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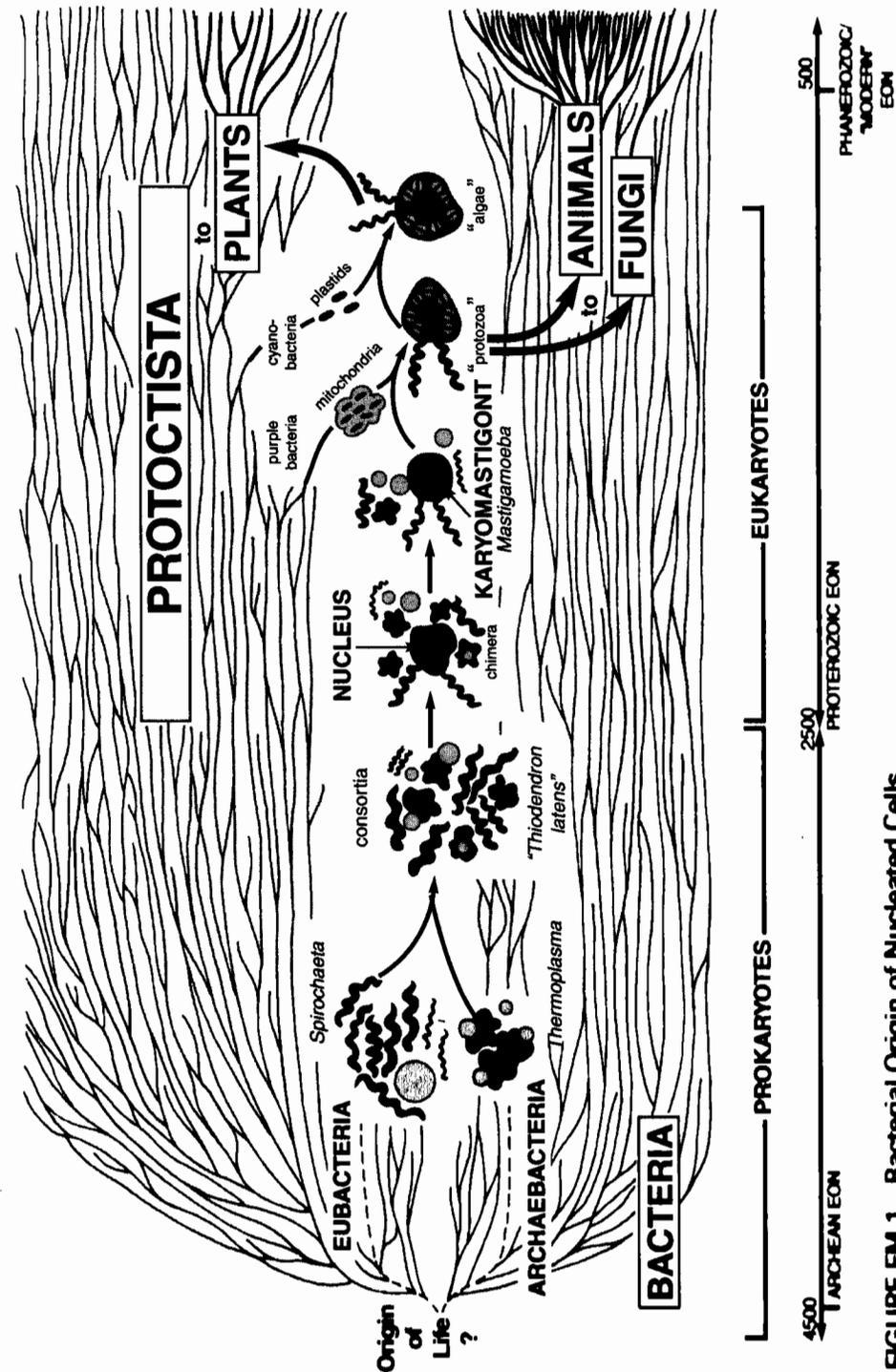


FIGURE FM.1 Bacterial Origin of Nucleated Cells

Any one whose disposition leads him to attach more weight to unexplained difficulties than to the explanation of a certain number of facts will certainly reject my theory.

Charles Darwin
The Origin of Species
1859

FOREWORD

When I got my degree at the University of Berlin, almost eighty years ago, biology consisted of two branches, zoology and botany. What dealt with animals was zoology, and everything else, including fungi and bacteria, was assigned to botany. Things have improved since then, particularly since the discovery of the usefulness of yeast and bacteria for molecular studies. Most of these studies, however, strengthened the reductionist approach and thus fostered a neglect of the major actors in evolution—individuals, populations, species, and their interactions.

The authors of *Acquiring Genomes* counter this tendency by showing the overwhelming importance of interactions between individuals of different species. Much advance in evolution is due to the establishment of consortia between two organisms with entirely different genomes. Ecologists have barely begun to describe these interactions.

Among the millions of possible interactions (including parasitism), the authors have selected one as the principal object of their book: symbiosis. This is the name for mutual interaction involving physical association between “differently named organisms.” The classical examples of symbiosis are the lichens, in which a fungus is associated with an alga or a cyanobacterium. At first considered quite exceptional, symbiosis was eventually discovered to be almost

universal. The microbes that live in a special stomach of the cow, for instance, and provide the enzymes for its digestion of cellulose are symbionts of the cow. Lynn Margulis has long been a leading student of symbiosis. She convinced the cytologists that mitochondria are symbionts in both plant and animal cells, as are chloroplasts in plant cells. The establishment of a new form from such symbiosis is known as symbiogenesis.

For many years, Margulis has been a leader in the interpretation of evolutionary entities as the products of symbiogenesis. The most startling (and, for some people, still unbelievable) such event was the origin of the eukaryotes by the fusion of an archaebacterium with some eubacteria. Both partners contributed important physiological capacities, from which ensued the great evolutionary success of the eukaryotes—the cells from which all animals, plants, and fungi are made.

Symbiogenesis is the major theme of this book. The authors show convincingly that an unexpectedly large proportion of evolutionary lineages had their origins in symbiogenesis. In these cases a combination of two totally different genomes form a symbiotic consortium which becomes the target of selection as a single entity. By the mutual stability of the relationship, symbiosis differs from other cases of interaction such as carnivory, herbivory, and parasitism.

The acquisition of a new genome may be as instantaneous as a chromosomal event that leads to polyploidy. The authors lead one to suggest that such an event might be in conflict with Darwin's principle of gradual evolution. Actually, the incorporation of a new genome is probably a very slow process extending over very many generations. But even if instantaneous, it will not be any more saltational than any event leading to polyploidy.

