

## FULL HOUSE

ous in the light of this book's central theme: maybe Cope's now more famous law of increasing body size only arises as a noncausal side consequence of Cope's other law of the unspecialized. Major lineages tend to be founded by species of unspecialized anatomy and behavior. Unspecialized species also tend to be small in body size. Cope's Rule of increasing size is therefore an artifact of these small beginnings near a left wall for the founders of major lineages. Cope never made all the connections, but we should record and honor his words:

The "Doctrine of the Unspecialized" . . . describes the fact that the highly developed, or specialized types of one geological period have not been the parents of the types of succeeding periods, but that the descent has been derived from the less specialized of preceding ages. . . . The validity of this law is due to the fact that the specialized types of all periods have been generally incapable of adaptation to the changed conditions which characterized the advent of new periods. . . . Such changes have been often especially severe in their effects on species of large size, which required food in great quantities. . . . Animals of omnivorous food-habits would survive where those which required special foods would die. Species of small size would survive a scarcity of food, while large ones would perish. It is true . . . that the lines of descent of Mammalia have originated or been continued through forms of small size. The same is true of all other Vertebrata.

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### *The Power of the Modal Bacter, or Why the Tail Can't Wag the Dog*

#### An Epitome of the Argument

I believe that the most knowledgeable students of life's history have always sensed the failure of the fossil record to supply the most desired ingredient of Western comfort: a clear signal of progress measured as some form of steadily increasing complexity for life as a whole through time. The basic evidence cannot support such a view, for simple forms still predominate in most environments, as they always have. Faced with this undeniable fact, supporters of progress (that is, nearly all of us throughout the history of evolutionary thought) have shifted criteria and ended up grasping at straws. (The altered criterion may not have struck the graspers as such a thin reed, for one must first internalize the argument of this

book—trends as changes in variation rather than things moving somewhere—to recognize the weakness.) In short, graspers for progress have looked exclusively at the history of the most complex organism through time—a myopic focus on extreme values only—and have used the increasing complexity of the most complex as a false surrogate for progress of the whole (again, see this book's opening example and Figure 1 for a striking case). But this argument is illogical and has always disturbed the most critical consumers.

Thus, James Dwight Dana, America's greatest naturalist in Darwin's era (at least after Agassiz's death), and a soul mate to Darwin in their remarkably parallel careers (both went on long sea voyages in their youth, and both became fascinated with coral reefs and the taxonomy of crustaceans), used this criterion when he finally converted to evolution in the mid-1870s. Dana's primary commitment to progress as the definition of life's organization held firm throughout his career, and in his personal transition from creationism to evolution. But Dana could validate progress only by looking at the history of extremes—"the grand fact that the system of life began in the simple sea-plant and the lower forms of animals, and ended in man" (Dana, 1876, page 593). Julian Huxley, grandson of Thomas Henry, sensed the same unease, but could think of no other criterion in 1959 (as quoted at the beginning of chapter 12). When Darwin's grandson challenged him to defend progress in the light of so many well-adapted but anatomically simplified parasites, Julian Huxley replied, "I mean a higher degree of organization in general, as shown by the upper level attained." But the "upper level attained" (the extreme organism at the right tail) is not a measure of "organization in general"—and Huxley's defense is illogical.

In debunking this conventional argument for progress in the history of life, I reach the crux of this book (although I will not disparage anyone who regards baseball as equal in importance to life's history, and therefore views the correct interpretation of 0.400 hitting as more vital to American life than understanding the central themes of 3.5 billion years in biological time)! Yet I can summarize my argument against progress in the history of life in just seven statements condensed into a few pages. I do not mean to be capricious or disrespectful in this brevity. If I have done my job in the rest of this book, I have already set the background and ar-

gument with sufficient thoroughness—so this focal application at grandest scale should follow quickly with just a few reminders and way stations for the new context.

I do not challenge the statement that the most complex creature has tended to increase in elaboration through time, but I fervently deny that this limited little fact can provide an argument for general progress as a defining thrust of life's history. Such a grandiose claim represents a ludicrous case of the tail wagging the dog, or the invalid elevation of a small and epiphenomenal consequence into a major and controlling cause.

I shall present, in seven arguments, my best sense of a proper case based on the history of expanding variation away from a beginning left wall. I shall then provide extended commentary for three of the statements that are particularly vital, and most generally misunderstood or unappreciated. Please note that the entire sequence of statements for life as a whole follows exactly the same logic, and postulates the same causes, as my previous story (at smallest scale) about the evolution of planktonic forams.

1. *Life's necessary beginning at the left wall.* The earth is about 4.5 billion years old. Life, as recorded in the fossil record, originated at least 3.5 billion years ago, and probably not much earlier because the earth passed through a molten period that ended about 3.8 billion years ago (the age of the oldest rocks). Life presumably began in primeval oceans as a result of sequential chemical reactions based on original constituents of atmospheres and oceans, and regulated by principles of physics for self-organizing systems. (The "primeval soup" has long been a catchword for oceans teeming with appropriate organic compounds prior to the origin of life.) In any case, we may specify as a "left wall" the minimal complexity of life under these conditions of spontaneous origin. (As a paleontologist, I like to think of this wall as the lower limit of "conceivable, preservable complexity" in the fossil record.) For reasons of physics and chemistry, life had to begin right next to the left wall of minimal complexity—as a microscopic blob. You cannot begin by precipitating a lion out of the primeval soup.

2. *Stability throughout time of the initial bacterial mode.* If we are particularly parochial in our concern for multicellular creatures, we place the major division in life between plants and animals (as the Book of Genesis

## FULL HOUSE

does in both creation myths of chapters 1 and 2). If we are more ecumenical, we generally place the division between unicellular and multicellular forms. But most professional biologists would argue that the break of maximal profundity occurs within the unicells, separating the prokaryotes (or cells without organelles—no nuclei, no chromosomes, no mitochondria, no chloroplasts) from the eukaryotes (organisms like amoebae and paramecia, with all the complex parts contained in the cells of multicellular organisms). Prokaryotes include the amazingly diverse groups collectively known as “bacteria,” and also the so-called “blue-green algae,” which are little more than photosynthesizing bacteria, and are now generally known as Cyanobacteria.

All the earliest forms of life in the fossil record are prokaryotes—or, loosely, “bacteria.” In fact, more than half the history of life is a tale of bacteria only. In terms of preservable anatomy in the fossil record, bacteria lie right next to the left wall of minimal conceivable complexity. Life therefore began with a bacterial mode (see Figure 28). Life still maintains a bacterial mode in the same position. So it was in the beginning, is now, and ever shall be—at least until the sun explodes and dooms the planet. How, then, using the proper criterion of variation in life’s full house, can we possibly argue that progress provides a central defining thrust to evolution if complexity’s mode has never changed? (Life’s *mean* complexity may have increased, but see chapter 4 for a discussion of why means are inappropriate, and modes proper, as measures of central tendency in

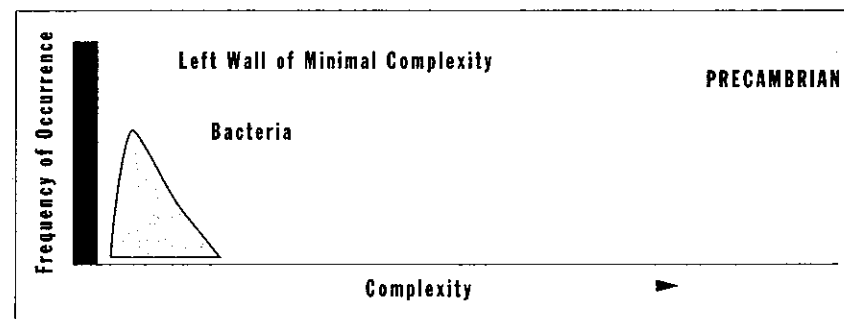


FIGURE 28

Life begins necessarily near the left wall of minimal complexity, and the bacterial mode soon develops.

## The Power of the Modal Bacter

strongly skewed distributions.) The modal bacter of this chapter’s title has been life’s constant paradigm of success.

3. *Life’s successful expansion must form an increasingly right-skewed distribution.* Life had to begin next to the left wall of minimal complexity (see statement 1). As life diversified, only one direction stood open for expansion. Nothing much could move left and fit between the initial bacterial mode and the left wall. The bacterial mode itself has maintained its initial position and grown continually in height (see Figure 29). Since space remains available away from the left wall and toward the direction of greater complexity, new species occasionally wander into this previously unoccupied domain, giving the bell curve of complexity for all species a right skew, with capacity for increased skewing through time.

