The Endosymbiont Hypothesis

Symbiosis in Cell Evolution. Life and Its Environment on the Early Earth. LYNN MARGULIS. Freeman, San Francisco, 1981. xxiv, 420 pp., illus. Cloth, $24.50; paper, $14.95.

Lynn Margulis's 1970 book (*Origin of Eukaryotic Cells*, Yale University Press) summarized in one place, and with the idiosyncratic fervor we have come to associate with her writing, arguments for the then not-too-reputable notion that mitochondria and plastids evolved from endosymbiotic respiring eubacteria and blue-green algae (cyanobacteria) respectively. That book is a classic, probably referred to more than any other publication bearing in any way on the origins of organelles. Much has happened in the ensuing decade. Arguments for the derivation of plastids from endosymbiotic oxygenic-photosynthetic prokaryotes have become almost irrefutable; data bearing on the origins of mitochondria are many but show few definite clues to the prokaryotic ancestry of mitochondrial genomes; the prokaryotes themselves have been divided into two distinct evolutionary lineages (eubacteria and archaebacteria); and our knowledge of Precambrian geochemistry and paleobiology has expanded enormously. Margulis covers all these topics and more in this new book, which is better than the first—tighter, more easily read, and graced with many attractive drawings, plates, and summary tables. No one in cellular evolution can afford to ignore the book, although probably no one will agree with all that Margulis says in it.

And indeed she says many things, because her approach to evolutionary biology has always been eclectic. This gives the book the virtue of breadth, and the reader's interest is well sustained by examples of bizarre and complex symbiotic relationships drawn from her own work and more than 1000 cited publications. The exposition of the endosymbiont hypothesis and the important consequences its acceptance has for understanding phylogenetic relationships among the four eukaryotic kingdoms is presented in three introductory chapters with a facility that comes only with practice; Margulis has already written much on the subject. The body of the book seems to be intended as (i) a discussion of the origins of the first cells; (ii) a review of recent paleobiological and geochemical data and how these, together with a knowledge of contemporary metabolic diversity, lead to what is becoming a consensus on Precambrian evolution; (iii) an analysis of modern symbioses, their diversity, ubiquity, and ecological and evolutionary importance; (iv) a selective summary of data that strongly supports the notion that plastids are degenerate endosymbiotic oxygenic-photosynthetic eubacteria and mitochondria are degenerate endosymbiotic respiring bacteria; and (v) a defense of the notion, of which Margulis is still the only vigorous promoter, that tubulin-containing spirochaetes associated in mobility symbioses with otherwise immobile protoeukaryotes gave rise to tubulin-containing structures involved not only in eukaryotic mobility but in mitosis, which Margulis sees both as polyphyletic and as essential to the subsequent evolutionary progress of the eukaryotes. I say the book "seems" to have these purposes because Margulis writes in a rather personal and reiterative way, playing variations on her central themes throughout. Some readers may find this irritating. I find it helps me to keep the themes in mind and suggest, for that reason, that portions of the book, or indeed all of it, would make thought-provoking reading for properly cautioned advanced undergraduate and graduate students with any interest whatsoever in evolutionary cell biology.

Caution is necessary because with so much breadth there is in places little depth. Margulis obviously feels uncomfortable with speculations about the origins of the machineries of transmission and expression of genetic information, and her coverage of these is skimpy. She makes much of the utility of the concept of "semes" (multigenic traits) in evolutionary analyses, without as far as I can see even once demonstrating how this concept can really be applied. She seems to accept the claims of Carl Woese and others that the archaebacteria diverged very early from eubacteria but devotes little discussion to the increasingly popular but still questionable claim that it is from the ranks of the former that the ancestor of the nucleocytoplasmic ("host") component of all eukaryotic cells was recruited. In fact she never seriously addresses the question of the ancestry of the host. Nor does she address the problems with the evidence for an endosymbiotic origin for mitochondria. Respiratory mechanisms and indeed the sequences of respiratory proteins unequivocally implicate the nonsulfur purple bacteria or their nonphotosynthetic derivatives (such as *Paracoccus denitrificans*) as directly ancestral, but all well-documented homologies involve nuclear gene products. Very little of the genomes of mitochondria (perhaps only the small-subunit ribosomal-RNA genes of plant mitochondria) is definitively eubacterial. One must assume that mitochondrial genomes evolve rapidly and under unique selection pressures. Margulis does discuss these pressures cogently, but without facing the fact that rapid evolution may make it impossible to eliminate the unattractive hypothesis that, although mitochondrial respiratory chains are unquestionably eubacterial, mitochondrial genomes may be something else altogether.

Margulis presents her pet hypothesis (the spirochaete origin of tubulin-containing organelles of eukaryotic motility and mitosis) in an appealing and vigorous way, but I remain unconvinced. It is unclear whether the tubulin-like protein found in spirochaetes is truly homologous with eukaryotic tubulin, unclear why spirochaetes have this remarkable "preadaptation" (apparently not for the motility that Margulis presumes led to their permanent engulfment and genetic dismemberment), and, more important, unclear how the hypothesis can ever be proved.

There are other speculative passages and unjustified generalizations with which one might take exception. I in particular regret that Margulis chose to conclude with an exposition of James Lovelock's "Gaia" hypothesis, which Margulis helped to develop and which proposes that biologically significant properties of the earth's atmosphere and oceans are maintained by homeostatic mechanisms resulting from symbiotic relationships that are global in scale and whose payoffs to individual partners may be delayed for thousands of generations. This is group selection writ very large—indeed, it reflects Lewis Thomas's Panglossian view of biology—and I wish she had left it out.