The authors refer to the act of symbiogenesis as an instance of speciation. Some of their statements might lead an uninformed reader to the erroneous conclusion that speciation is always due to symbiogenesis. This is not the case. Speciation—the multiplication

of species—and symbiogenesis are two independent, superimposed processes. There is no indication that any of the 10,000 species of birds or the 4,500 species of mammals originated by symbiogenesis.

Another of the authors' evolutionary interpretations is vulnerable as well. They suggest that the incorporation of new genomes in cases of symbiogenesis restores the validity of the time-honored principle of inheritance of acquired characters (what is called "Lamarckian inheritance"). This is not true. The two processes are entirely different. Lamarckian inheritance is the inheritance of modified phenotypes, while symbiogenesis involves the inheritance of incorporated parts of genomes.

Perhaps the greatest merit of this book is that it introduces the reader to the fascinating world of the microbes. It cannot be denied that the average student of animals and plants knows little (almost nothing!) about this world. The authors do not limit their account to symbiogenesis but also provide an enthralling description of protists and bacteria. What biologist realizes that animals have only a single set of metabolic pathways while different kinds of bacteria have more than twenty fundamentally different ones? While thousands of specialists study the physiology of vertebrates, the far more diverse physiologies of the bacteria are the province of just a few scores of microbiologists.

Chapters 9 through 11 are devoted to fascinating accounts of dozens of unusual consortia of plants and animals with microbes (protists, lower fungi, and bacteria). It is quite admirable how natural selection succeeded in fusing the most unlikely combinations into single consortia. No whodunit could be more spellbinding than some of these cases of symbiogenesis.

Given the authors' dedication to their special field, it is not surprising that they sometimes arrive at interpretations others of us find arguable. Let the readers ignore those that are clearly in conflict with the findings of modern biology. Let him concentrate instead on the authors' brilliant new interpretations and be thankful that

they have called our attention to worlds of life that, despite their importance in the household of nature, are consistently neglected by most biologists.

Let us never forget the important lesson taught by these authors: The world of life not only consists of independent species, but every individual of most species is actually a consortium of several species. The relations between larger organisms and microbes are infinite in number and in most cases make an indispensable contribution to both partners' fitness. Some knowledge of this vast branch of biology should be an essential component of the education of every biologist. There is more to biology than rats, *Drosophila*, *Caenorhabditis*, and *E. coli*. A study of symbiogenesis can't help but lead to a deeper understanding of the world of life, and there is no better way to gain this knowledge than to study *Acquiring Genomes*.

Ernst Mayr
Bedford, Massachusetts
February 2002

P R E F A C E

Amid all the recent interest in complexity, many point out that the future of science belongs more to biology, the study of complex systems, than to physics. Few beings, reader, are more complex than you. In this book we argue that to understand the true complexity of life—the main source of evolutionary novelty Charles Darwin sought—one must understand how organisms come together in new and fascinating ways, and how their genes are donated and acquired. This then will be the story of how species, and speciation itself, evolved through the acquisition of genomes. With more than a century of observation and experimentation by scientists around the world, and intense communication among them, let us now explain how new species come into being.

Neither an omnipotent deity nor fantastic good luck enters into it. The story that begins with Jean Baptiste Lamarck's studiousness, Charles Darwin's data, Gregor Mendel's garden peas, James Watson's willfulness, and Francis Crick's lack of humility ends, with a species of romantic irony, in the muck and slime. Its protagonists are speedy, determined bacteria and expert protist architects on a tectonically active Earth under an energetic sun. Wars, alliances, bizarre sexual encounters, mergers, truces, and victories are the dramas. Random DNA mutations, primarily destructive in their effects, account only for the beginnings. The role of randomness has been exaggerated in the evolutionary saga. Drugs,

chemical compounds, and other molecules are mere stimulants and components. Live beings by contrast are the protagonists.

The DNA molecule, like the computer disk, stores evolutionary information but does not create it. Selfish genes, since they are not “selves” in any coherent sense, may be taken as figments of an overactive, primarily English-speaking imagination. The living cell is the true self. An entity that cannot help creating more copies of itself, it plays center stage. The engine of evolution is driven by tiny selves of which we are only half conscious. We fear and malign them. The bacteria, these lively minute beings, escape our awareness except in freakish moments when they alarm or threaten us. We ignore or disdain the fact that they have lives of their own. But they do. The actions of the bacteria and other subvisible selves perpetuate old and generate new species.

On Saturday and every other night in the microbial world, something dramatic goes on. The spectacle has been playing for at least 3,000 million years, and the first acts are far too important for us to miss. Only at the very end of this long history does the social ape who walks upright and gossips nonstop take center stage. The ape who is nearly hairless, the one who cuts down rain forest trees with abandon, is deluded by visions of his importance. His sense of uniqueness and selfish interests combined with his technological profligacy have led to an unprecedented population explosion of primates. But this story is not about that ape, his lovemaking, his cohabitators, or his victims. Rather it is the tale of the nonhuman ancestors that preceded him. Before campfires, before proclamations of independence, before cities and urban sprawl, the Earth around the sun was populated by innumerable kinds of superficially alien life. The whole evolutionary saga of how species originate and how they extinguish may be the greatest tale ever to be told. It is everybody's story.

PART ONE

THE
EVOLUTIONARY
IMPERATIVE

ideas: variations occur, and only some offspring survive to produce their own offspring. Differences among organisms are selected by the environment through differential survival.

Thus he came to realize that organisms are connected through time and all descend from common ancestors. He called his idea descent with modification. Some of his best examples came from dogs and pigeons. He observed that people who bred chickens for eating selected those with bigger breast muscles, and the people who raised dogs for hunting selected those with the keenest senses. He noticed that selection relatively quickly produced differences in offspring, which in dogs, for instance, were codified as different breeds.

Darwin's basic concept, as modified, extended, and verified in the 20th Century, has been summarized by Ernst Mayr (2001) in his book *What Evolution Is*. This accessible introduction to the grand sweep of evolutionary science by an active participant expands on our brief resumé here.

In short, Darwin's argument goes: abundant production of too many organisms where only some survive to reproduce can always be shown. All offspring vary from their parents. Some of these variations are inherited. Therefore changes occur in the history of life. But what puzzled Darwin was, where does the inherited variation come from? Why, that is, aren't organisms always just like their parents, or just like their single parent? What is the source of evolutionary variation? In the end, Darwin didn't know. But he did note that much variation is never inherited: circumcised male children, most tailless mice, and yellowed leaves did not give rise to foreskinless babies, tailless mice, or plants with yellow leaves. Darwin often wrote that only variation that is inherited is important for "descent with modification," that is, evolution. The length of one's hair, as a variation, would not be of interest, because it is not inherited. But the length that hair might grow if permitted to grow maximally might be of interest as an example of inherited variation.