4. *The myopia of characterizing a full distribution by an extreme item at one tail.* Considering life’s full house of Figure 29, the only conceivable ar-

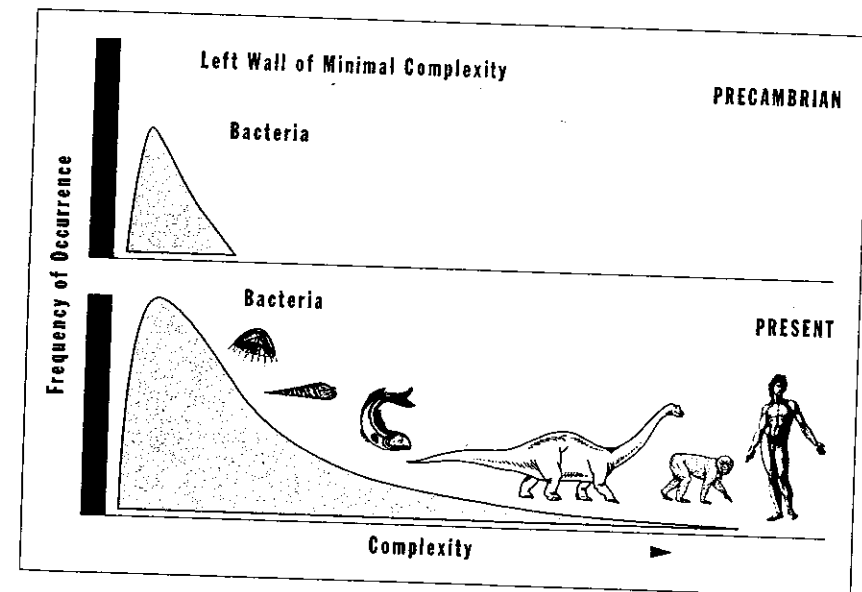


FIGURE 29

The frequency distribution for life’s complexity becomes increasingly right skewed through time, but the bacterial mode never alters.

gument for general progress must postulate that an expanding right tail demonstrates a predictable upward thrust of the whole. But such a claim only embodies the silly spectacle of a small tail wagging a large dog. (We have generally failed to grasp the evident absurdity because we have not visualized the dog properly; rather, in a move that recalls the Cheshire Cat of Wonderland, identified only by its smile, we have characterized the entire dog by its tail alone.)

A claim for general progress based on the right tail alone is absurd for two primary reasons: First, the tail is small and occupied by only a tiny percentage of species (more than 80 percent of multicellular animal species are arthropods, and we generally regard almost all members of this phylum as primitive and nonprogressive). Second, the occupants of the extreme right edge through time do not form an evolutionary sequence, but rather a motley series of disparate forms that have tumbled into this position, one after the other. Such a sequence through time might read: bacterium, eukaryotic cell, marine alga, jellyfish, trilobite, nautiloid, placoderm fish, dinosaur, saber-toothed cat, and *Homo sapiens*. Beyond the first two transitions, not a single form in this sequence can possibly be a direct ancestor of the next in line.

5. *Causality resides at the wall and in the spread of variation; the right tail is a consequence, not a cause.* The development of life's bell curve for complexity through time (Figures 28 and 29) does not represent a fully random phenomenon (though random elements play an important role). Two important causal influences shape the curve and its changes—but neither influence includes any statement about conventional progress. The two major causes are, first, necessary origin at the left wall of minimal complexity; and, second, increase of numbers and kinds, with predictable development of a right-skewed distribution. Given this point of origin at a wall and subsequent increase in variation, the right tail almost had to develop and extend. But this expansion of the right tail—the only (and myopic) source for any potential claim about progress—is an epiphenomenon and a side consequence of the two causes listed above, not a fundamental thrust produced by the superiority of complex forms under natural selection. In fact, as the paradigm of the drunkard's walk illustrates, such an extension of the right tail will occur in a regime of entirely random mo-

tion for each item, so long as the system begins at a wall. Thus, as the drunkard's walk shows in theory, and the evolution of planktonic forams confirms in fact, the expanding right tail of life's complexity may arise from random motion among all lineages. The vaunted progress of life is really *random motion away from simple beginnings, not directed impetus toward inherently advantageous complexity.*

6. *The only promising way to smuggle progress back into such a system is logically possible, but empirically false at high probability.* My argument for the whole system is sound: from a necessary beginning at the left wall, random motion of all items in a growing system will produce an increasingly right-skewed distribution. Thus, and with powerful irony, the most venerable evidence for general progress—the increasing complexity of the most complex—becomes a passive consequence of growth in a system with no directional bias whatever in the motion of its components.

But one potential (though much vitiated) argument for general progress remains. The entire system is free to vary only in the direction of greater complexity from an initial position next to the left wall. But what about a smaller lineage that begins at some intermediary position with freedom to expand in *either* direction (the first living thing starts at the left wall, but the first mammal, or the first seed plant, or the first clam, begins in the middle and its descendants can move toward either tail). If we studied all the smaller lineages free to vary in any direction, perhaps we would then detect a clear bias for net movement to the right, or toward greater complexity. If we found such a bias, we could legitimately speak of a general trend to greater complexity in the evolutionary history of lineages. (This more subtle position would still not explain the general pattern of Figure 29, which would still arise as a consequence of random motion in a growing system constrained to begin at the left wall. But a rightward bias in individual lineages would function as a "booster" or "helpmate" in the general production of right skew. The entire system would then be built by two components: random motion from the left wall, and a rightward bias in individual lineages—and the second component would provide an argument for general progress.)

The logic of this argument is sound, but two strong reasons suggest (though not all the evidence is yet in) that the proposition is empirically

false. (I shall summarize the two reasons here and provide more details later in this chapter.) First, while I know of no proven bias for rightward motion under natural selection—a mechanism that yields only local adaptation to changing environments, not general progress—a good case can be made for leftward bias because parasitism is such a common evolutionary strategy, and parasites tend to be anatomically more simplified than their free-living ancestors. (Ironically, then, the full system of increasing right skew for the whole might actually be built with a slight bias toward *decreased* complexity in individual lineages!) Second, several paleontologists are now studying this issue directly by trying to quantify the elusive notion of progress and then tracing the changing spread of their measure in the history of individual lineages. Only a few studies have been completed so far, but current results show no rightward bias, and therefore no tendency to progress in individual lineages.

7. *Even a parochial decision to focus on the right tail alone will not yield the one, most truly desired conclusion, the psychological impetus to our yearning for general progress—that is, the predictable and sensible evolution to domination of a creature like us, endowed with consciousness.* We might adopt a position of substantial retreat from an original claim for general progress, but still a bastion of defense for what really matters to us. That is, we might say, “Okay, you win. I understand your point that the evidence of supposed progress, the increasing right skew of life’s bell curve, is only an epiphenomenal tail that cannot wag the entire dog—and that life’s full house has never moved from its modal position. But I am allowed to be parochial. The right tail may be small and epiphenomenal, but I love the right tail because I dwell at its end—and I want to focus on the right tail alone because this little epiphenomenon is all that matters to me. Even you admit that the right tail had to arise, so long as life expanded. So the right tail had to develop and grow—and had to produce, at its apogee, something like me. I therefore remain the modern equivalent of the apple of God’s eye: the predictably most complex creature that ever lived.”

Wrong again, even for this pitifully restricted claim (after advancing an initial argument for intrinsic directionality in the basic causal thrust of all evolution). The right tail had to exist, but the actual composition of creatures on the tail is utterly unpredictable, partly random, and entirely con-

tingent—not at all foreordained by the mechanisms of evolution. If we could replay the game of life again and again, always starting at the left wall and expanding thereafter in diversity, we would get a right tail almost every time, but the inhabitants of this region of greatest complexity would be wildly and unpredictably different in each rendition—and the vast majority of replays would never produce (on the finite scale of a planet’s lifetime) a creature with self-consciousness. Humans are here by the luck of the draw, not the inevitability of life’s direction or evolution’s mechanism.

In any case, little tails, no tails, or whoever occupies the tails, the outstanding feature of life’s history has been the stability of its bacterial mode over billions of years!

#### **The Multifariousness of the Modal Bacter**

My interest in paleontology began in a childhood fascination with dinosaurs. I spent a substantial part of my youth reading the modest literature then available for children on the history of life. I well remember the invariant scheme used to divide the fossil record into a series of “ages” representing the progress that supposedly marked the march of evolution: the “Age of Invertebrates,” followed by the Age of Fishes, Reptiles, Mammals, and, finally, with all the parochiality of the engendered language then current, the “Age of Man.”

I have watched various reforms in this system during the past forty years (though see chapter 2, for persisting use of the old scheme). The language police, of course, would never allow an Age of Man anymore, so we could, at best and with more inclusive generosity, now specify an “age of humans” or an “age of self-consciousness.” But we have also come to recognize, with even further inclusive generosity, that one species of mammals, despite our unbounded success, cannot speak adequately for the whole. Some enlightened folks have even recognized that an “age of mammals” doesn’t specify sufficient equity—especially since mammals form a small group of some four thousand species, while nearly a million species of multicellular animals have been formally named. Since more than 80



percent of these million are arthropods, and since the great majority of arthropods are insects, these same enlightened people tend to label modern times as the "age of arthropods."

Fair enough, if we wish to honor multicellular creatures—but we are still not free of the parochialism of our scale. If we must characterize a whole by a representative part, we certainly should honor life's constant mode. We live now in the "Age of Bacteria." Our planet has always been in the "Age of Bacteria," ever since the first fossils—bacteria, of course—were entombed in rocks more than three and a half billion years ago.

On any possible, reasonable, or fair criterion, bacteria are—and always have been—the dominant forms of life on earth. Our failure to grasp this most evident of biological facts arises in part from the blindness of our arrogance, but also, in large measure, as an effect of scale. We are so accustomed to viewing phenomena of our scale—sizes measured in feet and ages in decades—as typical of nature. Individual bacteria lie beneath our vision and may live no longer than the time I take to eat lunch, or my grandfather spent with his evening cigar. But then, who knows? To a bacterium, human bodies might appear as widely dispersed, effectively eternal (or at least geological), massive mountains, fit for all forms of exploitation, and fraught with little danger unless a bolus of imported penicillin strikes at some of the nasty brethren.

