BOOK REVIEWS

Lynn Margulis, *Symbiosis in Cell Evolution: Life and its Environment on the Early Earth*, W. H. Freeman, 1981, 419 pp., $24.50 and $14.95 (paper).

One of the most intriguing controversies in evolutionary biology is the question of how eukaryotic cells and their distinctive cellular organelles arose. In the last 10 years, the symbiotic hypothesis – that eukaryotic cells arose by symbiotic associations of prokaryotic cells from divergent lines – has become a respectable explanation of the remarkable properties of mitochondria and chloroplasts. But the proponents of the autogenous or evolutionary hypothesis can argue that semi-autonomous organelles have arisen by gradual separation of gene-sets and functional proteins into mitochondria, chloroplasts, and nuclei. In many cases, the data can be interpreted either way. At this point, it would be useful for proponents of each view to clearly outline the major hypotheses, to summarize the evidence for and against these hypotheses, and to propose appropriate tests of these hypotheses.

This is what Margulis has attempted to do for the symbiotic hypothesis in *Symbiosis in Cell Evolution.* In this easily readable book, Margulis presents an extensive but admittedly one-sided view of the origins and evolution of eukaryotic forms of life. After an elementary introduction to the evolution of life and its geological context, she draws the battle lines: the 'botanical myth' of the autogenous or direct filiation hypothesis is contrasted with its old-yet-new challenger, the symbiotic hypothesis. She points out the huge structural discontinuity between prokaryotic and eukaryotic cells and the ease with which intracellular symbiotic associations can form. If a gradual evolutionary process produced eukaryotes, then organisms representing transitional stages might be expected to exist. Before going into the origins of specific organelles, Margulis provides an excellent review of the symbiosis literature relevant to metabolic and motility symbiotism of single cells.

The strongest case for endosymbiotic origins can be made for chloroplasts. Margulis describes organisms like *Cyanophora paradoxa*, which have cyanobacteria functioning as obligate photosynthetic symbionts in the cytoplasm of an otherwise heterotrophic eukaryotic flagellate. Protists like the red algae seem to have chloroplasts that are very different from those in green algae and that exhibit many similarities to certain cyanobacteria. Also, *Prochloron*, a prokaryotic symbiont of colonial ascidians, has been shown to have chlorophylls a and b like green algae and higher plants. Margulis suggests such prokaryotes are the descendants of the ancestors of green algal and plant chloroplasts, whereas certain blue-green algae have become the chloroplasts of other (e.g., red) algae to produce, through parallel symbioses, the variety of different chloroplasts seen in eukaryotic algae today. The recent partial sequence analysis of *Prochloron* 16S ribosomal RNA does not clarify the issue; *Prochloron* has highest affinity to certain cyanobacteria and is only distantly related to the plant or green algal chloroplasts to which it was compared (Seewalt and Stackebrandt, *Nature* **295**: 618, 1982). If the book provided a more comprehensive review of biochemical similarities and differences among cyanobacteria, chloroxybacteria, and the different types of chloroplasts, I believe a stronger case could be made for their origins as symbionts.

A good circumstantial case is made for the symbiotic origin of mitochondria, based on closer relationships to certain prokaryotes than to the nuclear-cytoplasmic system in genome morphology, antibiotic sensitivity, membrane properties, respiratory systems, and certain protein sequences. The case is strengthened by the similarities of mitochondria 5S rRNA sequences to those in certain bacteria, a prediction of the symbiotic hypothesis supported by data published since Margulis wrote this book. However, direct evolutionists are quick to point out that mutation rates can vary greatly between nucleus and organelles, so greater sequence homology is not necessarily proof of a closer phylogenetic relationship.

The most questionable part of Margulis' earlier *Origin of Eukaryotic Cells* (Yale University Press, 1970) was the suggestion that microtubule-containing organelles were first ectosymbiotic spirochetes that became integrated into eukaryotic cells as flagella and later organized tubulin molecules into mitotic spindles and other microtubular systems. The resemblance of cilia and flagella (her undulipodia) to the motility-symbiont spirochetes on organisms like *Mixotricha paradoxa* seemed superficial, but now Margulis and coworkers have demonstrated 'microtubules' and tubulin-like protein in several spirochetes. To the surprise of many of us, spirochetes may turn out to the inventors of microtubules and the contributors of these basic cytoskeletal elements (and a 9 + 2 pattern for undulipodia?) to eukaryotic cells. Margulis' classification of

Origins of Life **12** (1982) 119–121. 0302–1688/82/0121–0119$00.45.