In summary, any population displays measurable variation, much of which is irrelevant to evolution. But the same population

also shows variation that is inherited and therefore relevant to evolutionary change. Such variation can be detected and measured in any group. So our question becomes the one Darwin asked himself—what is the source of observable inherited variation?

SYMBIOSIS AS A SOURCE OF INHERITED VARIATION

The word among neodarwinists, primarily zoologists who today call themselves "evolutionary biologists," is that inherited variation derives from random changes in the chemistry of the genes. Variations that are heritable are caused by mutations, and mutations are random. Unpredictable, and uncorrelated with behavior, social conditions, food, or anything else, mutations are permanent genetic changes. As these random genetic changes accumulate with time, they determine the course of evolution. Such is the view offered by most evolutionary literature.

We certainly agree that random heritable changes, or gene mutations, occur. We also concur that these random mutations are expressed in the chemistry of the living organism. Altered proteins that can be traced back to gene mutations in living organisms have been massively demonstrated. The major difference between our view and the standard neodarwinist doctrine today concerns the importance of random mutation in evolution. We believe random mutation is wildly overemphasized as a source of hereditary variation. Mutations, genetic changes in live organisms, are inducible; this can be done by X-ray radiation or by addition of mutagenic chemicals to food. Many ways to induce mutations are known but none lead to new organisms. Mutation accumulation does not lead to new species or even to new organs or new tissues. If the egg and a batch of sperm of a mammal is subjected to mutation, yes, hereditary changes occur, but as was pointed out very early by Hermann J. Muller (1890–1967), the Nobel prizewinner who showed X-rays to be mutagenic in fruit flies, 99.9 percent of the mutations are

deleterious. Even professional evolutionary biologists are hard put to find mutations, experimentally induced or spontaneous, that lead in a positive way to evolutionary change.

We show here that the major source of inherited variation is not random mutation. Rather the important transmitted variation that leads to evolutionary novelty comes from the acquisition of genomes. Entire sets of genes, indeed whole organisms each with its own genome, are acquired and incorporated by others. The most common route of genome acquisition, furthermore, is by the process known as symbiogenesis.

What is symbiogenesis and how is it related to symbiosis? First, what is symbiosis? Symbiosis is simply the living together of organisms that are different from each other. When originally defined by Heinrich Anton de Bary (1831–1888), symbiosis was the living together of “differently named organisms.” Symbioses are long-term physical associations. Different types of organisms stick together and fuse to make a third kind of organism. The fusion is not random. Symbiotic relationships occur under specific environmental conditions. In some of these relationships, one partner in the symbiosis feeds off the other to its detriment and even death. Such exploitative associations are called “parasitic” or “pathogenic.” They tend to be highly sensitive to environmental stress. The parasite that invariably and virulently kills its partner kills itself. With time and circumstance the nature of associations tends to change. The relationships that interest us most here are modulated coexistence between former predators, pathogens and their hosts, their shelter and food sources. As members of two species respond over time to each other’s presence, exploitative relationships may eventually become convivial to the point where neither organism exists without the other.

Long-term stable symbiosis that leads to evolutionary change is called “symbiogenesis.” These mergers, long-term biological fusions beginning as symbiosis, are the engine of species evolution. A very specific example of symbiogenesis in live organisms illustrates the

point. We introduce you to photosynthetic animals, actual plant-animal hybrids. Slugs, the familiar shell-less mollusks eating your garden plants, have entirely green photosynthetic relatives. The ancestors of these slugs have eaten but not digested certain green algae, which years ago entered the tissues of the animal—and stayed there. All members of these species (for example *Elysia viridis*) are always green. These underwater slugs need not seek food. Rather they crawl near the shore. They never eat throughout their adult life. The slugs, newly evolved green animals, now sunbathe in the way plants sunbathe. They are permanently and discontinuously different from their gray, algae-eating ancestors. Such acquisition, use, and permanent inheritance of entire alga genomes only seems marginal—in fact it has occurred many times in evolutionary history. At least four or five times different lineages of green animals have been documented in videos and scientific papers. Green animals provide graphic examples of symbioses that lead to symbiogenesis.

A second example is lichen, the plantlike greenery that grows on rock and tree bark. Most biologists do not realize that they are Schwendenerists. A Schwendenerist is a scientist, usually a botanist, who believes that lichens are not plants. The Schwendenerism argument raged in the late nineteenth century. Simon Schwendener (1829–1919) explained, in a long, complex treatise written in German, the composite nature of the plantlike lichen-growths and why no lichen is a plant. Modern investigators all accept lichens as symbiogenetic in origin. One quarter of all documented fungi are now known to be “lichenized”—they must live photosynthetically with green algal or cyanobacterial partners. This accounts for some 25,000 species of lichens. Together the intertwined organisms act as units: They produce highly organized and structured tissue—stalks, leaves, and bulbous protrusions. The fungal and algal (or cyanobacterial) cells of lichens propagate together. No serious biologist today ever suggests that any lichen is a true plant. All concur that while lichens look like plants and photosynthesize as plants do, even

cursory morphological analysis shows they differ from plants fundamentally.

Lichens provide us with the classic example of symbiogenesis. Moreover, the lichen individual is something distinct from either of its two component parts. It is neither the green alga (or cyanobacterium) nor a fungus. It is lichen. Lichens, evolutionary novelties that evolved by cyanobacteria or algal genome acquisitions, have taken a unique path and display characteristics distinct from both sets of their ancestors. Though traditionally studied within botany, lichens have always been central to concepts of symbiosis and symbiogenesis in evolutionary thought. And yet their symbiotic nature has led them to be thought of as a marginal evolutionary phenomenon. Perhaps they have been accepted as an example of the power of symbiogenesis to generate evolutionary novelty because the partners are of the same size. The alga and fungus are both easily seen with low-power microscopy, so neither can be studied without simultaneous study of the other. In some green animals, by contrast, for example in the flatworm species *Convoluta roscoffensis*, the two partners differ greatly in size. The worm is large, centimeters, whereas the little photosynthetic microorganisms, the algae, are microscopic. Such size discrepancies make the symbiosis, and symbiogenesis, less obvious.