Consider just some of the criteria for bacterial domination:

**TIME.** I have already mentioned the persistence of bacterial rule. The fossil record of life begins with bacteria, some 3.5 to 3.6 billion years ago. About half the history of life later, the more elaborate eukaryotic cell makes a first appearance in the fossil record—about 1.8 to 1.9 billion years ago by best current evidence. The first multicellular creatures—marine algae—enter the stage soon afterward, but these organisms bear no genealogical relationship to our primary (if admittedly parochial) interest in this book: the history of animal life. The first multicellular animals do not enter the fossil record until about 580 million years ago—that is, after about five-sixths of life's history had already passed. Bacteria have been the stayers and keepers of life's history.

Moreover, bacteria do not record their history of Precambrian domination as invisible dots in rocks. Rather, they shaped their environments, and left their sedimentary records, in highly visible form—even though

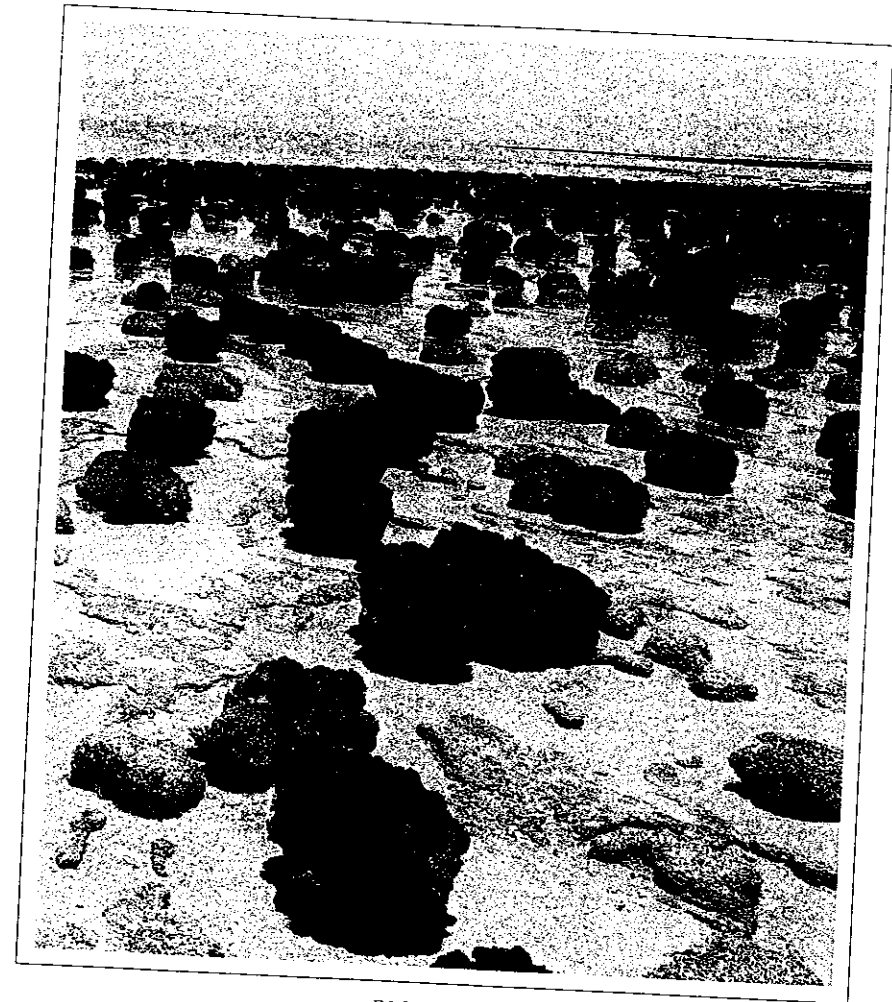


FIGURE 30

Modern stromatolites—layers of sediment trapped and bound by prokaryotic cells.

no multicellular animals then lived to view the effect. The fossil record of ancient bacteria consists largely of stromatolites—complexly concentric and laminated layers, often looking like a head of cabbage in cross-section (see Figure 30). These sizable structures are not bacteria themselves, but layers of sediments trapped and bound by mats of bacterial cells. Most stromatolites formed near the tide lines, and were constantly desiccated and regrown during fluctuations in sea level—thus leading to large, vertical

piles of wavy layers. Stromatolites still exist, but now can form only in unusual environments devoid of the multicellular animals that happily feed on such organisms and therefore prevent their formation in most places. But no potential feeders lived in these early years, during most of life's history, and stromatolites must have covered appropriate habitats throughout the planet.

**INDESTRUCTIBILITY.** Let us make a quick bow to the flip side of such long domination—to the future prospects that match such a distinguished and persistent past. Bacteria have occupied life's mode from the very beginning, and I cannot imagine a change of status, even under any conceivable new regime that human ingenuity might someday impose upon our planet. Bacteria exist in such overwhelming number, and such unparalleled variety; they live in such a wide range of environments, and work in so many unmatched modes of metabolism. Our shenanigans, nuclear and otherwise, might easily lead to our own destruction in the foreseeable future. We might take most of the large terrestrial vertebrates with us—a few thousand species at most. We surely cannot extirpate 500,000 species of beetles, though we might make a significant dent. I doubt that we could ever substantially touch bacterial diversity. The modal organisms cannot be nuked into oblivion, or very much affected by any of our considerable conceivable malfeasances.

**TAXONOMY.** The history of classification for the basic groups of life is one long tale of decreasing parochialism and growing recognition of the diversity and importance of single-celled organisms, and other "lower" creatures. Most of Western history favored the biblically sanctioned twofold division of organisms into plants and animals (with a third realm for all inorganic substances—leading to the old taxonomy of "animal, vegetable, or mineral" in such venerable games as Twenty Questions). This twofold division produced a host of practical consequences, including the separation of biological research into two academic departments and traditions of study: zoology and botany. Under this system, all single-celled organisms had to fall into one camp or the other, however uncomfortably, and however tight the shove of the shoehorn. Thus, paramecia and amoebae became animals because they move and ingest food. Photosynthesizing unicells, of course, became plants. But what about photosynthesizers with mobility? And, above all, what about the prokaryotic bacteria, which

bear no key feature suggesting either allocation? But since bacteria have a strong cell wall, and because many species are photosynthetic, bacteria fell into the domain of botany. To this day, we still talk about the bacterial "flora" of our guts.

By the time I entered high school in the mid-1950s, expansion and enlightenment had proceeded far enough to acknowledge that unicells could not be so divided by criteria of the multicellular world, and that single-celled organisms probably deserved a separate kingdom of their own, usually called Protista.

Twelve years later, as I left graduate school, even greater respect for the unicells had led to further proliferation at the "lower" end. A "five kingdom" system was now all the rage (and has since become canonical in textbooks)—with the three multicellular kingdoms of plants, fungi, and animals in a top layer (representing, loosely, production, decomposition, and ingestion as basic modes of life); the eukaryotic unicells, or Kingdom Protista, in a middle layer; and the prokaryotic unicells, or Kingdom Monera, representing bacteria and "blue-green algae," on a bottom rung. Most proponents of this system recognized the gap between prokaryotic and eukaryotic organization—that is, the transition from Monera to Protista—as the fundamental division within life, thus finally granting bacteria their measure of independent respect, if only as a bottom tier.

A decade later, starting in the mid-1970s, development of techniques for sequencing the genetic code finally gave us a key for mapping evolutionary relationships among bacterial lineages. (We know how to use anatomy for drawing genealogical trees of multicellular creatures more familiar to us—so we employ the internal skeleton of vertebrates, the external carapace of arthropods, and the multiplated test and radial symmetry of echinoderms to identify major evolutionary groups. But we are so ignorant of the bacterial world that we couldn't identify proper genealogical divisions—and we therefore tended to dump all bacteria together into a bag of little unicellular blobs, rods, and spirals. Yet we should have suspected deep divisions, far more extensive than those separating lines of multicellular animals—if only because bacteria have inhabited the planet for so long.)

As nucleotide sequences began to accumulate for key segments of bacterial genomes, a fascinating and unsuspected pattern emerged—and

has grown ever stronger with passing years and further accumulation of evidence. This group of supposed primitives, once shoved into one small bag for their limited range of overt anatomical diversity, actually includes two great divisions, each far larger in scope (in terms of genomic distinction and variety) than all three multicellular kingdoms (plants, animals, and fungi) combined! Moreover, one of these divisions seemed to gather together, into one grand sibship, most of the bacteria living in odd environments and working by peculiar metabolisms under extreme conditions (often in the absence of oxygen) that may have flourished early in the earth's history—the methanogens, or methane producers; the tolerators of high salinities, the halophiles; and the thrivers at temperatures around the boiling point of water, the thermophiles.

These first accurate genealogical maps led to the apparently inescapable conclusion that two grand kingdoms, or domains, must be recognized within the old kingdom Monera—Bacteria for most conventional forms that come to mind when we contemplate this category (the photosynthesizing blue-greens, the gut bacteria, the organisms that cause human diseases and therefore become “germs” in our vernacular); and Archaea for the newly recognized coherence of oddballs. By contrast, all eukaryotic organisms, the three multicellular kingdoms as well as all unicellular eukaryotes, belong to a third great evolutionary domain, the Eucarya.

