The chloroplast (pale green oval) originated when a cyanobacterium formed a symbiotic partnership with an ancestral plant cell.

#### EVOLUTION

# The complexity chronicles

**Nancy Moran** enjoys a treatise on symbiosis — the intimate association of species that transformed life and Earth.

In One Plus One Equals One, John Archibald melds two epic stories. One is the 3.8-billion-year tale of the fundamental biochemical inventions that underlie life on Earth, and how they were swapped and merged to produce complex life forms. The second follows the scientists who first mapped the domains of life and finally proved the central evolutionary role of symbiosis — the intimate associations between two or more distinct species.

Cells originated, became complex and expanded their capabilities: events that, as Archibald puts it, "led to a transformation of ocean, land, and atmosphere". He relates the scientific struggles behind the discoveries of these events with an appreciation of the strategies used. The microbiologist Carl Woese, for example, catalogued ribosomal RNA fragments harvested from large volumes of microbial cultures to transform our understanding of the tree of life. He delineated the ancient lineages that were later recognized as the fundamental players in the symbiotic formation of complex cells.

Archibald also offers glimpses into the

personalities of these pioneers. I loved the story of how, in 1978, Woese was so eager to see how the first determined ribosomal RNA gene sequence (from *Escherichia coli*) fitted with his own data that he could not wait for his issue of *FEBS Letters* to arrive in Illinois by post. Instead, he called biochemist Ford Doolittle in Halifax, Canada — who already had a copy — and got him to read out the 1,542-letter sequence

over the telephone.

The origins of mitochondria and chloroplasts from bacterial ancestors are arguably the two biggest innovations in the history of life. In eukaryotes, organisms in which the genomic DNA of each cell is packaged in a membrane-bound nucleus, mitochondria serve as energy factories; plants and algae also have chloroplasts



One Plus One Equals One: Symbiosis and the Evolution of Complex Life JOHN ARCHIBALD Oxford University Press: 2014.

that allow the harvest and storage of energy from sunlight. As their remnant genomes show, mitochondria and chloroplasts each arose from a specific bacterial group ( $\alpha$ -proteobacteria and cyanobacteria, respectively). And each arose from a single endosymbiotic event in which the bacterium was engulfed by an ancestral cell that 'chose' to coexist with it, rather than digest it. Those two choices made all the difference.

From 1905, when Constantin Mereschkowsky first postulated that higher plants depend on "little green slaves" (chloroplasts), until the 1980s, the endosymbiotic theory provoked controversy. The evolutionary biologist Lynn Margulis was a proponent from the late 1960s onwards, along with botanist Peter Raven and microbiologist Jostein Gøksoyr; botanist Arthur Cronquist was among the detractors. Proof came with the molecular era. As Archibald describes, a constellation of biologists, biochemists and bioinformaticians - prominently Michael Gray, Doolittle and Margaret Dayhoff exploited molecular technologies as they became available.

The consequences of symbiosis are ubiquitous and ongoing. Symbiotic cells have themselves been engulfed as symbionts of hosts, from algae to insects. Archibald gives many examples, including the citrus mealybug *Planococcus citri*, which contains one bacterial symbiont nested within another. And sequencing data are revealing many ghosts of symbioses past, in the form of genes transferred between interacting genomes. Many nuclear genes in plants were transferred from the chloroplast ancestor, for example.

Mysteries remain. A central one is the origin of eukaryotic cells. Their distinctive nuclei, as well as other attributes such as a cytoskeleton and endomembrane system, clearly show that these cells arose only once. The few eukaryotes that lack recognizable mitochondria, such as the protozoan parasite *Giardia lamblia*, descend from ancestors that had them, as evidenced by sprinklings of mitochondrion-derived genes in their nuclear genomes. If any proto-eukaryote had a nucleus but no mitochondrion, it left either no descendants, or descendants so few or secluded that they remain undiscovered.

Why would the ancestral mitochondrion have been retained? The 'ox-tox' hypothesis posits that the mitochondrion provided an 'oxygen antidote' for the anaerobic host cell, which would have struggled to thrive in conditions of rising atmospheric oxygen. This seems paradoxical, because modern mitochondria generate oxygen by-products that would have been toxic to the host.

