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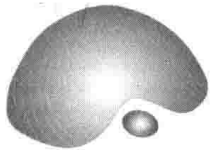
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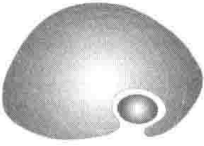
symbiosis and the
evolution of complex life

JOHN ARCHIBALD



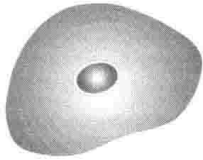
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symploysis and the evolution
of complex life



JOHN ARCHIBALD



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ONE PLUS ONE EQUALS ONE

For Shauna, Cameron, and Miles

Colin Turnbull (1961) took a pygmy friend, Kenge, out of the forest for the first time in his life, and they climbed a mountain together and looked out over the plains. Kenge saw some buffalo 'grazing lazily several miles away, far down below. He turned to me and said. "What insects are those?" ... At first I hardly understood, then I realized that in the forest vision is so limited that there is no great need to make an automatic allowance for distance when judging size. Out here in the plains, Kenge was looking for the first time over apparently unending miles of unfamiliar grasslands, with not a tree worth the name to give him any basis for comparison ... When I told Kenge that the insects were buffalo, he roared with laughter and told me not to tell such stupid lies.'

Richard Dawkins, 1982, *The Extended Phenotype*, p. 7

ACKNOWLEDGEMENTS AND NOTE TO READER

The idea for this book crystallized during the evening of 4 July 2008. I was sitting in a cozy dining room with about 40 other scientists, spouses, students, and friends atop Citadel Hill, a beautiful National Historic Site in the heart of Halifax, Nova Scotia. The occasion was the closing banquet of a meeting entitled *Mitochondria, Ribosomes and Cells: A Symposium in Honour of Mike Gray*. Professor Emeritus Michael Gray was retiring, and the preceding two days had been filled with talks covering much of the scientific territory he and his lab had roamed over since 1971. As I sat listening to speeches from Gray Lab members past and present, I realized how little I actually knew about the history of my field. I decided to do something about it. The end result is this book, and a much greater appreciation of science as a process. I sincerely thank Michael and my mentor-turned-colleague Ford Doolittle for 15 years of inspiration and support, and for teaching me the importance of looking backwards as well as forwards.

On more than one occasion before and during the writing of this book I was warned of the dangers of telling stories about scientists and the science they do. As with any text dealing with historical aspects of research, not everyone will agree with what I've written. Errors of fact are of course mine alone; so too are errors of interpretation, where possible to discern. I must emphasize the fact that there is much interesting and important science that was carried out during the time span covered in this book that I have glossed over or ignored entirely. Jan Sapp, Professor of Biology and History at York University

in Canada, has written extensively on many of the topics discussed herein; I encourage those interested in digging deeper into the history of endosymbiotic theory to consult his numerous articles and books. I have learned a great deal from Jan's work and thank him for his insights.

I have accumulated a great many additional debts over the past two years. I thank Professor Christopher Howe and Adrian Barbrook for being gracious hosts during my sabbatical stint as a Visiting By-Fellow at the University of Cambridge. I am grateful to Chris, Adrian, and all the Howe Lab members in the Department of Biochemistry for discussions and companionship. Churchill College served as home base for much of the front-end research for this book, and helped make my 'Cambridge experience' rewarding and inspirational in ways that I hadn't anticipated.

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Numerous additional people, scientists and non-scientists alike, read some or all of the text in draft format (in several cases more than once). I am immensely grateful for their encouragement and critical comments. In alphabetical order, these people are: Martha Archibald, Shauna Archibald, Andrzej Bodył, Bruce Curtis, Ford Doolittle, Mark Farmer, Martin Embley, Laura Eme, Victor Fet, Gillian Gile, Michael Gray, Michelle Leger, William Martin, John McCutcheon, Michael Melkonian, Nancy Moran, Thomas Richards, Courtney Stairs,