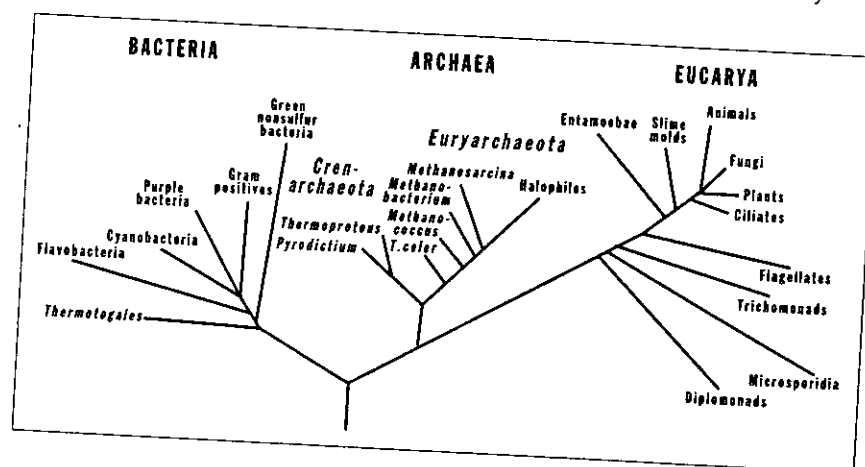


FIGURE 31

Life's evolutionary tree, showing two prokaryotic domains and only one eukaryotic domain, with plants, animals, and fungi as small twigs at an extreme of the eukaryotic domain.

### *The Power of the Modal Bacter*

The accompanying chart (Figure 31), from the work of Carl Woese, our greatest pioneer in this new constitution of life, says it all, with the maximally stunning device of a revolutionary picture. We now have a system of three grand evolutionary domains—Bacteria, Archaea, and Eucarya—and two of the three consist entirely of prokaryotes: that is, “bacteria” in the vernacular, the inhabitants of life's constant mode. Once we place two-thirds of evolutionary diversity at life's mode, we have much less trouble grasping the centrality of this location, and the constant domination of life by bacteria. For example, the domain of Bacteria, as presently defined, contains eleven major subdivisions, and the genetic distance between any pair is at least equal to the average separation between eukaryotic kingdoms such as plants and animals (Fuhrman, McCallum, and Davis, 1992).

Note, by contrast and in closing, the restricted domain of all three multicellular kingdoms. On this genealogical chart for all life, the three multicellular kingdoms form three little twigs on the bush of just one among three grand domains of life. Quite a change in one generation—from my parents' learning that everything living must be animal or vegetable, to the icon of my mature years: the kingdoms Animalia and Plantae as two little twigs amid a plethora of other branches on one of three bushes—with both other bushes growing bacteria, and only bacteria, all over.

UBIQUITY. The taxonomic criterion (Figure 31), while impressive, does not guarantee bacterial domination—and for a definite reason common to all genealogical schemes. Bacteria form the root of life's entire tree. For the first 2 billion years or so, about half of life's full history, bacteria alone built the tree of life. Therefore all multicellular creatures, as late arrivals, can only inhabit some topmost branches; the roots and trunk must be exclusively bacterial. This geometry does not make the case for calling our modern world an “Age of Bacteria” because the roots and trunk might now be atrophied, with only the multicellular branches flourishing. We need to show not only that bacteria build most of life's tree, but also that these bacterial foundations remain strong, healthy, vigorous, and fully supportive of the minor superstructure called multicellular life. Bacteria, indeed, have retained their predominant position, and hold sway not only by virtue of a long and illustrious history, but also for abundant reasons of contemporary vigor. Consider two aspects of ubiquity:



1. *Numbers.* Bacteria inhabit effectively every place suitable for the existence of life. Mother told you, after all, that bacterial "germs" require constant vigilance to combat their ubiquity in every breath and every mouthful—and the vast majority of bacteria are benign or irrelevant to us, not harmful agents of disease. One fact will suffice: during the course of life, the number of *E. coli* in the gut of each human being far exceeds the total number of people that now live and have ever inhabited the earth. (And *E. coli* is only one species in the normal gut "flora" of all humans.)

Numerical estimates, admittedly imprecise, are a stock in trade of all popular writing on bacteria. The *Encyclopaedia Britannica* tells us that bacteria live by "billions in a gram of rich garden soil and millions in one drop of saliva." Sagan and Margulis (1988, page 4) write that "human skin harbors some 100,000 microbes per square centimeter" ("microbes" includes nonbacterial unicells, but the overwhelming majority of "microbes" are bacteria); and that "one spoonful of high quality soil contains about 10 trillion bacteria." I was particularly impressed with this statement about our colonial status (Margulis and Sagan, 1986): "Fully ten percent of our own dry body weight consists of bacteria, some of which, although they are not a congenital part of our bodies, we can't live without."

2. *Places.* Since the temperature tolerance and metabolic ranges of bacteria so far exceed the scope of all other organisms, bacteria live in all habitats accessible to any form of life, while the edges of life's toleration are almost exclusively bacterial—from the coldest puddles on glaciers, to the hot springs of Yellowstone Park, to oceanic vents where water issues from the earth's interior at 480°F (still below the boiling point at the high pressures of oceanic bottoms). At temperatures greater than 160°F, all life is bacterial. I shall say more in the following pages about new information on bacteria of the open oceans and the earth's interior, but even conventional data from terrestrial environments prove the point. *Thermophila acidophilum* thrives at 140°F, and at a pH of 1 or 2, the acidity of concentrated sulfuric acid. This species, found on the surface of burning coals, and in the hot springs of Yellowstone Park, freezes to death below 100°F.

UTILITY. Importance for human life forms the most parochial of cri-

### The Power of the Modal Bacter

teria for assessing the role of any organism in the history and constitution of life—though the conventional case for bacteria proceeds largely in this mode. I will therefore expand a bit toward utility (or at least "intrinsicness") for all of life, and even for the earth.

1. *Historical.* Oxygen, the most essential constituent of the atmosphere for human needs, now maintains itself primarily through release by multicellular plants in the process of photosynthesis. The earth's original atmosphere apparently contained little or no free oxygen, and this otherwise unlikely element both arose historically, and is now maintained, by the action of organisms. Plants may provide the major input today, but oxygen started to accumulate in the atmosphere about 2 billion years ago, substantially before the evolution of multicellular plant life. Bacterial photosynthesis supplied the atmosphere's original oxygen (and, in concert with multicellular plants, continues to act as a major source of resupply today).

But even if plants release most of today's oxygen, the source of resupply remains, ultimately and evolutionarily, bacterial. The photosynthetic organelle of the eukaryotic cell—the chloroplast—is, by ancestry, a photosynthesizing bacterium. According to an elegant and persuasive notion—the endosymbiotic theory for the origin of the eukaryotic cell—several organelles of eukaryotes arose by greater coordination and integration of an original symbiotic assemblage of prokaryotic cells. In this sense, the eukaryotic cell began as a colony, and each unit of our own body can be traced to such a cooperative beginning.

The case has been made persuasively only for the mitochondrion—the "energy factory" of all cells—and the chloroplast—the photosynthetic organelle—though some proponents extend the argument more generally to cilia (seen as descendants of spirochete bacteria) and other parts of cells. The evidence seems entirely convincing for mitochondria and chloroplasts: both are about the same size as bacteria (prokaryotes are substantially smaller than eukaryotes, so several bacterial cells easily fit inside a eukaryote); they look and function like bacteria; they have their own DNA programs (small because most genetic material has, through evolutionary time, been transferred to the nucleus)—all indicating ancestral status as independent organisms. Thus, even today, atmospheric oxygen is a bac-

terial product—released either directly by bacterial photosynthesis, or by bacterial descendants in eukaryotic cells.

Bacterial symbiosis—with bacteria remaining as coherent creatures, taxonomically independent if ecologically dependent, and not fully incorporated like mitochondria and chloroplasts—is a vital and potent phenomenon in many of life's central processes and balances. We could not digest and absorb food properly without our gut "flora." Grazing animals, cattle and their relatives, depend upon bacteria in their complex, quadripartite stomachs to digest grasses in the process of rumination. About 30 percent of atmospheric methane can be traced to the action of methanogenic bacteria in the guts of ruminants, largely released into the atmosphere—how else to say it—by belches and farts. (The most cultured and distinguished British ecologist, G. Evelyn Hutchinson, once published a famous calculation on the substantial contributions to atmospheric methane made by the flatulence of domestic cattle. Sagan and Margulis [1988, page 113] advance the "semiserious suggestion that the primary function served by large mammals is the equitable distribution of methane gas throughout the biosphere.")

In another symbiosis essential to human agriculture, plants need nitrogen as an essential soil nutrient, but cannot use the ubiquitous free nitrogen of our atmosphere. This nitrogen is "fixed," or chemically converted into usable form, by the action of bacteria like *Rhizobium*, living symbiotically in bulbous growths on the roots of leguminous plants.

Some symbioses are eerie in their complexity and almost gory precision. Nealson (1991) documents the story of a nematode (a tiny roundworm) parasitic upon insects and potentially useful as a biological control upon pests. The nematode enters the insect's mouth, anus, or spiracle (breathing organ) and migrates into the hemocoel (or blood cavity). There the nematode ejects millions of bacterial symbionts from its own intestine into the insect's circulatory system. These bacteria, though harmless to the nematode, kill the insect within hours. (Bacteria need the nematode to feast upon the insect because bacteria entering by themselves never reach the hemocoel and therefore do not attack the insect.) The dead insect becomes bioluminescent (another consequence of bacterial action) and darkly pigmented, but does not putrefy (perhaps because the nematode also releases antibiotics that kill other bacteria but leave their own symbionts harmless).