The usual attitude is, "Well, symbiosis is acceptable for the evolution of microbial things that interest you" (as if we had a kind of bizarre personal issue with microorganisms). "But we don't believe symbiosis is an important evolutionary mechanism for 'higher' organisms (mainly mammals) that really interest us." But this book is replete with examples where symbiogenesis serves as the source of evolutionary novelty in familiar animals. For example, cows. Cows are "forty-gallon fermentation tanks on four legs," according to Sir David C. Smith (Smith and Douglas, 1987). Cows ingest grass, but they never digest it because they are incapable of cellulose breakdown. Digestion in cows is by microbial symbionts in the rumen. The rumen is a special stomach, really an overgrown esophagus,

that has changed over evolutionary time. Cows that lack rumens don't exist; cows (and bulls) deprived of their microbial symbionts are dead.

Random DNA base changes of course play a role in the evolutionary process. They are like printers' errors that crop up in the copying of books. They rarely clarify or enhance meaning. Such small random changes are nearly always inconsequential or detrimental to the work as a whole. We do not deny the importance of mutations. Rather we insist that random mutation, a small part of the evolutionary saga, has been dogmatically overemphasized. The much larger part of the story of evolutionary innovation, the symbiotic joining of organisms (similar, if we extend the printing analogy, to the fusion of texts in plagiarism or anthologies) from different lineages, has systematically been ignored by self-proclaimed evolutionary biologists (Sapp, 2002).

In the familiar phylogenetic tree, the acquisition of heritable genomes can be depicted as an anastomosis, a fusing of branches. The major proposition put forth here, of fusion of evolutionary lineages, is sometimes decried as an alternative to classical darwinism. But symbiogenetic acquisition of new traits by inheritance of acquired genomes is rather an extension, a refinement, and amplification of Darwin's idea. Such evolution requires new thought processes. New metaphors to reflect on permanent associations are needed. Symbiosis, merger, body fusion, and the like cannot be reduced to replacing "competition" as a major motive force in evolution with "cooperation." Ultimately, an anthropocentric term like "competition" has no obvious place in the scientific dialogue. Rather we would propose a new search in the social sciences for terms to replace the old, tired social darwinist metaphors. If survival is owed to symbiosis, rather than overemphasized intraspecific competitive struggles, what then are the consequences for nonbiologists interested in evolution?

In this book we have been careful to never use either "cooperation" or "competition" to describe biological or other evolutionary phenomena. These words may be appropriate for the basketball

court, computer industry, and financial institutions, but they paint with too broad a brush. Far too often they miss the complex interactions of live beings, organisms who cohabit. Competition implies an agreement, a set of actions that follow rules, but in the game of real life the “rules”—based on chemistry and environmental conditions—change with the players. To compete, people—for example on opposite teams—must basically cooperate in some way. “Competition” is a term with limited scientific meaning, usually without reference to units by which it can be measured. How does the green worm or the lichen fungus assess its competitive status? By the addition of points in its score or by dollars or Swiss francs? No. Then what are the units of competition? If you ask what are the units of biomass we can tell you in grams or ounces. If you ask how light or biotic potential is to be measured, we answer in lux or foot-candles or number of offspring per generation. But if you ask “what are the units of competition” we reply that yours is not a scientific notion. Vogue terms like “competition,” “cooperation,” “mutualism,” “mutual benefit,” “energy costs,” and “competitive advantage” have been borrowed from human enterprises and forced on science from politics, business, and social thought. The entire panoply of neodarwinist terminology reflects a philosophical error, a twentieth-century example of a phenomenon aptly named by Alfred North Whitehead: “the fallacy of misplaced concreteness.” The terminology of most modern evolutionists is not only fallacious but dangerously so, because it leads people to think they know about the evolution of life when in fact they are confused and baffled. The “selfish gene” provides a fine example. What is Richard Dawkins’s selfish gene? A gene is never a self to begin with. A gene alone is only a piece of DNA long enough to have a function. The gene by itself can be flushed down the sink; even if preserved in a freezer or a salt solution the isolated gene has no activity whatsoever. There is no life in a gene. There is no self. A gene never fits the minimal criterion of self, of a living system. The time has come in serious biology to abandon

words like competition, cooperation, and selfish genes and replace them with meaningful terms such as metabolic modes (chemoautotrophy, photosynthesis), ecological relations (epibiont, pollinator), and measurable quantities (light, heat, mechanical force). So many current evolutionary metaphors are superficial dichotomizations that come from false clarities of language. They do not beget but preclude scientific understanding.

Would not society be better served, then, if we adopted symbiotic metaphors instead of competitive ones? No. Society will be better served by more accurate scientific understanding, and this is not to be gained by substituting one pole of oversimplified metaphors for another. But of course organisms do vie in various ways with each other for space and food. Such vying however (or competition) among members of the same species does not in itself lead to new species; a source of genetic novelty—usually symbiogenesis—is needed. Only a small fraction of any population survives. Is this not then competition? Is it not then a “struggle for existence”? Not really. When Darwin referred to struggle, he meant the tendency of all organisms to grow, to reproduce, and to attempt to leave their own descendants. He did not mean that God battles with angels or that fistfights ensue among the mistresses of the king. In the sense of the tendency of some but not all to leave offspring, Darwin’s proper term is natural selection. The “struggle” is the bald fact, a rule of all life, that biotic potential is never reached. Only a few of us produce offspring who go on to produce offspring who themselves produce more fertile offspring. To call the tendency to leave offspring or fail to do so “competition,” as biologists frequently do, is misguided.

As a highly social species so often concerned with relationships among ourselves, we tend to be oblivious to our relationships with other species. Biologically, for example, there is no such thing as a symbiosis between a mother and her unborn infant. Symbiosis is always a physically close relationship between organisms of *different*

kinds. We humans have a symbiotic relationship with our eyelash mites. Most of us ignore the fact that we live symbiotically with our eyelash mites or with our underarm or gut bacteria or with the spirochetes in our gum tissue. But we do have eyelash mites and intestinal and underarm bacteria. We are inattentive to our immense populations of oral spirochetes until our gums bleed or our tooth aches. Each of us harbors bacteria in our intestines that make K and B vitamins that are absorbed through the intestinal walls. We seem reluctant to acknowledge our symbiotic bacteria even when we see them with a scanning electron microscope. We all enjoy silent, unconscious relationships with microbes.