Pelomyxa palustris as a very primitive ameboid eukaryote lacking microtubules is countered by Griffin's (*Trans. Amer. Micros. Soc.* **98**: 157, 1979) demonstration that they contain aberrant, non-motile axonemes with 9 + 1 to 9 + 5 microtubular arrays. In contrast to her assertion that no animal cells with undulipodia can divide, many insect spermatocytes go through one or both divisions of meiosis with flagella assembled on one of the centrioles at each pole.

Margulis also suggests that undulipodia preceded all other eukaryotic microtubule systems, such as microtubule-mediated mitotic movements, in the evolution of eukaryotic motility and that kinetochores on nuclear chromosomes derived from undulipodia. In accepting these as given premises, she keeps her 1970 scheme of the evolution of mitosis, which now seems out of step with more recent reviews. The inclusion of Heath's extensive tables on mitotic variations in the protists is helpful; it could be more easily used if the organisms listed were arranged in some obvious order, such as her phylogeny of mitosis.

On the whole, the book is useful, stimulating, and, like its author, colorful and controversial. Her lack of qualifications for unsupported opinions may mislead the uninitiated and turn off the expert. Although few non-believers or agnostics will be converted by this book, Margulis does point out that there are hypotheses to be tested on both sides of the controversy. Hopefully, the origins of eukaryotic cells are not so buried by intervening changes that our early evolutionary history is unknowable.

Department of Zoology
University of Maryland
College Park, Maryland 20742

DENNIS GOODE

The Origins of Life and Evolution, Harlyn O. Halvorson and K. E. Van Holde (eds.), Alan R. Liss, Inc., New York, 1980, 126 pp., $ 16.00.

The material presented in this first volume of what promises to be a stimulating series of books is a compilation of material presented at an informal workshop held at the Marine Biological Laboratories at Woods Hole in 1979. The workshop was set up in an effort to synthesize a cogent body of data concerning the origins of life, since, prior to that time, there was a dearth of 'hard' experimental information concerning this topic. The papers presented here are easily grouped into three main sections: paleobiology, protobiology, and evolutionary biology.

In the first group are two papers, which deal with the appearance of microfossils in the range 3.4 to 3.7 BYBP. Strother and Barghoorn's work on the presence of organic 'microspheres' in the Swartkoppie formation is not presented as an attempt to 'prove' that these spheroids are microfossils, but rather that they are compatible with a biogenic derivation. By careful measurements of the sizes of these formations, they generate a series of size-frequency plots, which results are consistent with values derived from analysis of living unicellular algal populations. Subject to several caveats, for example, concerning the requirement for binary fission as a reproductive mode, their claim that "...if these microspheres were found in younger rocks, their biogenicity would not be questioned" stands up quite well, and argues forcefully for the biogenic origin of these materials. As a natural follow-up to this first paper is that of Des Marais, who deals with organic geochemical, or 'chemical' fossils. After an excellent (albeit short) introduction concerning the types of chemical processes that have been at work on Precambrian material, he discusses the implications of some recent work in this area, and indicates just where future work is required. This chapter provides an excellent review of this controversial field.