The pigment and glow then attract other nematodes to the insectan feast. The nematodes grow and reproduce by eating the insect; they also take on the helpful bacteria as symbionts. This source can yield up to 500,000 nematodes per gram of infected insects.

The recent discovery of the remarkable deep-sea "vent faunas," at zones of effusion for hot, mineral-laden waters from the earth's interior to the ocean floor, has provided another striking case of bacterial necessity and symbiosis. An old saw of biological pedagogy (I well remember the phrase emblazoned on the chapter heading of my junior high school textbook) proclaims, "All energy for biological processes comes ultimately from the sun." (I remember the pains that teachers took to trace even the most indirect pathways to a solar source—worms on the sea bottom eating decomposed bodies of fishes, which had fed on other fishes in shallow waters, with the little fishes eating shrimp, shrimp eating copepods, copepods ingesting algal cells, and algal cells growing by photosynthesis from that ultimate solar source.)

The vent faunas provide the first exception to this venerable rule, for their ultimate source of energy comes from the heat of the earth's interior (which warms the emerging waters, contributes to the solubility of minerals, and so on). Bacteria form the base of this unique and independent food chain—mostly sulfur-oxidizing forms that can convert the minerals of emerging waters into metabolically useful form. Some rift organisms form amazing symbiotic associations with these bacteria. The largest animal of this fauna, the vestimentiferan worm *Riftia pachyptila*, grows to several feet in length, but has no mouth, gut, or anus. This creature is so morphologically simplified that taxonomists have still not been able to determine its zoological affinity with confidence (current opinion favors a status within a small group of marine worms, the phylum Pogonophora). *Riftia* does contain a large and highly vascularized organ called the trophosome, filled with specialized cells (bacteriocytes) that house the symbiotic sulfur bacteria. Up to 35 percent of the trophosome's weight consists of these bacteria (Vetter, 1991).

2. *Current.* As discussed above, bacteria produced our atmospheric oxygen, fix nitrogen in our soil, facilitate the rumination of grazing animals, and build the food web of the only nonsolar ecosystem on our planet. We

## FULL HOUSE

could also compile a long list of more parochial uses for particularly human needs and pleasures: the degradation of sewage to nutrients suitable for plant growth; the possible dispersion of oceanic oil spills; the production of cheeses, buttermilk, and yogurt by fermentation (we make most alcoholic drinks by fermentation of eukaryotic yeasts); the bacterial production of vinegar from alcohol, and of MSG from sugars.

More generally, bacteria (along with fungi) are the main reducers of dead organic matter, and thus act as one of the two major links in the fundamental ecological cycle of production (plant photosynthesis and, come to think of it, bacterial photosynthesis as well) and reduction to useful form for renewed production. (The ingesting animals are just a little blip upon this basic cycle; the biosphere could do very well without them.) Sagan and Margulis write in conclusion (1988, pages 4–5):

All of the elements crucial to global life—oxygen, nitrogen, phosphorus, sulfur, carbon—return to a usable form through the intervention of microbes. . . . Ecology is based on the restorative decomposition of microbes and molds, acting on plants and animals after they have died to return their valuable chemical nutrients to the total living system of life on earth.

NEW DATA ON BACTERIAL BIOMASS. This range of bacterial habitation and necessary activity certainly makes a good case for domination of life by the modal bacter. But one claim, formerly regarded as wildly improbable but now quite plausible, if still unproven, would really clinch the argument. We may grant bacteria all the above, but surely the main weight of life rests upon eukaryotes, particularly upon the wood of our forests. Another truism in biology has long proclaimed that the highest percentage of the earth's biomass—pure weight of organically produced matter—must lie in the wood of plants. Bacteria may be ubiquitous and present in nearly uncountable numbers, but they are awfully light, and you need several gazillion to equal the weight of even a small tree. So how could bacterial biomass even come close to that of the displacing and superseding eukaryotes? But new discoveries in the open oceans and the earth's inte-

## *The Power of the Modal Bacter*

rior have now made a plausible case for bacterial domination in biomass as well.

As Ariel, in *The Tempest*, proclaimed his ubiquity in all manifestations of life—"where the bee sucks, there suck I / In a cowslip's bell I lie"—so, in this world, do bacteria dwell in virtually every spot that can sustain any form of life. And we have underestimated their global number because we, as members of a kingdom far more restricted in potential habitation, never appreciated the full range of places that might be searched.

For example, the ubiquity and role of bacteria in the open oceans have been documented only in the past twenty years. Conventional methods of analysis missed up to 99 percent of these organisms (Fuhrman, McCallum, and Davis, 1992) because we could identify only what could be cultured from a water sample—and most species don't grow on most culture media. Now, with methods of genomic sequencing and other techniques, we can assess taxonomic diversity without growing a large, pure culture of each species.

Scientists had long known that the photosynthesizing Cyanobacteria ("blue-green algae" of older terminology) played a prominent role in the oceanic plankton, but the great abundance of heterotrophic bacteria (non-photosynthesizers that ingest nutrients from external sources) had not been appreciated. In coastal waters, these heterotrophs constitute from 5 to 20 percent of microbial biomass and can consume an amount of carbon equal to 20 to 60 percent of total "primary production" (that is, organic material made by photosynthesis)—giving them a major role near the base of oceanic food chains. But Jed A. Fuhrman and his colleagues then studied the biomass of heterotrophic bacteria in open oceans (that is, needless to say, by far the largest habitat on earth by area) and found that they dominate in these environments. In the Sargasso Sea, for example (Fuhrman et al., 1989), heterotrophic bacteria contribute 70 to 80 percent of microbial carbon and nitrogen, and form more than 90 percent of biological surface area.

When I visited Jed Fuhrman's lab at the University of Southern California, I asked him if he could estimate the earth's total bacterial biomass relative to contributions from the other kingdoms of life. These "back of the envelope" calculations have a long and honorable history in biological

barroom discussions—and no one would want to grant them any more technical or firmer status. They must, of necessity, be based on a large number of assumptions and “best estimates” that may be wildly wrong for lack of better available data (average number of bacteria per milliliter of sea water for all the world’s oceans, for example). Still, such calculations serve a useful function in defining ballparks. Fuhrman made his best estimate for me, and came up with an oceanic bacterial biomass equal to about one-fiftieth of the entire terrestrial biota, including wood. This may not sound impressive, but whenever such a calculation gets you within an “order of magnitude” or two of a key number, then you are “in the same ballpark.” (An order of magnitude—the standard measure of comparison for such rough calculations—is a multiple of ten. Thus, 1/50 is between one [1/10] and two [1/100] orders of magnitude from the terrestrial figure—and definitely in the same ballpark.) This figure is even more impressive when you realize (1) that all traditional estimates have granted domination to the multicells by orders of magnitude because the biomass of wood must be so high; (2) that Fuhrman has not included terrestrial bacteria of soil, gut floras, nodules of leguminous plants, etc.; and (3) that an even greater potential source of biomass from a “new” environment—the earth’s interior—has been similarly excluded. If we then turn to some stunning, and controversial, data on the earth’s interior, we may really be in for a surprise.

I shall present this new information by snippets in chronological order—a good way to mark successive claims for “internal” bacteria: first around deep sea vents, then in oil reservoirs, and finally in ordinary interior rocks, a finding that, at one extreme of interpretation, makes our surficial biota puny and exceptional, and suggests that interior bacterial biotas may be life’s standard and universal mode.

In the late 1970s, marine biologists discovered the bacterial basis of food chains for deep-sea vent faunas—and the unique dependence of this community upon energy from the earth’s interior, rather than from a solar source (as discussed on page 185). Two kinds of vents had been described: cracks and small fissures with warm water emerging at temperatures of 40° to 70°F; and large conical sulfide mounds, up to thirty feet in height, and spouting superheated waters at temperatures that can exceed 600°F. Bacteria had been identified in waters from small fissures of

### *The Power of the Modal Bacter*

the first category, but, unsurprisingly, they “had previously not been thought to exist in the superheated waters associated with sulfide chimneys” (Baross et al., 1982, page 366).

But, in the early 1980s, John Baross and his colleagues discovered a bacterial biota, including both oxidative and anaerobic species, in superheated waters emanating from the sulfide mounds (also known as “smokers”). They cultured bacteria from waters collected at 650°F and then grew vigorous communities in a laboratory chamber with waters heated to 480°F at a pressure of 265 atmospheres. Thus, bacteria can (and do) live in high temperatures (and pressures) of waters flowing beneath the earth’s surface (Baross et al., 1982; Baross and Deming, 1983).

Writing about this work in a commentary for *Nature*, Britain’s leading journal of professional science, A. E. Walsby (1983) commented, “I must admit that my first reaction on reading the manuscript of Baross and Deming, arriving as it did on the eve of April Fool’s day, was one of incredulity.” Walsby began his comment by noting that these deep-sea bacteria grow at a heat exceeding the title of Ray Bradbury’s famous story, *Fahrenheit 451*—the temperature at which paper ignites (and thought can therefore be more easily controlled by destruction of radical literature). Pressure is the key to an otherwise paradoxical situation. Life needs liquidity, not necessarily coolness. At the enormous pressures of the sea floor, water does not boil at temperatures tolerated by these bacteria. Baross and Deming end their article, prophetically as we shall see, by noting (1983, page 425):

These results substantiate the hypothesis that microbial growth is limited not by temperature but by the existence of liquid water, assuming that all other conditions necessary for life are provided. This greatly increases the number of environments and conditions both on Earth and elsewhere in the Universe where life can exist.