But none of us has a symbiotic relationship with his or her mother-in-law, father, or adolescent child. Why? Because all people belong to the same *Homo sapiens* species. "Symbiosis" is an ecological term that describes two or more organisms of different kinds in protracted physical contact. Even bees and flowers, associated as they are by pollination ecology, do not have a symbiotic relationship. They enjoy other kinds of relationships, but they are not in physical contact long enough to be symbionts. Eyelash mites and the human body are symbionts. The odors that your socks emanate come from some of the bacteria and fungi that live between your toes; they have special habitats. The estimate is that any person is about ten percent dry weight symbioses. Most human symbionts, by weight, are the many types of bacteria that thrive in the colon (the large intestine). Our relation to these microbes is one of association—not "benefits" or "costs" or "cooperation" or "competition." Symbiosis and its evolutionary consequence, in some cases "symbiogenesis," is simply a fact of life.

In short, much of the modern evolutionist's (not the quaint darwinist's) terminology should be abandoned. Both in popular culture and especially in the scientific "evolutionary biology" subculture, the terminology is not scientific, but misleading to the point of being destructive. Honest critics of the evolutionary way of thinking

who have emphasized problems with biologists' dogma and their undefinable terms are often dismissed as if they were Christian fundamentalist zealots or racial bigots. But the part of this book's thesis that insists that such terminology (Table 1.2) interferes with real science requires an open and thoughtful debate about the reality of the claims made by zoocentric evolutionists.

THE MYTH OF THE INDEPENDENT INDIVIDUAL

Perhaps you are suspicious of the suggestion that organisms aren't as self-contained as we thought. The idea that we people are really walking assemblages, beings who have integrated various other kinds of organisms—that each of us is a sort of loose committee—opens up too many challenging speculations. When "the committee" gets sick, is simply a single animal getting sick, or is illness more a rearrangement of the members? We imagine that pathogenic microbes attack us, but if such pathogens are part of the committee that makes up each of us to begin with, isn't health less a question of resistance to invasion from the outside and much more an issue of ecological relationships among committee members? Yes.

We humans, like all organisms, live embedded in ecological communities. If, as individuals, we feel we are falling apart, it is probably because we multicomponented beings *are*, in fact, falling apart. Each person, each dog, each tree is composed of many different living parts that can be detected and identified. The relations among our living component parts are absolutely critical to our health, and therefore to our happiness. The completely self-contained "individual" is a myth that needs to be replaced with a more flexible description. The symbionts of people are difficult to study, however, for many reasons: complexity of disparate sizes, inability to carry out experiments in human heredity, politics, and social prejudice. Lichens provide better cases for understanding

Table 1.2—Evolutionary Terms as Battle Cries*

(No adequate quantitative measure of these exists; therefore they are deficient, even pseudoscientific terms.)

altruism	indirect fitness
benefit	levels of selection
game payoff matrix	lower organism
gene, selfish gene	mate competition
group selection	mutualism
higher organism	parental investment
inclusive fitness	reciprocal altruism

* Only a few of many examples listed here. See for example E. F. Keller and E. A. Lloyd, 1992, and L. Keller, 1999, for wholesale acceptance of neodarwinist “holy writ.” See Margulis, 1990, for spirited criticism against this fallacious language of misplaced concreteness.

symbionts. If certain lichens are placed in the dark, the photosynthetic member, the photobiont (usually a cyanobacterium such as *Nostoc* or a green alga such as *Trebouxia*), cannot live. The fungus often just grows and grows—it digests its green former partner. If lichens are placed underwater for a long time and in the light, the fungus drowns but the green alga will just grow and grow. Lichens, therefore, are composite organisms that require mixed light: They do not survive persistent *all-light* or *all-dark* conditions. So, too, they cannot live when the environment is entirely wet or entirely dry but require cycling between extremes. Change in the environment is essential to their survival. This lichen proclivity for change should not trouble us. The cycles, the alternations between wet and dry and light and dark, are what maintain the living composite, the apparent individual. Certain ratios of changes are required for most living beings to persist and propagate.

We must begin to think of organisms as communities, as collectives. And communities are ecological entities.

To go beyond animals, think of plants. We stick their seeds or seedlings in the garden soil and marvel as plants do their thing.

Most plant roots live in the rhizosphere. This is an ecological zone of many different organisms that all grow and metabolize at the same time. Some rhizosphere inhabitants provide nutrients to what we see as the plant, generally the part above the ground. But, like animals, plants are also confederacies of once-separate and different kinds of organisms. As we will see, symbioses in the roots, in the leaves, and even on the stems are known to have produced new forms of plant life—and may be responsible for the origin of those once-monstrous growths without which humanity as we know it would never have evolved—fruits.

The book *What Is Life?* (Margulis and Sagan 2000) has a photo taken from a distance by Connie Barlow that shows a stand of poplar trees in Colorado. Anyone can count these trees—there are hundreds if not thousands of them. But although it has many parts, this stand is really only one single organism. Under the ground the “tree” is continuous. It forms a connected structure with many upright shoots that emerge from the soil, straining our everyday notion of a single tree. The “individual,” whose roots are completely continuous, extends for kilometers laterally and for meters into the ground and up into the air vertically. This poplar stand is believed to be one of the largest “organisms” alive today.

Plants must be integrally incorporated into our conception of the evolutionary process. As stated, a problem with modern “evolutionary biologists” is that their examples are nearly always derived from people or other animals, especially other land mammals. Occasionally fruit flies or other insects serve as their illustrations of evolution. When they say “lower organisms,” they are generally speaking of animals other than mammals. As zoologists they tend not to know the microbial world—they are often ignorant of bacteria, fungi, and the myriad other “larger” microbes called protists. Zoologists tend to study very little botany, very little protistology, and no bacteriology. They write about “individuals,” but what is generally meant is people, pets, and our zoo and food animals. Occasionally, modern

evolutionists factor agricultural plants into their analyses, but they often do so in a limited and scientifically inadequate way. Although zoocentrism may be adequate for the kinds of mammals that are deployed for breeding further populations of mammals, it is a tame approximation—a kind of Apollonian hallucination—of what is going on with life as a whole.

A nineteenth-century question still with us today is whether evolutionary progress exists. Is increasing complexity on a large evolutionary scale to be understood as progress?

Evidence for evolutionary expansion is easy to show. In the fossil record evidence for the outward expansions of life forms abounds. Life, of course including human life, loves to be where water, ocean or lake, contacts the air as well as the soil. We all know from real estate values that shorelines are popular environments. Life enjoys habitats where water meets land meets air. Most life forms within a few millimeters of such surfaces.

