139
6.4.2	Ecosystem Functioning	140

6.5	Microphytobenthos as Ecosystem Engineers	141
6.5.1	Sediment Stabilization	141
6.5.2	Beyond the Benthos	143
6.5.3	Diatom Architects	144
6.5.4	Working with Others: Combined Effects	144
6.5.5	The Dynamic of EPS	145
6.5.6	Nutrient Turnover and Biogeochemistry	145
6.6	Niche Construction and Epipellic Diatoms	146
6.7	Conclusion	149
	Acknowledgments	150
	References	150
7	Diatom Motility: Mechanisms, Control and Adaptive Value	159
	<i>João Serôdio</i>	
7.1	Introduction	159
7.2	Forms and Mechanisms of Motility in Diatoms	160
7.2.1	Motility in Centric Diatoms	160
7.2.2	Motility in Pennate Raphid Diatoms	161
7.2.3	Motility in Other Substrate-Associated Diatoms	162
7.2.4	Vertical Migration in Diatom-Dominated Microphytobenthos	163
7.3	Controlling Factors of Diatom Motility	164
7.3.1	Motility Responses to Vectorial Stimuli	164
	7.3.1.1 Light Intensity	164
	7.3.1.2 Light Spectrum	165
	7.3.1.3 UV Radiation	166
	7.3.1.4 Gravity	166
	7.3.1.5 Chemical Gradients	167
7.3.2	Motility Responses to Non-Vectorial Stimuli	167
	7.3.2.1 Temperature	167
	7.3.2.2 Salinity	168
	7.3.2.3 pH	168
	7.3.2.4 Calcium	168
	7.3.2.5 Other Factors	169
	7.3.2.6 Inhibitors of Diatom Motility	169
7.3.3	Species-Specific Responses and Interspecies Interactions	169
7.3.4	Endogenous Control of Motility	170
7.3.5	A Model of Diatom Vertical Migration Behavior in Sediments	170
7.4	Adaptive Value and Consequences of Motility	172
7.4.1	Planktonic Centrics	172
7.4.2	Benthic Pennates	173
7.4.3	Ecological Consequences of Vertical Migration	175
	7.4.3.1 Motility-Enhanced Productivity	175
	7.4.3.2 Carbon Cycling and Sediment Biostabilization	176
	Acknowledgments	176
	References	176

8	Motility in the Diatom Genus <i>Eunotia</i> Ehrenb.	185
	<i>Paula C. Furey</i>	
8.1	Introduction	185
8.2	Accounts of Movement in <i>Eunotia</i>	188
8.3	Motility in the Context of Valve Structure	194
8.3.1	Motility and Morphological Characteristics in Girdle View	194
8.3.2	Motility and Morphological Characteristics in Valve View	196
8.3.3	Motility and the Rimoportula	198
8.4	Motility and Ecology of <i>Eunotia</i>	198
8.4.1	Substratum-Associated Environments	199
8.4.2	Planktonic Environments	201
8.5	Motility and Diatom Evolution	202
8.6	Conclusion and Future Directions	203
	Acknowledgements	204
	References	205
9	A Free Ride: Diatoms Attached on Motile Diatoms	211
	<i>Vincent Roubex and Martin Laviale</i>	
9.1	Introduction	211
9.2	Adhesion and Distribution of Epidiatomic Diatoms on Their Host	213
9.3	The Specificity of Host-Epiphyte Interactions	215
9.4	Cost-Benefit Analysis of Host-Epiphyte Interactions	217
9.5	Conclusion	219
	References	219
10	Towards a Digital Diatom: Image Processing and Deep Learning Analysis of <i>Bacillaria paradoxa</i> Dynamic Morphology	223
	<i>Bradly Alicea, Richard Gordon, Thomas Harbich, Ujjwal Singh, Asmit Singh and Vinay Varma</i>	
10.1	Introduction	224
10.1.1	Organism Description	224
10.1.2	Research Motivation	227
10.2	Methods	228
10.2.1	Video Extraction	228
10.2.2	Deep Learning	230
10.2.3	DeepLabv3 Analysis	234
10.2.4	Primary Dataset Analysis	234
10.2.5	Data Availability	235
10.3	Results	235
10.3.1	Watershed Segmentation and Canny Edge Detection	235
10.3.2	Deep Learning	236
10.4	Conclusion	243
	Acknowledgments	245
	References	245