Then, in the early 1990s, several groups of scientists found and cultured bacteria from oil drillings and other environments beneath oceans and continents—thus indicating that bacteria may live generally in the earth’s interior, and not only in limited areas where superheated waters

## FULL HOUSE

emerge at the surface: from four oil reservoirs nearly two miles below the bed of the North Sea and below the permafrost surface of Alaska's North Slope (Stetter et al., 1993); from a Swedish borehole nearly four miles deep (Szewzyk et al., 1994); and from four wells about a mile deep in France's East Paris Basin (L'Haridon et al., 1995). Water migrates extensively through cracks and joints in subsurface rocks, and even through pore spaces between grains of sediments themselves (an important property of rocks, known as "porosity" and vital to the oil industry as a natural mechanism for concentrating underground liquids—and, as it now appears, bacteria as well). Thus, although such data do not indicate global pervasiveness or interconnectivity of subsurface bacterial biotas, we certainly must entertain the proposition that much of the earth deep beneath our feet teems with microbial life.

The most obvious and serious caution in these data emerges from another general property of bacteria: their almost ineradicable ubiquity. How do we know that these bacteria, cultured from waters collected at depth, really live in these underground environments? Perhaps they were introduced into deeper waters by the machinery used to dig the oil wells and boreholes that provided sites for sampling; perhaps (with even more trepidation) they just represent contamination from ubiquitous and ordinary bacteria of our surface environments, stubbornly living in laboratories despite all attempts to carry out experiments in sterile conditions. (A fascinating, and very long, book could be written about remarkable claims for bacteria in odd places—on meteorites, living in geological dormancy within 400-million-year-old salt deposits—that turned out to be ordinary surface contaminants. I well remember the first "proven" extraterrestrial life on meteorites, later exposed as ordinary ragweed pollen. Ah-choo!)

This well-known possibility sends shivers down the spine of any scientist working in this area. I am no expert and cannot make any general statement. I would not doubt (and neither do the authors of these articles) that some reports may be based on contamination. But all known and possible precautions have been taken, and best procedures for assuring sterility have been followed. Most persuasively, many of the bacteria isolated from these deep environments are anaerobic hyperthermophiles (jargon for bacteria growing at very high temperatures in the absence of oxygen) that could thrive in subterranean conditions, and cannot be laboratory con-

## *The Power of the Modal Bacter*

taminants because they die in ordinary surface environments of "low" temperature and pressure and abundant oxygen.

Writing in *The New York Times* on December 28, 1993, William J. Broad summarized the case nicely:

Some scientists say the microbes may be ubiquitous throughout the upper few miles of the Earth's crust, inhabiting fluid-filled pores, cracks, and interstices of rocks while living off the Earth's interior heat and chemicals. Their main habitats would be in the hot aquifers beneath the continents and in oceanic abysses, fed perpetually by the nutrients carried by the slow circulation of fluids like oil and deep ground water.

We might ask one further question that would clinch the case for underground ubiquity: Moving away from the specialized environments of deep-sea vents and oil reservoirs, do bacteria also live more generally in ordinary rocks and sediments (provided that some water seeps through joints and pore spaces)? New data from the mid-1990s seem to answer this most general question in the affirmative as well.

R. J. Parkes et al. (1994) found abundant bacteria in ordinary sediments of five Pacific Ocean sites at depths up to 1,800 feet. Meanwhile, the United States Department of Energy, under the leadership of Frank J. Wobber, had been digging deep wells to monitor contamination of groundwater from both inorganic and potentially microbial sources (done largely to learn if bacteria might affect the storage of nuclear wastes in deep repositories!). Wobber's group, taking special pains to avoid the risk of contamination from surface bacteria introduced into the holes, found bacterial populations in at least six sites, including a boring in Virginia at 9,180 feet under the ground!

William J. Broad wrote another article for the *Times* (October 4, 1994), this time even more excited, and justifiably so:

Fiction writers have fantasized about it. Prominent scientists have theorized about it. Experimentalists have delved into it. Skeptics have ridiculed it. But for decades,



nobody has had substantial evidence one way or another on the question of whether the depths of the rocky earth harbor anything that could be considered part of the spectacle of life—until now. . . . Swarms of microbial life thrive deep within the planet.

Stevens and McKinley (1995) then described rich bacterial communities living more than three thousand feet below the earth's surface in rocks of the Columbia River Basalt in the northwestern United States. These bacteria are anaerobic and seem to get energy from hydrogen produced in a reaction between minerals in the basaltic rocks and groundwater seeping through. Thus, like the biotas of the deep-sea vents, these bacteria live on energy from the earth's interior, entirely independent of the photosynthetic, and ultimately solar, base of all conventional ecosystems. To confirm their findings in the field, Stevens and McKinley mixed crushed basalt with water free from dissolved oxygen. This mixture did generate hydrogen. They then sealed basalt together with groundwaters containing the deep bacteria. In these laboratory conditions, simulating the natural situation at depth, the bacteria thrived for up to a year.

Following a scientific tradition for constructing humorous and memorable acronyms, Stevens and McKinley have named these deep bacterial floras, independent of solar energy, and cut off from contact with surficial communities, SLiME (for subsurface lithoautotrophic microbial ecosystem—the second word is just a fancy way of saying “getting energy from rocks alone”). Jocelyn Kaiser (1995), writing a comment for *Science* magazine on the work of Stevens and McKinley, used a provocative title: “Can deep bacteria live on nothing but rocks and water?” The answer seems to be yes.

My colleague Tom Gold of Cornell University may be one of America's most iconoclastic scientists. (One prominent biologist, who shall remain nameless, once said to me that Gold ought to be buried deep within the earth along with all his putative bacteria.) But no one sells him short or refuses to take him seriously—for he has been right far too often (we only threaten to bury alive the people we fear).

In a remarkable article entitled “The deep, hot biosphere” and published in the prestigious *Proceedings of the National Academy of Sciences* in

1992, Gold set out the full case (truly universal, or at least potentially so) for the importance of bacterial biotas deep within the earth. (He did this, characteristically, a few years before firm data existed for rich bacterial communities in ordinary subsurface rocks. But he was right again, in this factual claim at least, if not necessarily in all his implications. Gold began his case by asking, “Are the ocean vents the sole representatives of this [deep bacterial life], or do they merely represent the examples that were discovered first?”)

Of all living things that might expand the range of life beyond conventional habitats of land and oceans, bacteria are the obvious candidates. They are small enough to fit nearly anywhere, and their environmental range vastly exceeds that of all other organisms. Gold writes: “Of all the forms of life that we now know, bacteria appear to represent the one that can most readily utilize energy from a great variety of chemical sources.”

Gold then makes a key estimate—for my argument about domination of the modal bacter, at least—of possible bacterial biomass, given the vast expansion of range into rocks and fluids of the earth's interior. Gold's effort is, of course, another back-of-the-envelope calculation, and must be treated with all the caution always accorded to this genre (but remember that the estimates may also be too low, rather than inflated). A large number of assumptions must be made: How deep do bacteria live? At what temperatures? How much of rock volume consists of pore space where bacteria may live in percolating waters? How many bacteria can these waters hold? Since we do not know the actual values for any of these key factors, we must make a “most reasonable” estimate. If actual values differ greatly from the estimate (as they may well do), then the final figure may be very far wrong. (I trust that nonscientific readers will now grasp why, in this enterprise, we are satisfied with “ballpark” estimates that might be “off” by even an order of magnitude or two.)

In any case, Gold based his number for total bacterial biomass on reasonable, even fairly conservative, estimates for key factors—so if most rocks permeable by water do contain bacteria, then his figure is probably in the right ballpark. Gold assumes an upper temperature range of 230° to 300°F and a depth limit of three to six miles. (If bacteria actually live deeper, their biomass might be much higher.) He calculates the mass of water available for bacterial life by assuming that about 3 percent of rock volume

## FULL HOUSE

consists of pore spaces. Finally, he estimates that bacterial mass might equal about 1 percent of the total mass of available underground water.

Putting all these estimates together, Gold calculates a potential mass of underground bacteria at  $2 \times 10^{14}$  tons. This figure, he writes, is equivalent to a layer five feet thick spread out over the earth's entire land surface—an amount of biomass, Gold states, that would “indeed be more than the existing surface flora and fauna.” As a cautious conclusion to his calculation of underground bacterial biomass, Gold writes:

We do not know at present how to make a realistic estimate of the subterranean mass of material now living, but all that can be said is that one must consider it possible that it is comparable to all the living mass at the surface.

When one considers how deeply entrenched has been the dogma that most earthly biomass lies in the wood of our forest trees, this potentially greater weight of underground bacteria represents a major revision of conventional biology—and quite a boost for the modal bacter. Not only does the earth contain more bacterial organisms than all others combined (scarcely surprising, given their minimal size and mass); not only do bacteria live in more places and work in a greater variety of metabolic ways; not only did bacteria alone constitute the first half of life's history, with no slackening in diversity thereafter; but also, and most surprisingly, total bacterial biomass (even at such minimal weight per cell) may exceed all the rest of life combined, even forest trees, once we include the subterranean populations as well. Need any more be said in making a case for the modal bacter as life's constant center of maximal influence and importance?