Life apparently evolved from propagation at the seaside and only afterward expanded into the polar regions, high montagne lakes, and ocean abyss. Only since the Cenozoic era, which began 64 million years ago, did animal and algal life forms leave body fossils in the high Arctic and Antarctic. (For the geological time scale, simplified, see Table 9.1, p.147.) The continuous core of life on Earth has expanded and extended its range. Is this progress? Examples of fossil reptiles that sported more vertebrae and more morphological complexity than any now living have been unearthed. Since they are extinct, they stand in opposition to the concept of evolutionary progress. The very term “progress,” with its moral overtones, denotes a complex quantity that is unmeasurable and unassessible. The descendants of these reptiles lost complexity—they are simplified relative to their ancestors—but we can not say that they “regressed.” They evolved to have fewer vertebrae, that’s all. That some directional progress in evolution led to us, *Homo sapiens*, on our peak at some Olympian summit is an untenable

concept. As more of Earth became covered with more life, life *did* expand, but whether it “progressed” is questionable. Life’s apparent progress is best seen in the context of its conformity to the second law of thermodynamics, as we see in Chapter 2. We trace life’s history from the Precambrian to the present, always mindful of the question “How do new species evolve?” We recast the concept of “evolutionary progress” and “life’s purpose” in terms of the new thermodynamics, which unites and integrates, in a way distinct from but complementary to genetics and molecular biology, the physical and biological sciences.

environmental energy to “purposefully” reduce their gradients. The key point is that living and nonliving “selves” come into being to reduce gradients naturally. The reproducing self of biology is a higher-order cycle whose antecedents can be inferred from the cycles of the nonliving world. Nucleotide replication and cell reproduction do not emerge from nowhere. They are born in an energetic universe from thermodynamic tendencies inherent in nature.

CHAPTER 3

RELATIVE INDIVIDUALITY

We recognize individuals with ease. A group of individuals of the same species, in the same place at the same time, we call a population. Taken together with other forms of life, for example food plants and animals, different populations at the same time and place are recognized to form communities. Sometimes the largest and most dominant members of communities may be smaller than a millimeter in their largest dimension; if so, we speak of microbial communities. No life on Earth consists of unassociated individuals of the same population, like jailed adolescents or rows of corn plants—at least not for long.

INDIVIDUALITY FROM COMMUNITY

Communities are natural groups; in the natural world we recognize them easily without formal training—treetop communities, pond

water communities, shoreline communities, cliff-dwelling or woodland communities. A rule of thumb that we all use unselfconsciously is that individuals who seem to have everything important in common, individuals who seem "the same" in all major aspects of their lives, belong to the same species.

In the eighteenth century, Linnaeus, naturalists, and others interested in natural history began to name and document species the world over. A flurry of documentation and publication began as Europeans explored the tropics of America, Africa, and Southeast Asia. The Linnaean task of safe documentation and proper naming of all organisms has never been completed. Even now an effort is under way to encourage the monied interests of global corporations to use their profits for an "All-Species Inventory." With the international use of high-speed computers, satellite technologies, and real-time transfer of copious quantities of data, the leader of this project, naturalist Peter Warshall, has argued that we ought to record the world's living diversity before we destroy it. Extinction of species, like a death in the family, is an irreversible loss.

Even while the "All-species whole-Earth data set" is far from complete, some salient features emerge. Some ten to thirty million different species of organisms are estimated to be alive today, whereas fewer than two million of these have been documented in professional literature. Species of extinct organisms, registered in the paleontological literature based on fossil evidence of their former existence, number only about 150,000. Most scientists concur that over 99 percent of species that ever lived are extinct. Hence the guess for the number of species that have ever come or gone, since life on the Earth began 4,000 million years ago, is 200,000,000 million. No one we know can distinguish more than a few thousand species, and in fact we know almost no one who can even recognize that many, even with the aid of appropriate library books. In the field, especially in the flagrantly diverse new world tropics, most of us are hopeless. Even Mayer Rodriguez, consummate Ecuadorian

guide on the Tiputini branch of the Napo tributary of the Amazon river, cannot identify more than about 500 species. And no one knows that region better than he does.

All known organisms can be placed unambiguously into one of two inclusive groups that depend upon the types of cells of which they are composed. The first, presumably earlier group is by far the more diverse (from the viewpoint of metabolic modes) and essential to the environment at the planet's surface. These are the bacteria, all of which are composed of cells that lack nuclei (prokaryotic cells). The familiar life forms (animals and plants) as well as the two groups of smaller but visible beings (fungi and protoctists) belong to the second, newer group. These larger life forms are known as eukaryotes, truly nucleated organisms, because the cells of their bodies contain nuclei.

Hence life on Earth is neatly classifiable into five groups that we, in the great tradition of biological taxonomy, consider to be kingdoms. (Table 3.1) Kingdoms are the "highest," which only means the most inclusive, taxa. This tradition uses all information available about an organism to place it in a group as reflective as possible of its evolutionary history. Very briefly, members of the bacteria kingdom are composed of small single cells with threads of genes, not bound to protein, called chromonemes. When seen in electron microscopes the genetic structures are called nucleoids, to distinguish them from the nuclei of eukaryotes. The other four great kingdoms of life (the nucleated organisms whose DNA, wrapped in protein, is inside membrane-bounded nuclei and packaged into chromosomes) can be summarized too. First we have the embryo-forming groups: plants, which grow at one stage in the tissues of their mothers and at another stage from spores that contain only a single set of chromosomes; and animals, which grow after fusion of an egg with a sperm to form an embryo called a blastula. The less-known eukaryote kingdoms are the fungi (molds, mushrooms, yeasts, and their relatives) and the protoctista, unruly microorganisms and their larger descendants that gave rise to the

Table 3.1—Kingdoms: Largest Groups of Living Organisms

Time*	Type of cell	Chromosome sets	Comments	Examples
BACTERIA (3500)	Prokaryotic (no nucleus)	None. Chromosomal genetic organization	unidirectional DNA transfer from donor to host	<i>E. coli</i> "bluegreen algae" = cyanobacteria; archaebacteria
PROTOCTISTS (2000)	Eukaryotic (membrane-bounded nucleus)	haploid (1) and diploid (2), variable	variations abound, cell and nuclear fusions	algae, amebas, ciliates, slime molds
FUNGI (450)	Eukaryotic (membrane-bounded nucleus)	haploid (1)	grow from zygo-asco- or basidio-spores, chitin cell walls	molds, yeasts, mushrooms
PLANTS (450)	Eukaryotic (membrane-bounded nucleus)	haploid (1) and diploid (2)	maternally retained embryos, cellulosic cell walls	mosses, ferns, flowering plants
ANIMALS (600)	Eukaryotic (membrane-bounded nucleus)	diploid (2)	blastula embryos, no cell walls	mollusks, arthropods, fish, mammals

*Approximate time of appearance in the fossil record, measured in millions of years before present

fungi, animals, and plants. These latter organisms form some fifty natural groups, of which most people have only heard of three or four. Among them are the red and green seaweeds, the brown algae including the giant kelp, the slime molds and water molds, shelled foraminifera, glassy diatoms, ciliates like *Paramecium*, the amebas, and the euglenids.