Having established the presence of biogenic materials on Archaen Earth, the question naturally arises as to what processes were at work that resulted in the origin of these materials. The next section of the book, comprised of three chapters, addresses this point. Van Holde offers a cogent argument in favor of reassessment of some of the long-held views that life originated in an aqueous environment, by presenting thermodynamic requirements which demonstrate that, since polymer formation is the result of dehydration reactions, such polymer formation could not, perforce, have taken place in the primitive oceans. He presents two hypotheses which are consistent with this requirement. The importance of his arguments is not that they are any more testable than the previous ones, but that they force the reader to reexamine the erstwhile dogma. John Oró's paper on 'Prebiological Synthesis of Organic Molecules and the Origin of Life' provides excellent background material on organic cosmochemistry, and then applies these results to conditions extant on primitive Earth. Beginning with chemical precursors, he proceeds through the formation of monomeric species, to the synthesis of oligomers and membranes. With the availability of these requisite materials, Oró continues into the realm of protobiological evolution. His entire presentation is made within the established guidelines of the chemical evolution hypothesis, propounded by Oparin and Haldane, but does not preclude other interpretations, as mentioned above with regard to Van Holde's work. This alternative view of chemical evolution is further explored in the next chapter by Carl Woese, who argues successfully that the Oparin hypothesis, while providing an excellent springboard for the initial studies on the origin of life, has now stultified work in this area. Woese provides cogent arguments in criticism of the Oparin view, and presents his synthesis of present-day thinking and data to conclude that life probably arose in the form of droplets, as an aerosol, which obviates many of the problems *he* sees in the Oparin/Haldane hypothesis. In this regard, his conclusions hearken back to those presented earlier in this volume by Van Holde. As was mentioned in that case, the major importance of Woese's work here is that it forces a rethinking in an effort to more clearly explicate those processes at work in chemical evolution leading to protobionts. Furthermore, he argues that photosynthesis was probably an early property of organisms on the Earth, and that it was this process that converted the primitive Earth, with many of the attibutes of the greenhouse effect (similar to Venus) into a planet that would support life as we know it. Unfortunately, his hypothesis is no way addresses the problem of information transfer (i.e., genetics), which does not serve to weaken the work, but it does leave it incomplete. All in all, a fascinating critique.

The next section of the book approaches the question of genetics and evolution of early organisms from a number of perspectives. K. C. Atwood uses some interesting statistical derivations to conclude that all genes, regardless of size, are descended from sequences of less than sixty bases, and probably much less than this. He also argues that photosynthesis resulted in this upper limit, which was even smaller before the onset of this transduction process. He introduces the concept of sequence space, and demonstrates that "...if life is monophyletic, it goes back to a particular point of entry into sequence space. This point marks the beginning of biological evolution as distinct from mere synthesis".

Almost as if in response to this type of analysis, Margulis presents her scheme for organizing microorganisms, specifically bacteria, into phyla; an approach that has not hitherto been explored. She would claim that her work, presented in this volume, is designed to reincorporate these organisms into the mainstream of biological thinking. Since bacteria have been at work on the Earth for well over two billion years, this approach has its merits. Perhaps because of the sheer amount of material required to document this approach, her chapter seems to be more of an advertisement for the handbook she mentions, but that does not detract from the work presented here. The applicability of Margulis' approach is, in effect, tested by the next paper, which presents a phylogenetic analysis of photosynthetic bacteria by using the well-established technique of analysis of 16S ribosomal RNA components. The conclusion that Gibson draws from her work is that photosynthesis was probably established early in the anaerobic phase of the evolution of life, and that present day, nonphotosynthetic aerobes are descended from these antecedents, having lost the capacity to carry out these reactions.

The question of rethinking of previously-established dogma is continued in the last chapter of the book, wherein Mahler presents some arguments concerning the evolution and possible origin of mitochondria. Drawing on numerous data bases, from electron microscopy to standard restriction nuclease analyses of the mitochondrial genome, Mahler concludes that the mosaic organization of mitochondrial genomes is the result of the most primitive mechanism of genetic recombination. The conclusion that he would like to draw is that the organization of the mitochondrial genetic system is such as to force consideration of the mitochondrion system as unique, and that "facile attempt" as its classification are futile.

In toto, the book provides an excellent background into some of the areas that are currently being addressed concerning the origins of life and evolution. Clearly, the material presented is provided by some of the foremost workers in their respective fields. The bibliographies for each chapter provide excellent starting material for further literature research. While there appears to be no obvious organization to the book, consideration of the various chapters in the light alluded to at the beginning of this report allows seeing the work as a *gestalt*.

The only criticism I have concerns the supposed "editorial excellence and high physical quality" claimed for this volume (and, presumably succeeding ones). I found a distracting number of typographical errors, which should not have passed the proofreaders.

Laboratory of Chemical Evolution
Department of Chemistry
University of Maryland
College Park, Maryland 20742

MITCHELL K. HOBISH