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I communicated with a great many academics during the research and writing of this book, everything from one-off emails to lengthy face-to-face interviews. Several people deserve special mention. Professor William Martin of the Botany Department at Heinrich Heine University in Düsseldorf, Germany, was incredibly generous with his time, providing detailed insight into endosymbiosis research as well as translations from German. I benefited greatly from time spent discussing organelle research in the pre- and post-molecular era with Bill and Professor Klaus Kowallik; both kindly made their extensive reprint collections available during my visit to Düsseldorf, saving me much time and energy. Nick Lane, senior lecturer at University College London, has been a regular source of inspiration and support, and provided sound advice on the structure of the book in its early stages. Professor Tom Cavalier-Smith and Professor Emeritus Philip John graciously accepted me into their homes for interviews during a visit to Oxford in December 2012. Professor Emeritus Max Taylor did the same on a trip to British Columbia (Max also kindly shared portions of his memoirs with me), as did Francisco Carrapiço and Ricardo Santos on trips to Portugal. Francisco and Ricardo provided me with interesting perspectives on the nature of science and the careers of numerous scientists, in particular Constantin Mereschkowsky and Lynn Margulis. For additional insight, through their publications and/or in person, I thank the following individuals: John Allen, Steven Ball, Debashish Bhattacharya, Neal Blackstone, Andrzej Bodył, Linda Bonen, Sam Bowser, Donald Bryant, Martin Embley, Paul Falkowski, Mark Farmer, Viktor Fet, Arthur Grossman, Kwang Jeon, Andrew Knoll, James Lake, Antonio Lazcano, Brian Leander, Uwe Maier, John McCutcheon, Geoff McFadden, Michael Melkonian, Maureen O'Malley, Eva Nowack, Thomas Richards, Andrew Roger, Mary Beth Saffo, Jan Sapp, Joseph Seckbach, Alastair Simpson, and Mitchell Sogin.

ACKNOWLEDGEMENTS AND NOTE TO READER

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JOHN ARCHIBALD

November 2013

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INTRODUCTION

We are in the midst of a revolution. It is a scientific revolution built upon our understanding of DNA, the hereditary material of life. Using the tools of molecular biology, we probe and prod the world around us in ways unimaginable a few decades ago. Big or small, past or present, no organism is immune. Need to identify and track a bacterium at the root of a hospital outbreak? No problem: the offending germ's complete genetic profile can be obtained in 24 hours. Curious about how we humans differ from our closest relatives, the now-extinct Neanderthals? Anthropologists are tackling this very question with DNA extracted from fossilized bone. With a simple cheek swab and a hundred dollars you can delve into your family history in ways that traditional genealogy cannot, and the same technology can reveal susceptibility to Alzheimer's disease and certain cancers. It can even solve a crime. We insert human DNA into *E. coli* bacteria to produce our insulin; we isolate spider silk protein from the milk of transgenic goats; we dream of solving the energy crisis with microbes engineered to produce alternative biofuels; we can clone our pets.

Precisely when and how this revolution began is debatable, but it is safe to say that it would not have happened without the advent of DNA 'sequencing'. The iconic DNA double helix is a ladder-like molecule whose rungs are comprised of four chemical 'bases'. In the 1970s scientists did a remarkable thing: they figured out how to take a piece of DNA and determine the precise order of these bases from one end of the molecule to the other. The microbiologist Carl Woese referred to it as 'biology's ultimate technique', and for good reason. Buried within the four-letter chemical read out—within the DNA

sequence—are an organism's genes, collectively the set of 'instructions' it uses to synthesize the proteins needed to sustain life at the cellular level. The genetic alphabet is simple but the information it stores is complex and powerful. As we learned the language of life we learned to manipulate it with increasing ease, transforming countless areas of basic and applied research. Science would never be the same again.

