Preface

Molecular studies of bacterial phylogeny have effected a profound revolution in biology. Beginning in the 1970s, 16s ribosomal RNA phylogenetics by Carl Woese and his collaborators led to a natural classification of bacteria and to the construction of a universal phylogenetic tree, with three Domains or Urkingdoms: the Archaea, the Eubacteria, and the Eucarya. Studies of molecular evolution have also led to new concepts for understanding evolutionary change, and to the confirmation of old concepts, including the paramount role of symbiosis in the origin of the eukaryotic cell from which all plants and animals have sprung. The origin of mitochondria from alpha-proteobacteria and the origin of chloroplasts from cyanobacteria are well established.

Neo-Darwinian evolutionary theory, based on gene mutations and recombination between individuals of a species, did not include bacteria (*sensu lato*, or in the broad sense); nor could it. The evolutionary synthesis was constructed in the 1930s and early 1940s, before bacterial genetics was established, before the bacterium's mechanisms of heredity were elucidated, and before bacterial phylogenetics was considered possible. My own historical introduction highlights the controversies over microbial classification from Pasteur to the present. It illustrates the difficulties of constructing a microbial phylogeny before the advent of the field of molecular evolution, the revolution in microbial evolution by rRNA phylogenies, how the current controversies have arisen with the rise of genomics, and how the general concepts of microbial evolution contrast with classical neo-Darwinian theory.

Microbial evolutionary biology has been undergoing another transformation, with the birth of bacterial genomics, since the mid-1990s. These new data have led to several conceptual modifications and to wholly new issues. The importance of lateral gene transfer (between "species") across the bacterial phylogenetic spectrum is a subject of heated debate. Even the standard symbiotic scenario for evolution is being reconsidered, and the complex twists and turns in chloroplast evolutionary history have been revealed. Although the origin and evolution of mitochondria and plastids continue to be rich veins of research, several researchers have proposed further that the eukaryotic cell nucleus also evolved from a symbiotic event of some kind. The scope and significance of hereditary symbiosis among animals also remain subjects of controversy.

This volume brings together leading microbial evolutionists, often with markedly different viewpoints, to discuss these issues. Does the phylogenetic "tree" based on rRNA phylogenies still stand in the age of genomics? What is the scope and significance of lateral gene transfer across the bacterial phylogenetic spectrum? Can one trace bacterial genealogies at all in the face of lateral gene transfer? Is the course of the first 2 billion years or so of evolution unknowable? These issues are discussed in the first ten chapters. A full range of views are expressed in this volume.

Pace, Ludwig, and Schleifer (in chaps. 2 and 3) articulate the significance of rRNA-based microbial phylogenies. Woese (chap. 4) discusses why our understanding of the cell can never be separated from its evolution, the conceptual problems with the eukaryote–prokaryote dichotomy, the importance of lateral gene transfer in cell evolution, and the nature of the translation apparatus. Pace (chap. 2) provides a tour of the macrostructure of the phylogenetic tree and emphasizes how understanding of the tree has expanded through recent molecular studies of microbial diversity in the environment. Ludwig and Schleifer (chap. 3) compare the weighty data based on rRNA phylogenies to evidence based on other gene phylogenies.

While these authors elaborate on the importance of rRNA phylogenies, others qualify such studies as providing a definitive tree. A range of alternative views are offered here. At one pole, Doolittle (chap. 5) argues that lateral gene transfer may be so pervasive as to completely erase bacterial phylogenetic tracks. Martin (chap. 6) proposes that lateral gene transfer does not completely dash hopes for tracing the early evolution of life, but that one has to supplement genomics and rRNA histories with other data from biochemical evolution and from the fossil record. Morowitz and his collaborators (chap. 7) offer arguments for the robustness of metabolic phenotype compared to a noisy changing bacterial genotype. Gupta (chap. 8) and Lake and his collaborators (chap. 9) agree that it is indeed possible to trace genealogies, but they also suggest modifications to the model based on rRNA. On the opposite pole, Kurland (chap. 10) argues that the actual evidence for evolutionary significant lateral gene transfer is weak and that its phylogenetic importance has been grossly exaggerated.

Gray (chap. 11) offers us an overview of the central questions and controversies in research on mitochondrial evolution: What was the nature of the proto-mitochondria? Did mitochondria arise only once? How has the mitochondrial proteome evolved? Kurland (chap. 10) also considers some modifications to the standard symbiotic scenario for mitochondria, and Martin (chap. 6) argues for a radical change to theory, one that joins the symbiotic origin for mitochondria with that of nucleus. Archibald and Keeling (chap. 12) provide a lucid overview of the recent issues in chloroplast evolution: What was the nature of the proto-chloroplasts? Have chloroplasts evolved only once? Although all plastids may have descended from a single common ancestor, photosynthesis has spread horizontally among unrelated protist groups by symbioses involving two protists (secondary symbiosis). In still other cases, such secondary plastids have been replaced with those of an unrelated alga.

Although there have been several propositions that the nucleus is also a chimera of sorts, there is no consensus among scientists. Gupta (chap. 8) argues that the nucleus originated from a fusion between a diderm (gram negative) and monoderm (gram positive) bacteria, which he believes is the fundamental dichotomy among bacteria. Lake and his colleagues (chap. 9) consider that the nucleus involved an engulfment of one kind of bacteria by another, whereas Martin (chap. 6) has proposed that the ancestor of the mitochondria was involved in the origin of the nucleus. Margulis and her collaborators (chap. 13) maintain, instead, that the nucleus involved the merger of a spirochete-like eubacterium and an archaebacterium, which would account for the eukaryotic cell cytoskeleton and protist motility. The need to account for the origin of eukaryotic cell cytoskeleton is discussed by Dolan (chap. 14).

Werren's overview (chap. 15) of the importance of hereditary bacterial symbiosis in insects, shrimp, spiders, and worms, detected by techniques of molecular screening, reminds us that the scope of microbial symbiosis extends far and wide. This chapter effectively contradicts the assertions of leading neo-Darwinian theorists that hereditary symbiosis among animals is a rare occurrence.