But Gold does take one further, and equally striking, step. We are now fairly certain that ordinary life exists nowhere else in our solar system—for no other planetary surface maintains appropriate conditions of temperature and liquid water. Moreover, such earthly surface conditions are probably rare in the universe, making life an unusual cosmic phenomenon.

But the environment of the earth's shallow interior—liquid flowing through cracks and pore spaces in rocks—may be quite common on other worlds, both in our solar system and elsewhere (frozen surfaces of distant planets will not permit life, but interior heat may produce liquid—and a

## *The Power of the Modal Bacter*

possible environment for life at bacterial grade—within underground rocks). In fact, Gold estimates that “there are at least ten other planetary bodies [including several moons of the giant planets] in our solar system that would have had a similar chance for originating microbial life” because “the circumstances in the interior of most of the solid planetary bodies will not be too different from those at a depth of a few kilometers in the Earth.”

Finally, we may need to make a complete reversal of our usual perspective and consider the possibility that our conventional surface life, based on photosynthesis, might be a very peculiar, even bizarre, manifestation of a common universal phenomenon usually expressed by life at bacterial grade in the shallow interior of planetary bodies. Considering that we didn't even know only ten years ago such interior life existed, the transition from unknown to potentially universal must be the most astonishing promotion in the history of favorable revisions! Gold concludes:

The surface life on the Earth, based on photosynthesis, for its overall energy supply, may be just one strange branch of life, an adaptation specific to a planet that happened to have such favorable circumstances on its surface as would occur only very rarely: a favorable atmosphere, a suitable distance from an illuminating star, a mix of water and rock surface, etc. The deep, chemically supplied life, however, may be very common in the universe.

The modal bacter, in other words, may not only dominate, even by weight, on earth, but may also represent life's only common mode throughout the universe.

## No Driving to the Right Tail

A proper theory of morality depends upon the separation of intentions from results. Tragic deaths may occur as unintended consequences of decent acts—and we rightly despise the cold-blooded killer, while holding sympathy for the good Samaritan, even if an unnecessary death becomes

the common result of such radically different intentions (the robber who shoots the store owner, and the policeman who kills the same owner because he fired at the robber and missed).

Similarly, any proper theory of explanation in natural history depends upon the distinction of causes and consequences. Darwin's central theory holds that natural selection acts to increase adaptation to changing local environments. Therefore, features built directly by natural selection—the thick coat of the woolly mammoth in my example on page 139, for example—evolve for adaptive reasons by definite cause. But many features that become vital to the lives of their bearers may arise as uncaused (or at least indirectly produced) and “unintended” sequelae or side consequences. For example, our ability to read and write has acted as a prime mover of contemporary culture. But no one could argue that natural selection acted to enlarge our brains for this purpose—for *Homo sapiens* evolved brains of modern size and design tens of thousands of years before anyone thought about reading or writing. Selection made our brains large for other reasons, while reading and writing arose later as a fortuitous or unintended result of an enlarged mental power directly evolved for different functions.

Our intuitions tell us—quite rightly in this case, I believe—that this distinction between *results directly caused* and *consequences incidentally arising* is both important in explaining any particular feature of the organic world and fundamental to any general understanding of evolution. The main issue is not predictability—for a phenomenon may be predictable whether it arises directly for cause or incidentally as a consequence. The key question centers on the nature and character of explanation. The purposeful killer and the erring policeman produce the same result (and with equal predictability in the old-fashioned Newtonian sense of potential for deducing the outcome once we know the positions of all people, the sight line of the gun, the timings, etc.)—yet we yearn to judge the meaning differently based on the distinction between intention and accident.

In the same way, a right tail of increasing maximal complexity might arise on the bell curve of life either (as tradition has held) because evolution inherently drives life to higher levels of complexity or (as I argue in the major claim of this book) as an incidental side consequence of life's necessary origin at the left wall of minimal complexity followed by success-

ful expansion thereafter with retention of an unvarying bacterial mode. Our intuitions detect a radical difference in meaning between these two pathways to predictable production of the same result—and our intuitions are right again. We do, and should, care profoundly about the different meanings—for, in one case, increasing complexity is the driving *raison d'être* of life's history; while, in the other, the expanding right tail is a passive consequence of evolutionary principles with radically different main results. In one case, progress rules and shapes the history of life as the central product of fundamental causes; in the other, progress is secondary, rare, incidental, and shaped by no cause working directly in its interest.

This issue of directly caused results versus incidental consequences has reverberated throughout the history of evolutionary thought. A large literature, both scientific and philosophical, has been devoted to explicating these vital distinctions. A daunting and somewhat jargony terminology has arisen (some, I confess, of my own construction) to carry this debate in the technical literature—adaptations versus exaptations, aptations versus spandrels, selection versus sorting (see Sober, 1984; Gould and Lewontin, 1979; Gould and Vrba, 1982; Vrba and Eldredge, 1984). We will stick to the vernacular here, and make our main distinction between intended results and incidental consequences.

As the main claim of this book, I do not deny the phenomenon of increased complexity in life's history—but I subject this conclusion to two restrictions that undermine its traditional hegemony as evolution's defining feature. First, the phenomenon exists only in the pitifully limited and restricted sense of a few species extending the small right tail of a bell curve with an ever-constant mode at bacterial complexity—and not as a pervasive feature in the history of most lineages. Second, this restricted phenomenon arises as an incidental consequence—an “effect,” in the terminology of Williams (1966) and Vrba (1980), rather than an intended result—of causes that include no mechanism for progress or increasing complexity in their main actions.

At most, one might advance Thomas's (1993) claim that “progressive emergence of increasing complexity over the long term is the main effect of evolution. As such, it compels our attention.” In other words, Thomas admits that increasing complexity is an incidental consequence, an effect

rather than a main result of causes framed in its interest. He holds, however, that progress still compels our attention as the "main" effect among all of evolution's incidental consequences. But what possible criterion can validate this claim beyond the parochial and subjective desire to designate as primary an effect that both led to human life and placed us atop a heap of our own definition? I think that any truly dominant bacterium would laugh with scorn at this apotheosis for such a small tail so far from the modal center of life's main weight and continuity. I do realize that bacteria can't laugh (or cogitate)—and that philosophical claims for our greater importance can be based on the consequences of this difference between them and us. But do remember that we can't live on basalt and water six miles under the earth's surface, form the core of novel ecosystems based on the earth's interior heat rather than solar energy, or serve as a possible model for cosmic life in most solar systems.

In other words, progress as a purely incidental consequence (and limited to a small right tail) just won't do as a validation for our traditional hopes about intrinsic human importance—the spin-doctoring that prevents the completion of Darwin's revolution in Freud's crucial sense of pedestal smashing (see chapter 2). I think that virtually every evolutionist who has ever considered the issue in the terms of this book (that is, as a history of variation in all life—the full house—rather than as a tale told by abstracted means or extreme values only) has come to the conclusion that the appearance of progress as an expanding right tail must arise as an incidental consequence, not as a main result.

The traditional hope for intrinsic progress as an explicit result must therefore rest upon a fallback position—not nearly so grand as the original formulation, but a source of some potential solace nonetheless. Even if we must admit that an expanding right tail arises as an incidental consequence of origin at a left wall with subsequent proliferation, could we not also hold that other forces operate as well on life's bell curve—and that some of these other forces do include an intrinsic and predictable drive to progress?

As stated in point 6 of my epitome (see page 173), such an argument could be true, would take the following form, and can be tested empirically: life as a whole begins at the left wall and is therefore free to expand in only one direction. Therefore we cannot use life-as-a-whole to test for

drives to progress—because upward movement of the mean must, in part, reflect the left wall's constraint, not any potential drive. But if we could study the history of smaller lineages with founding members far from the wall—and therefore free to vary in either direction—then we could devise a clear test for general progress. Do such "free" lineages show a tendency for increases in complexity to be more frequent, or greater in effect, than decreases? If most free lineages show a trend to increasing complexity, then we could assert a general principle of progress as a main result for its own sake. The full phenomenon of life's expanding right tail would then arise by two separate and reinforcing processes: an incidental consequence based on constraints of origin at the left wall, and a direct result of intrinsic bias to greater complexity in lineages free to vary in both directions.

This conjecture is logically sound but, by all evidence so far in hand, empirically wrong. I would raise two arguments against intrinsic progress, the first briefly and subjectively, the second at greater length and based upon some compelling recent evidence.

First, if I were a betting man, I would wager a decent sum (but not the whole farm) on a small natural preference for *decreasing* complexity within lineages, and not for the traditional increase, if any general bias exists at all. I make this surprising claim because natural selection, in its purest form, only yields adaptation to changing local environments. These changes should be effectively random (with respect to "progress"), for fluctuations in climate show no temporal trend. A bias for or against increasing complexity therefore requires a general advantage for one direction as life plays its Darwinian game. I can think of a reason why a bias for decreasing complexity might exist, but I cannot defend any corresponding preference for increases. Hence I would bet that a slight overall bias for decreasing complexity might well prevail in the aggregate of all lineages.

I have long been entirely underwhelmed by the standard arguments for general advantages of increasing complexity in the Darwinian game—adaptive benefit of more elaborate bodily form in competition for limited resources, for example. Why should more complex conformations generally prevail? I can imagine such an argument for mammalian brains—if complexity translates to rising flexibility and com-

envisage just as many situations where more elaborate forms might be a hindrance—more parts to fail, less flexibility because all parts must interact with precision.