It is natural to look at biotechnology in the twenty-first century with an uneasy mix of wonder and fear. Biotechnology is, however, not as 'unnatural' as one might think. Indeed, biotechnology would be utterly impossible if not for the following indisputable fact: all life on Earth is related. All living organisms use the same fundamental molecular processes to maintain and replicate their genetic material; all organisms use the same basic genetic code to 'read' their genes. From wombats to whales, yaks to yeasts, barnacles to bacteria, the similarities are written in their DNA. And here's the astonishing thing: evolution has been 'plugging-and-playing' with the molecular components of life from the very beginning, generating new organisms with novel biochemical capabilities. It continues to do so today. The evidence is there for all to see. In fact we *are* the evidence; we need look no further than the inner workings of our own cells.

Molecular biology has allowed us to gaze back more than three billion years to the ancient roots of unicellular life. It has revealed how, from simple precursors, complex life forms came into existence. This book tells the story of how we have come to realize that our cells are natural chimaeras, and the importance it holds for us as human beings. It is some of the most exciting and important scientific detective work most people have never heard of.

1

LIFE AS WE DON'T KNOW IT

The yin and yang of life

Spring, summer, autumn, and winter—the temperate seasons of Earth. The further we are from the equator the more extreme they become, and the more our lives turn with them. Our blue-green gem of a planet orbits the sun at a breathtaking 30 kilometres per second. It is a journey that takes 365 and one-quarter days. And all the while Earth spins like a top, its axis of rotation tilted 23.5 degrees relative to its orbital plane. It may not seem like much of an angle, but the northern and southern hemispheres alternate summer and winter precisely because of it. In summer, the days are longer and the sun's rays strike the Earth more directly. It's a simple matter of physics. From the perspective of biology it makes all the difference in the world.

Nothing serves to focus the mind on the wonders of nature quite like a walk. Any season will do, although a sunny day in late spring or summer is apt to be most enlightening. If you're so inclined, pretend you are Isaac Newton and sit under a tree. Maybe it's an apple, or perhaps a majestic oak. Relax. Lean back, stare upward, and consider what's happening. If the tree is deciduous, its branches will be covered with leaves, a sea of green against a bright blue sky. Inside those leaves the world's most important biochemical reactions are taking place. With little more than carbon dioxide, water, and some nutrients drawn up by its roots, the tree is harnessing the energy of light, light that has travelled 150 million kilometres from the sun. Individual particles of light—photons—pass cleanly through the waxy outer

layers of its leaves and on towards specialized structures called *chloroplasts* buried within the cells beneath. Inside these sub-cellular factories, which give leaves their colour, photon absorption by chlorophyll pigments triggers a series of reactions that ultimately produce sugar and release oxygen as a by-product. This is the process of *photosynthesis*. With minor variations it is happening pretty much everywhere: within the plants on your porch, inside the needles of towering dawn redwoods, in slimy beach kelp, in desert cacti, even in single-celled algae drifting aimlessly in the sea. Photosynthesis makes the world go around.

The collective efforts of these and a myriad of other photosynthetic organisms have, over many millions of years, shaped the chemical composition of Earth's atmosphere. Their influence can still be felt. Carbon dioxide levels wax and wane as day turns to night and back again—as its name suggests, photosynthesis does not occur in the absence of light. During spring and summer, with leaves aplenty and the engines of photosynthesis running full tilt, average atmospheric carbon dioxide levels gradually decline. But with the arrival of autumn, and the transition from green to red, orange, and brown that accompanies it, rates of photosynthesis slow: carbon dioxide accumulates once more. One could be forgiven for assuming that the northern and southern hemispheres cancel one another out in this regard, alternating summer and winter as they do. Not so. Because there is more land mass and more vegetation in the northern hemisphere than south of the equator, its collective thirst for carbon dioxide is greater. Consequently, global carbon dioxide levels fluctuate on an annual basis as a result of photosynthesis. Year in year out, levels decline when the North Pole is tilted towards the sun, and rise again when it tilts away. As we breathe, so too does our planet.

Leaves, pine needles, and kelp blades make sense to us. We can see them, touch them, and easily picture their flat surfaces catching light like solar panels on a roof. Chloroplasts? More than a thousand of them could fit on the head of a pin. What exactly are these invisible light-eating factories, and where did they come from? Despite being