This Week's Citation Classic®

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All life on Earth is bacterial or derives, by symbiogenesis, from communities of bacteria. A century of evolutionary theory without symbiogenesis is enough. [The *SCI*® indicates that this book has been cited in more than 340 publications.]

The Inheritance of Acquired Microbes

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I would rather not talk about myself, my four children, other liaisons or incessant pressures from those who would silence, or even more insidiously, marginalize me and my work. Rather, I welcome this joyful *Citation Classic*[1]' opportunity that permits expression of my views on the question Darwin never answered: How do species originate?

The public and even many biologists still consider life divisible into three groups: animals (organisms that move, including people), plants (organisms that photosynthesize, producing food and fiber) and the rest: germs. Germs, invisible, and lodged in bothersome scum, are randomly-attacking disease bacteria, viruses, and parasites. The new second edition of my book *(SCE2)* reverses such anthropocentrism by distinguishing microbes, profoundly respecting the powers of the subvisible world and the relevance of microbial diversity to evolution; thus it replaces the dim-witted dichotomy of plant versus animal with the logic of five kingdoms. By drawing on disciplines as disparate as DNA technology, ultrastructure, and pre-Phanerozoic geology, it establishes a modern basis for Darwin's concept of the common ancestry of life. Furthermore, *SCE2* rejects central tenets of neoDarwinian distortion of Darwin's vision, e.g., I assert that the gradual accumulation of random mutations is insufficient to explain speciation. Rather, speciation occurs mainly by symbiogenesis, of course supplemented by DNA mutations.

Symbiosis itself is merely protracted physical association of organisms who are members of different species. Symbiogenesis is the resulting evolutionary change that occurs by permanent integration of symbionts. That symbiogenesis formed new species was argued by I.E. Wallin (1883-1969), an American, and by at least three Russians[1]: K.S. Merezhkovsky (1855-1921), B.M. Kozo-Polyansky (1890-1957) and A. S. Famintsyn (1835-1918), yet it is still ignored in today's evolutionary literature. By the early Proterozoic eon (two billion years ago) different types of bacteria became so literally incorporated that they emerged as new kinds of larger individuals at more complex levels of organization. The appearance of eukaryotic cell organization from fermenting, motile, and eventually respiring and photosynthetic components of the microcosm provides principles of evolution within the framework of the fact that all life on Earth forms one complex interacting system with physical continuity through space and time.

Two major changes distinguish *SCE2* from *SCE* (1981): the evidence that undulipodia preceded mitochondria and the discovery of kinetosome-centriole DNA. The [9(2)+2] microtubule systems are motility structures surprisingly constant in width, at 0.25 urn, and usually 5-10 urn long. [Although they are quite uniform in width in all cells, they can vary from fewer than one to greater than 3,000 µm (= 3 mm) in length.] Familiar by their confusing names, these motility structures of eukaryotes are always underlain by kinetosomes. They include sperm tails; oviduct, tracheal and sensory cilia; ciliate cilia; gill cilia of molluscs; the eukaryotic "flagella" of trypanosomes, euglenids, and other swimming algae. The evolutionary homology is indisputable: the [9(2)+2] axoneme structure invariably forms from a [9(3)+0] kinetosome, a structure that often develops from a mitotic centriole. The generic term for the membrane-covered kinetosome-axoneme is undulipodium.

My book describes many independently-studied structures that are really modified undulipodia: olfactory cilia and the auditory kinocilium in mammals, rods and cones of some retinas, balance-organ cilia, insect mechanoreceptors, the haptonema of prymnesiophytes and the clumped bundles of ctenophore (comb jelly) undulipodia (the "macrocilia") are all outgrowths from [9(3)+0] kinetosomes. The symbiotic acquisition of the undulipodium (prior to mitochondria) implies that the first eukaryotes were motile undulipodiate anaerobes, whose descendants include G/ard/a(and other diplomonads), *Trichomonas* (and other parabasalids), retortamonads, and probably microsporidians. Acquisition of eubacterial motility symbionts into a *Thermoplasma-toke* archaebacterial host to form the first protists is reconstructed. The thorny issue of the origin of undulipodia is illuminated by the discovery of kinetosome-centriole DNA by Rockefeller University scientists.[2] The implications of the discovery in David Luck's lab for symbiogenetic theory are presented as a progress report because (unlike the definitive proof that both mitochondria and plastids are of symbiotic origin from O_2-respiring and phototrophic bacteria, respectively) the kinetosome-centriole work is not complete. The kinetosome-DNA has been severely criticized by Joel Rosenbaum[3] and others.[4] Furthermore, we now know that the protein we called "tubulin-like" that we found in some spirochetes lacks tubulin sequence homology; rather, like "symbionin" reported by Ishikawa and his colleagues,[5] this fibrous protein is a groEL chaperonin homologue. Although the postulate of spirochete origin of undulipodia, with its implications for evolution of mitosis and meiotic sexuality, is not definitively established, progress on serial endosymbiotic theory is still impressive. The discovery of kinetosome-centriole DNA, of morphogenesis in free-living spirochetes (*Spirosymplokos),*[6,7] of amitochondriate mastigotes and other relevant protoctists,[8] and of an expanded excellent prePhanerozoic fossil record establish eukaryosis as one of many examples[9] of the importance of symbiosis in evolution. Symbiogenesis, even in the larger animals and plants, the relevance of an "RNA world" connecting prebiotic chemistry and the first cells, the concept of autopoiesis and new support for the Gaia hypothesis are also reviewed in *SCE2.*

I have tried to resist the confusing pressures to fragment and technologize from which we all suffer in today's information glut. The work itself plunges ahead against the disdain, dismissal and ignorance of specialists and rejection by granting agencies. *SCE2* was written to bypass these keepers of the gates of truth and to engage the minds of those students and teachers, evolutionists and microbiologists, geologists and ecologists who love the field more than the laboratory and refuse to apologize for their direct sensory interest in the natural world and its history.

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