An alternative idea is the hydrogen hypothesis. This posits that the eukaryotic cell evolved from a separate-but-equal partnership between a hydrogen-producing  $\alpha$ -proteobacterium and a methane-producing archaean. In this idea, the nuclear envelope arose after the symbiosis. Archibald weighs up the arguments, but the jury is still out.

Just as distinct organismal lineages swap and combine biochemical inventions, generating ecological breakthroughs, scientific disciplines exchange technology and ideas, instigating unexpected leaps forward. One could venture that molecular biology did for evolutionary biology what chloroplasts did for the eukaryotic ancestor of plants. In both cases, it is hard to say which side benefited more from the partnership. And with time, the merger has become so complete that the original duality is not evident. But tracing the origins of the threads from which the present is spun is exhilarating, for both cells and science. One Plus One Equals One is an eloquent account, at times verging on the poetic. With serious scholarship, it illuminates a rare scientific endeavour.

**Nancy A. Moran** is professor of integrative biology at the University of Texas at Austin. e-mail: nancy.moran@austin.utexas.edu

# **Books in brief**



## How Not to Be Wrong: The Power of Mathematical Thinking

Jordan Ellenberg PENGUIN (2014)

Mathematicians from Charles Lutwidge Dodgson to Steven Strogatz have celebrated the power of mathematics in life and the imagination. In this hugely enjoyable exploration of everyday maths as "an atomic-powered prosthesis that you attach to your common sense", Jordan Ellenberg joins their ranks. Ellenberg, an academic and *Slate*'s 'Do the Math' columnist, explains key principles with erudite gusto — whether poking holes in predictions of a US "obesity apocalypse", or unpicking an attempt by psychologist B. F. Skinner to prove statistically that Shakespeare was a dud at alliteration.



Starlight Detectives: How Astronomers, Inventors, and Eccentrics Discovered the Modern Universe

Alan Hirshfeld BELLEVUE LITERARY PRESS (2014) From 1850 to 1930, a handful of technological adepts transformed astronomy. That race to see deep space is told with palpable relish by physicist Alan Hirshfeld. Among the brilliant amateurs whose work he showcases are William Bond, Harvard University's 'astronomical observer', and astrophotographic pioneer Henry Draper. No less rousing is Hirshfeld's rendition of the coda, as Edwin Hubble using the 2.5-metre reflector telescope at Mount Wilson, California discovered the expansion of the Universe and opened up the cosmos.



#### Deep: Freediving, Renegade Science and What the Ocean Tells Us About Ourselves

James Nestor HOUGHTON MIFFLIN HARCOURT (2014) Freediving, the sport that harnesses the mammalian dive reflex to survive deep plunges, can be a boon for marine researchers, avers James Nestor. We meet a salty cast of them, such as the "aquanauts" of Aquarius, a marine analogue of the International Space Station submerged off the Florida Keys. Equally mesmeric are Nestor's own adventures, whether spotting bioluminescent species from a submarine in the bathypelagic zone, or freediving himself — and voyaging into humanity's amphibious origins in the process.



The Collapse of Western Civilization: A View from the Future

Naomi Oreskes and Erik M. Conway COLUMBIA UNIVERSITY PRESS (2014) In Merchants of Doubt (Bloomsbury, 2010), science historians Naomi Oreskes and Erik Conway laid out the costs of science denialism. In this trenchant sci-fi novella, they carry the consequences to their illogical conclusion. A future historian in the "Second People's Republic of China" looks back at the last gasp of Western culture in 2093, drowned, burnt and broken by climate change, neoliberal-powered ignorance and market failure. Packed with salient science, smart speculation and flashes of mordant humour.



### Is the Planet Full?

lan Goldin Oxford University Press (2014)

Indefatigable economist lan Goldin follows up *The Butterfly Defect* (Princeton University Press, 2014), on the risks of globalization, with this edited volume on the equation of planetary resources and human population. Standouts among the agile analyses are lan Johnson's reappraisal of the Club of Rome's trailblazing 1972 *The Limits to Growth*, in which Massachusetts Institute of Technology researchers tackled the same overall question; and Goldin's discussion of governance, ever the elephant in this particular room. **Barbara Kiser**