Still, this is a very useful and provocative book. Ideas with which most of us

agree are well summarized. Ideas with which many of us may disagree are presented with persuasive enthusiasm—the kind of enthusiasm that forces one, once and for all, to decide why one disagrees with them.

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Polar Cap Aeronomy

Exploration of the Polar Upper Atmosphere. Proceedings of an institute, Lillehammer, Norway, May 1980. C. S. DEEHR and J. A. HOLTET, Eds. Reidel, Boston, 1981 (distributor, Kluwer Boston, Hingham, Mass.). xvi, 498 pp., illus. $58. NATO Advanced Study Institutes Series C, vol. 64.

"Aeronomy" is the name coined by Sydney Chapman in 1950 to designate the study of the physics and chemistry of the upper atmosphere of the earth. Needless to say, in the last three decades this field has undergone major transformations. Progress in the aeronomy of the earth's polar region, however, has lagged far behind the work carried out for other regions such as the equator, mid-latitudes, or auroral zone. This state of affairs will change with the advent of a number of recent initiatives. These include the launching of the NASA Dynamic Explorer satellites A and B, the move to Greenland of the incoherent scatter radar currently located at Chatanika, Alaska, and the attainment of operational status by the European incoherent scatter facility, EISCAT. Thus, the review of polar cap aeronomy in this book is timely.

The book summarizes our current understanding of the subject clearly and succinctly. This has been accomplished partly through the device of tutorial papers limited to 15 pages or less that review progress on seven subjects. The book contains 36 such papers on such aspects of polar cap aeronomy as the composition of the neutral atmosphere and ionosphere, optical emissions and related applications, the coupling of the polar cap ionosphere to the magnetosphere and the solar wind, the electrodynamics of the polar cap and auroral zone ionosphere, and the wave-particle interactions in the polar cap. A closing section of four papers covers the applications of polar cap aeronomy to communications and ionospheric weather forecasting. Notable papers presenting new material are those by P. M. Banks and co-workers on the determination of the polar cap electrostatic potentials deduced from ion velocity measurements by the Atmospheric Explorer satellites, by R. W. Smith on the measurements of the neutral wind in the polar cap with a Fabry-Perot interferometer, and by R. M. Thorne and L. J. Andreoli on relativistic electron precipitation. Excellent reviews are contributed by M. A. Geller on middle atmosphere dynamics, by J.-C. Gérard on optical F-region processes, by J. G. Roederer on the solar wind-magnetosphere-ionosphere system, and by G. G. Shepherd on the remote sensing of the optical emissions of the polar cap. As this listing shows, the book is strong on optical studies and provides a representation of the other branches of aeronomy. A section of four papers on the early exploration of the polar upper atmosphere through the visual observations of auroras in Nordic countries since medieval times gives the book historical flavor.

My own interests are in optical emissions of the atmosphere, and I found the papers on this subject to be interesting and reflective of the current status of research. For any graduate student contemplating aeronomy as a specialty, and for any experienced researcher desiring a review of recent activities in polar cap aeronomy, this book is recommended. The book also serves as a useful introduction to the important work being done by European scientists, who do not often publish in the English literature.

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A Colony in Greenland

Haabetz Colonie 1721–1728. A Historical-Archaeological Investigation of the Danish-Norwegian Colonization of Greenland. H. C. GULLØV and HANS KAPEL. National Museum of Denmark, Copenhagen, 1979. 246 pp., illus. Paper, DKr 116.40. Ethnohistorical Studies of the Meeting of Eskimo and European Cultures, 1. Publications of the National Museum, Ethnographical Series, vol. 16.

In 1721 the Danish-Norwegian Moravian missionary Hans Egede, accompanied by his wife, four children, and 40 followers, established the first post-Norse European settlement in Greenland. Egede's "Hope Colony" was located on a wet, exposed island outside Godthaab Fiord in West Greenland, an area exploited by European whalers and once occupied by the Greenland Norse. The colony remained here for eight years before being shifted to a more favorable spot at Nuk (Godthaab), the present-day administrative center of the Greenland Home Rule Government. Written records of the colony survived, but knowledge of its physical location was lost until 1903.

Interest in Hope Colony revived in preparation for the 250th anniversary celebration of Egede's arrival in Greenland, and in 1969–70 the Danish National Museum and the Greenland Landsmuseum conducted excavations to document the site archeologically. In addition to its historic, cultural, and political significance, the investigation of this small early-18th-century European outpost was an interesting anthropological problem. The project was aided by the existence of extensive written records pertaining to the settlement, its demography, economic ties with Europe, and relationships with the Eskimo village located at Kangek, only four kilometers away. Subsequent to their excavation at Hope Colony, the authors turned their attention to Kangek, where they investigated, among other things, the impact of the Egede colony on a contemporary native cultural system. The paucity of such reciprocal studies of cultural relationships in North America has been a serious failure of archeological and anthropological research. The present volume, however, concerns only the work at Hope Colony. A future volume will present the Kangek data.

The first chapter describes the authors' theoretical approach, establishing an anthropological perspective through quotation of Stanley South and Robert Schuyler on the role of American historical archeology studies. A historical sketch details reasons for colonization. In particular, the authors note the growing religious zeal to locate and reconvert the "lost" Norse colonists, mercantile interests in expansion of the whaling industry into Greenland waters, and national territorial expansion. (Only the last was achieved.) The authors describe the colony as portrayed in Egede's diaries, official accounts, ledgers, and inventories. Chapter 2 presents contemporary maps, providing information on the geographic setting of the colony and the location of specific buildings. A chapter describing in detail the structures and features actually excavated confirms the identification of the main dwelling house, smithy, stable, and a warehouse. Chapter 4 (140 pages of the 250-page monograph) describes the artifacts recovered, discussing object function and provenience and relating such items to those that appear on inventory lists. The