For the numbers of living species of these kingdoms we have only crude estimates that may be wildly incorrect. Animals, probably because people are good at distinguishing beetles, dominate. Over 10 million—perhaps as many as 30 million—are thought to exist. Some 500,000 plants, 100,000 fungi, and 250,000 protoctists are suggested to be lurking in the woods and waters of this world. As for bacteria, although thousands have been named as species and

no doubt thousands can be distinguished, the species concept doesn't apply. Although bacteria can be grouped on the basis of common features, these groups change so quickly that they are never fixed and recognizable like eukaryote species. Bacteria pass genes back and forth. All can simply reproduce, and thus at any given time have but a single parent. The intervention of sex, the formation of a new bacterium with genes from more than a single source, is a unidirectional affair. The genes pass from a donor individual to a recipient . . . but donors can change to recipients and vice versa in minutes. Furthermore the gene swapping is entirely optional. If a bacterium can survive and grow under conditions in which it finds itself, sex is dispensable at all times. Indeed bacteria are willing and able to "have sex" with naked DNA molecules that they absorb from the water in which they are bathed.

Life originated with bacteria; therefore we can say that the origin of life was concurrent with the origin of bacteria. But we agree with Professor Sorin Sonea and his colleague Lucien Mathieu, of the Université de Montreal, that bacteria do not have species at all (or, which amounts to the same thing, all of them together constitute one single cosmopolitan species). Speciation is a property only of nucleated organisms. It began with the earliest protoctists, long after bacteria had evolved nearly all the important metabolic traits displayed by life on Earth. Thus the origin of species itself was not at all concurrent with the origin of life; rather it occurred long after, in the Proterozoic Eon. Individuality does not come exclusively from diversification and branching evolution, as the neodarwinists would have us believe. It comes equally frequently, if not even more often, from the integration and differentiation of fused beings, once independent, but over time individualized and selected as wholes. This simply is another way of stating our thesis: speciation by (and in the aftermath of) symbiogenesis.

The creative force of symbiosis produced eukaryotic cells from bacteria. Hence all larger organisms—protoctists, fungi, animals,

and plants—originated symbiogenetically. But creation of novelty by symbiosis did not end with the evolution of the earliest nucleated cells. Symbiosis still is everywhere.

Many examples of evolution by symbiosis strike us as remarkably beautiful. Pacific coral reefs such as the Great Barrier of Australia represent associations between modern (scleractinian) coral and dinomastigotes such as *Gymnodinium microadriaticum*. New England lichens, New Guinea ant plants, and even milk cows serve as examples of the power of living fusions. Members of different species, and in the case of cows and corals, even of different kingdoms, under identifiable stresses formed tightly knit communities that became individuals by merger. Details abound that support the concept that all visible organisms, plants, animals, and fungi evolved by “body fusion.” Fusion at the microscopic level led to genetic integration and formation of ever-more complex individuals. The thermodynamic drive toward more complex gradient-reducing systems finds expression in the continual creation of newer, more intricate forms of association between life forms, including symbioses.

STRENGTH IN NUMBERS

Terry Erwin, a professor at the University of Alabama who shakes insects from nets in the Amazon canopy and counts them, tells us that, routinely, two-thirds of the species he finds are new to science. If ten million species of animals are so far documented in the annals of the learned, and if his counts represent the world, he suggests that at least thirty million living animal species must exist. Joseph Leidy, sage of nineteenth-century Philadelphia and one of the founders of that city’s Academy of Natural Science, summarized his philosophy of a good life: “How,” he wrote, “can life be tiresome when there is still another rhizopod to describe?” Whether counted in Leidy’s rhizopods (amebas), Erwin’s beetles, or the thousands of

orchid species of the mountains of Colombia, life’s diversity staggers the imagination. The Linnaean task of classifying all living things is as unfinished in the twenty-first century as in the eighteenth when Mrs. Linnaeus sold her husband’s whole collection to London to pay off his debtors and his daughter’s dowries. His jars, bottles, and dry plant specimens still reside in the basement of the Linnaean Society in Burlington House, just off noisy Picadilly Circus.

The goal to catalogue species of life on the planet remains noble, indeed more noble and useful than in Linnaeus’s times when species were catalogued and classified in a practical way without regard to preservation of planetary biodiversity. He never believed the forms of life reflected an evolutionary history but that all biological abundance and diversity were the works of a good and prodigious deity. His concept of species was of a fixed and unchanging kind, identifiable by visual characteristics. Most of the names he gave to his 10,000 species are in current use. *Panthera leo* is the name he gave to lions and *Felix catus* is what he called our cats. *Malus deliciosus* was how he recorded our apples and *Mytilus edulis* referred to the delicious blue mussels of the Atlantic shore. The first appellation, always capitalized, refers to the larger group or “kind” of life (people, dogs, apples, mussels)—the genus—and the second, the “specific epithet,” indicates the species (wise people, familiar dogs, delicious apples, and edible mussels). As for fungi *Lactarius deliciosus* (delicious milky mushroom) or *Penicillus chrysogenum* (little golden pencil), these of course, since they weren’t animals, were for Linnaeus plants.