11 Diatom Triboacoustics	249
<i>Ille C. Gebeshuber, Florian Zischka, Helmut Kratochvil, Anton Noll, Richard Gordon and Thomas Harbich</i>	
Glossary	249
11.1 State-of-the-Art	251
11.1.1 Diatoms and Their Movement	251
11.1.2 The Navier-Stokes Equation	252
11.1.3 Low Reynolds Number	253
11.1.4 Reynolds Number for Diatoms	254
11.1.5 Further Thoughts About Movement of Diatoms	254
11.1.6 Possible Reasons for Diatom Movement	255
11.1.7 Underwater Acoustics, Hydrophones	256
11.1.7.1 Underwater Acoustics	256
11.1.7.2 Hydrophones	257
11.2 Methods	257
11.2.1 Estimate of the Momentum of a Moving Diatom	257
11.2.2 On the Speed of Expansion of the Mucopolysaccharide Filaments	258
11.2.2.1 Estimation of Radial Expansion	258
11.2.2.2 Sound Generation	261
11.2.3 Gathering Diatoms	266
11.2.3.1 Purchasing Diatom Cultures	267
11.2.3.2 Diatoms from the Wild	267
11.2.4 Using a Hydrophone to Detect Possible Acoustic Signals from Diatoms	269
11.2.4.1 First Setup	269
11.2.4.2 Second Setup	271
11.3 Results and Discussion	272
11.3.1 Spectrograms	272
11.3.2 Discussion	277
11.4 Conclusions and Outlook	277
Acknowledgements	279
References	279
12 Movements of Diatoms VIII: Synthesis and Hypothesis	283
<i>Jean Bertrand</i>	
12.1 Introduction	283
12.2 Review of the Conditions Necessary for Movements	284
12.3 Hypothesis	285
12.4 Analysis – Comparison with Observations	288
12.4.1 Translational Apical Movement	288
12.4.2 The Transapical Toppling Movement	290
12.4.3 Diverse Pivoting	290
12.5 Conclusion	291
Acknowledgments	292
References	292

13 Locomotion of Benthic Pennate Diatoms: Models and Thoughts	295
<i>Jiadao Wang, Ding Weng, Lei Chen and Shan Cao</i>	
13.1 Diatom Structure	295
13.1.1 Ultrastructure of Frustules	295
13.1.2 Bending Ability of Diatoms	297
13.2 Models for Diatom Locomotion	300
13.2.1 Edgar Model for Diatom Locomotion	300
13.2.2 Van der Waals Force Model (VW Model) for Diatom Locomotion	302
13.2.2.1 Locomotion Behavior of Diatoms	302
13.2.2.2 Moving Organelles and Pseudopods	304
13.2.2.3 Chemical Properties of Mucilage Trails	307
13.2.2.4 Mechanical Properties of Mucilage Trails	310
13.2.2.5 VW Model for Diatom Locomotion	314
13.3 Locomotion and Aggregation of Diatoms	319
13.3.1 Locomotion Trajectory and Parameters of Diatoms	319
13.4 Simulation on Locomotion, Aggregation and Mutual Perception of Diatoms	323
13.4.1 Simulation Area and Parameters	323
13.4.2 Diatom Life Cycle and Modeling Parameters	323
13.4.3 Simulation Results of Diatom Locomotion Trajectory with Mutual Perception	326
13.4.4 Simulation Results of Diatom Adhesion with Mutual Perception	327
13.4.5 Adhesion and Aggregation Mechanism of Diatoms	331
References	332
14 The Whimsical History of Proposed Motors for Diatom Motility	335
<i>Richard Gordon</i>	
14.1 Introduction	336
14.2 Historical Survey of Models for the Diatom Motor	338
14.2.1 Diatoms Somersault via Protruding Muscles (1753)	338
14.2.2 Vibrating Feet or Protrusions Move Diatoms (1824)	338
14.2.3 Diatoms Crawl Like Snails (1838)	342
14.2.4 The Diatom Motor Is a Jet Engine (1849)	344
14.2.5 Rowing Diatoms (1855)	346
14.2.6 Diatoms Have Protoplasmic Tank Treads (1865)	350
14.2.7 Diatoms as the Flame of Life: Capillarity (1883)	354
14.2.8 Bellowing Diatoms (1887)	355
14.2.9 Jelly Powered Jet Skiing Diatoms (1896)	355
14.2.10 Bubble Powered Diatoms (1905)	358
14.2.11 Diatoms Win: "I Have No New Theory to Offer and See No Reason to Use Those Already Abandoned" (1940)	360
14.2.12 Is Diatom Motility a Special Case of Cytoplasmic Streaming? (1943)	360
14.2.13 Diatom Adhesion as a Sliding Toilet Plunger (1966)	365
14.2.14 Diatom as a Monorail that Lays Its Own Track (1967)	366

14.2.15	The Diatom as a “Compressed Air” Coanda Effect Gliding Vehicle (1967)	368
14.2.16	The Electrokinetic Diatom (1974)	371
14.2.17	The Diatom Clothes Line or Railroad Track (1980)	372
14.2.18	Diatom Ion Cyclotron Resonance (1987)	374
14.2.19	Diatoms Do Internal Treadmilling (1998)	375
14.2.20	Surface Treadmilling, Swimming and Snorkeling Diatoms (2007)	376
14.2.21	Acoustic Streaming: The Diatom as Vibrator or Jack Hammer (2010)	378
14.2.22	Propulsion of Diatoms Via Many Small Explosions (2020)	379
14.2.23	Diatoms Walk Like Geckos (2019)	380
14.3	Pulling What We Know and Don’t Know Together, about the Diatom Motor	381
14.4	Membrane Surfing: A New Working Hypothesis for the Diatom Motor (2020)	393
	Acknowledgments	397
	References	397
	Appendix	420
	Index	421

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 epiphytic 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,