Species, in short, were and still are the lowest common denominator. From the days of Linnaeus on, species have been “banked” in the literature: the name, the place of collection, the published description, and its author are publicly deposited in an herbarium or a natural history museum. As familiarity with microscopic life abounded, species proliferated and naming practices grew to include bacteria (as plants, even when they swam) and other unicells

DARWIN REVISITED:
SPECIES IN THE
EVOLUTIONARY
DIALOGUE

*I*n this book we have questioned the adequacy of the popular modern evolutionist explanation of the origins of new, heritable features of life and the evolution of new species and higher, more inclusive taxa. The reliance on accumulation of random mutations in DNA is not so much “wrong” as oversimplified and incomplete: It misses the symbiotic forest for the genetic trees. The neodarwinists’ inventive literature and valiant attempts to nite the genetic stability in the unblended mixture of Gregor Mendel’s factors to the gradual evolutionary change promoted by Darwin’s natural selection were as brilliant as they were incorrect. The hegemony of R. A. Fisher, J. B. S. Haldane, and Sewall Wright is gone forever, and their latter-day saints—Richard Dawkins and J. Maynard Smith, or at least their students—will have to learn something

about chemistry, microbiology, molecular biology, paleontology, and the air. Better-informed scientists have reinstated, in the light of new knowledge, the Darwinian, not neodarwinian, concepts of evolution as the organizing principles for the understanding of life. We suggest that at least some of Jean Baptiste de Lamarck's "acquired characteristics" that sensitively respond to the exigencies of the environment are foreign genomes. Tiny masters of metabolism and movement are often ready and willing to associate with larger forms when environmental pressures encourage togetherness. Evolution's menagerie is far more responsive to immediate environmental forces than the "random mutation" contingent would have us believe. The branches of the evolutionary tree fork, but they also fuse. Genomes integrate; the mergers persist past the point of no return. Evolution is irreversible. Even the evolution of the eye has a symbiotic, as well as a random mutation, component to its history. And like all evolutionary novelty, it must be seen as the several results of protracted biological, geological, and historical paths. Indeed, the evolution of vertebrate organs as complex as eyes has always fascinated everyone concerned with the origin of genuine innovation. How does an eyeless animal "grow an eye"? (Samuel Butler remarked that "We don't remember when we first grew an eye.") Anthropocentric writers with a proclivity for the miraculous and a commitment to divine intervention tend to attribute historical appearances like eyes, wings, and speech to "irreducible complexity" (as, for example, Michael Behe does in his book, *Darwin's Black Box*) or "ingenious design" (in the tradition of William Paley who used the functional organs of animals as proof for the existence of God). Here we feel no need for supernatural hypotheses. Rather, we insist that today, more than ever, it is the growing scientific understanding of how new traits appear, ones even as complex as the vertebrate eye, that has triumphed. What is the news?

The fundamental idea is that inherited characteristics of extraordinary importance to natural selection, such as fruits, eyes, wings, or

speech, always enjoy a long history of precedence. Awareness of the microbial antecedents and eukaryotic genetics and development converts what may seem divine intervention to evolution as usual. The evolutionary appearance of eyes is no exception. The capacity to specifically respond to visible light appears in many molecules common to all cells. The photosensitive ability of the human (and all vertebrate) retinal tissue is a property of the rods and cones of retinal cells. Chemically, these cells harbor rhodopsin, a purplish light-sensitive protein-pigment complex. The opsin portion of rhodopsin is a protein that varies from one organism to another but shares common features and is present in a huge range of animals, some bacteria, and protists. The actual light reactions occur in the second, smaller portion of the molecule: the retinal. The name, "*rhodo*," Greek for purple, refers to the retinal part, and *opsin*, where the "op" is the same as in optician or optical, refers to "eye." Loosely then, the apt name of the active molecule is purple eye protein. The small molecular portion that receives the light directly dates back in the history of life to a time long before animals and plants. Rhodopsin is conspicuously active in the entire group of archaeobacteria called halophils. These salt-loving prokaryotes bathe in sunlight; they use their light-sensitive rhodopsin to generate energy in the form of the ubiquitous molecule ATP. The fundamentals of photosensitivity are already well developed in the bacterial world.

The rods (used mainly for night vision) and cones (mainly for daylight) are elongate membrane-rich cells that line the retina in the eyes of animals. In our own eyes these cells bear the standard 9(3)+0 microtubular kinetosomes that underlay the microtubular shaft, the 9(2)+2 axoneme that we of course have studied in the context of the origin of intracellular motility. The rod is simply a greatly overgrown parallel infolding of the undulipodial (cilia) membrane. The cone is the same, although the folded membranes are in tapered stacks, rather than in parallel stacks, giving the entire cell a cone-like shape. If we concur that the entire undulipodial system derives

from spirochete symbionts then, yes, symbiosis is also a prerequisite to the evolution of the eye. What has been shown by the computer-generated natural selective pattern of Richard Dawkins and extensive study of the literature by Ernst Mayr and his colleagues is that any population of organisms with surface photosensitivity will tend to refine and expand this capacity in the direction of an organ that is protected, that can focus and move and even form an image. According to Mayr, eyes evolved in animal lineages at least forty times. The most conspicuous and best-studied examples are the simple eyes of vertebrates and mollusks (like squid and clams) and the compound eyes of insects. Not included in their list is the evolution of a cameralike eye in two genera of single-celled protists (the erythrocinid dinomastigotes) where the entire cell has become a functional modified eye; indeed *Erythrocinopsis* is entirely analogous to a wide-angle lens camera. The single cell whose plastid and other pigment-coated membranes form the retinal-equivalent sits attached as it waits for its microbial prey to cast a shadow overhead. As in any endeavor that seeks the origin of a complex, and superficially perfect, trait, one needs to study, in Darwin's words, "the oddities and peculiarities" of its antecedents.

The language of evolutionary change is neither mathematics nor computer-generated morphology. Certainly it is not statistics. Rather, natural history, ecology, genetics, and metabolism must be supplemented with accurate knowledge of microbes. Microbial physiology, ecology, and protistology are essential to understand the evolutionary process. The behavior of microbes within their own populations and in their interactions with others determined life's winding, expanding evolutionary course. The living subvisible world ultimately underlies the behavior, development, ecology, and evolution of the much larger world of which we are a part and with which we co-evolved. While some may feel belittled by this perspective of evolution punctuated and driven forward by microbial mergers, we believe, echoing Darwin, that there is grandeur, too, in this view of

life. Numberless forms and variation come not just gradually and at random, but suddenly and forcefully, by the co-opting of strangers, the involvement and infolding of others—viral, bacterial, and eukaryotic—into ever more complex and miscegenous genomes. The acquisition of the reproducing other, of the microbe and its genome, is no mere sideshow. Attraction, merger, fusion, incorporation, cohabitation, recombination—both permanent and cyclical—and other forbidden couplings, are the main sources of Darwin's missing variation. Sensitivity, co-optation, merger, acquisition, fusion, accommodation, perseverance and other capabilities of the microbes are not at all irrelevant to the evolutionary process. Far from it. The incorporation and integration of "foreign" genomes, bacterial and other, led to significant, useful heritable variation. The acquiring of genomes has been central to the evolutionary processes throughout the land and circuitous history of life.

Indeed, as Wallin said in 1927, "It is a rather startling proposal that bacteria, the organisms which are popularly associated with disease, may represent the fundamental causative factor in the origins of species." We agree.