But one common mode of Darwinian success (local adaptation) does entail an apparent preference for substantial decreases in complexity—namely, the lifestyle of parasites. We are not speaking here of an organic rarity, but of a mode of life evolved by probably hundreds of thousands of species—a substantial percentage of all living forms. Not all parasites gain adaptive benefit through simplification, but one large group of species certainly does—those that live deep within the bodies of their hosts, permanently attached and receiving all their nutrition by commandeering the blood supply, or some of the food already digested by the host. Such species require neither organs of locomotion nor digestion, and natural selection favors their loss. One or a few novel organs might evolve for special needs—hooks for attaching to the host, or suction devices to drain off food, for example—but these elaborations are more than offset by a far greater number of lost organs.

Often these immobile parasites become little more than bags or tubes of reproductive tissue—simple machines for propagation attached to the internal organs of their host. *Sacculina*, the famous barnacle parasite of crabs and other crustaceans, consists of a formless sac (acting as a brood pouch) attached to the crab's abdomen, with a stalk protruding inside to a system of roots that drain food from the crab's blood spaces. A twenty-foot-long tapeworm in a human intestine may contain of hundreds of sections (strobilae), each little more than a simple sac containing members of the next generation. The entire phylum Pentastomida, parasites of the respiratory tract of vertebrates, builds an elaborate organ for sucking blood, but no internal parts for locomotion, respiration, circulation, or excretion.

Thus, if "standard" natural selection on free-living creatures produces no bias in either direction, and if parasites tend to become simplified while no countervailing bias toward greater complexity exists, then a small overall tendency toward decreasing complexity may characterize the history of most lineages (as their parasitic species simplify, while their free-living species show no trend). Please note that the right tail for the full bell curve of life will still expand through time—even if a bias toward decreasing complexity operates in most lineages. For species moving left to less com-

plexity enter a domain already inhabited, while rarer species moving right may enter a previously unoccupied realm of complexity. The drunkard will end up in the road even if, for some reason, he moves more often toward the wall than toward the gutter—for he bounces off the wall but falls prostrate (and permanently) in the gutter. An entire system can extend its extreme in one direction even if individual lineages have a bias for excursions in the other direction.

But I can also think of an argument against my own claim for parasites. Adult forms do indeed tend to evolve toward greater simplicity, but when we confine our attention to adults, we fall into another conventional bias (not as general or pervasive, no doubt, as our preferences for progress, but a seriously distorting limitation nonetheless). A human being is not defined by the nongrowing form of adult years; kids are people too. Evolution shapes a full life cycle, not only an adult body. The immobile blood-sucking or food-draining adult parasite may have evolved toward greater simplicity compared with free-living ancestors, but full parasitic life cycles often change in the other direction toward great elaboration, sometimes with adaptation to two or three different hosts in the course of a full ontogeny.

The adult *Sacculina* may be an external blob attached to some internal roots, but the larval life cycle is astonishingly complex (see Gould, 1996)—several free-living planktonic forms, followed by a settling phase that cements to the crab, grows a dart that pierces the crab's body, and then injects the few cells that eventually grow into the adult blob and roots. Similarly, pentastome larvae first bore through the gut of an initial host. When a vertebrate eats its first home, the matured pentastome moves to the respiratory tract either by crawling from the vertebrate's stomach to the esophagus and then boring through, or by tunneling through the intestinal wall and into the bloodstream. The pentastome then attaches to its final site by means of complex hooks surrounding the mouth.

I therefore have little confidence that we can specify a clear bias one way or the other on general principles. But we do have a wealth of empirical data available for study. After all, the founding species of most multicellular lineages does not begin at a wall—and subsequent evolution remains free to produce either more or less complex species. If we can agree on a measure of complexity, and document enough lineages, we may be



able to extract a general conclusion. This subject has just begun to interest paleontologists in the past few years. We have not yet compiled nearly enough cases for any confident general solution. But the initial studies offer great promise, for we have at least made this vital subject tractable and testable. And the first few cases all point in the same radical direction—no bias toward increasing complexity has yet been measured.

This line of research has been pioneered by Dan McShea of the University of Michigan, now at Santa Fe's Institute for the Study of Complexity. Much of the technical literature must focus on providing an unambiguous and quantifiable definition for a very fuzzy vernacular term with a wide variety of meanings, some contradictory—namely, complexity itself. What do we mean when we say that a thing is more complex than something else? Several criteria fit our vernacular sense, depending upon the context. Complexity has morphological, developmental, and functional aspects. A junk heap (to use an example favored by McShea and Thomas) may be morphologically very complex (in consisting of so many highly varied and independent parts) but functionally quite simple (just glop for a landfill). On the other hand, what is functionally simple for us might be quite complex to other users—in this case, to the seagull who must distinguish all the little bits while searching for morsels of food.

I do not wish to address this technical subject at length in a book for general readers (but see McShea, 1992, 1993, 1994, and Thomas, 1993, for interesting discussion), though the importance and nature of the problem must be recorded. I do not think that any general solution can be found—because “complexity” is a vernacular term with several legitimately different meanings, and we may well be interested in all of them. For science as “the art of the soluble” (to use P. B. Medawar's felicitous phrase)—an enterprise dedicated to posing answerable questions—we must only resolve that we will choose a rigorously quantifiable definition of complexity and be very clear about which aspects of vernacular meaning will be thus addressed, and which omitted. (Someone else, or you yourself in a subsequent study, may then measure other aspects of complexity.) The literature has been admirable on this account, and therefore happily free of the muddiness that accompanies so much science.

McShea has favored a morphological definition—not because he views this meaning as closer to some vernacular norm, but because it permits

well-defined measurement and rigorous testing. He writes (1996): “The point is to rescue the study of biological complexity from a swamp of impressionistic evaluations, biased samples, and theoretical speculations, and to try to place it on more solid empirical ground.” McShea employs the following conceptualization to construct his quantifications:

The complexity of a system is generally acknowledged to be some function of the number of different parts it has, and of the irregularity of their arrangement. Thus, heterogeneous, messy, or irregularly configured systems are complex, such as organisms, automobiles, compost heaps, and junk yards. Order is the opposite of complexity. Ordered systems are homogeneous, redundant, or regular, like picket fences and brick walls (1993, page 731).

In his major study of the vertebrate spinal column, for example, McShea (1993) operationalizes this definition by measuring complexity as the

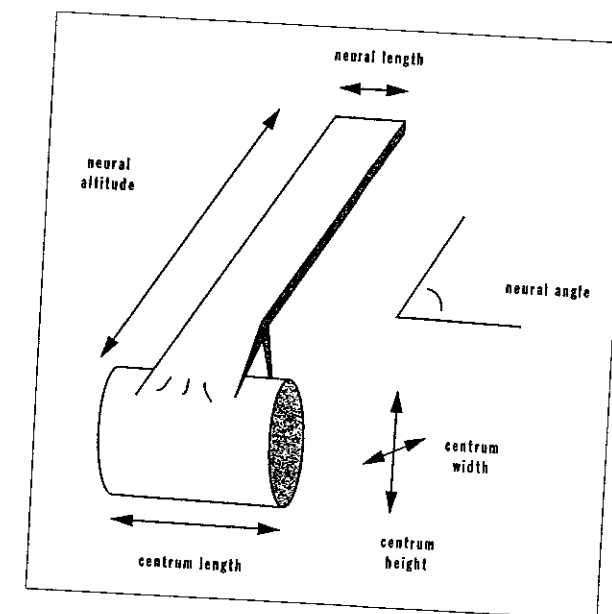


FIGURE 32  
Measurements used by McShea to assess the history of complexity in vertebrae.

degree to which individual vertebrae differ among themselves. (In the less complex backbone of a fish, forty or more vertebrae may be effectively alike as simple discs of similar size; the more complex mammalian spine has fewer vertebrae differentiated into the varied forms and sizes of neck bones, back vertebrae, and sacral discs that support the pelvis.) In practice (see Figure 32), McShea measures six variables (five linear dimensions and an angle) on each vertebra and then calculates the difference among vertebrae. He uses three assessments of complexity as variation among vertebrae: (1) the maximal difference between any two vertebrae of the same spinal column; (2) the average difference between each vertebra and the mean for all vertebrae; and (3) the average difference between each pair of adjacent vertebrae.

McShea's framework for testing harmonizes perfectly with the perspective of this book. He holds that trends come in two basic modes with strikingly different fundamental causes. He names these categories *driven* and *passive*, and argues that they represent natural "kinds," not just conceptual conveniences for human understanding. He writes (1994, page 1762): "These results do raise the possibility that the passive and driven mechanisms may be natural categories and that they may correspond to distinct and well-defined causes of large-scale trends."

Driven trends correspond to the traditional view of an overall movement achieved because each element evolves with a bias for change in this direction. A driven trend to complexity would arise because evolution generally favors more complex creatures—and each species of a lineage therefore tends to change in this manner. (In other words, natural selection acts as a driver, conveying each vehicle in a favored direction.) Passive trends (see Figure 33) conform to the unfamiliar model, championed for complexity in this book, of overall results arising as incidental consequences, with no favored direction for individual species. (McShea calls such a trend passive because no driver conducts any species along a preferred pathway. The general trend will arise even when the evolution of each individual species confirms to a "drunkard's walk" of random motion.) For passive trends in complexity, McShea proposes the same set of constraints that I have advocated throughout this book: ancestral beginnings at a left wall of minimal complexity, with only one direction open to novelty in subsequent evolution.

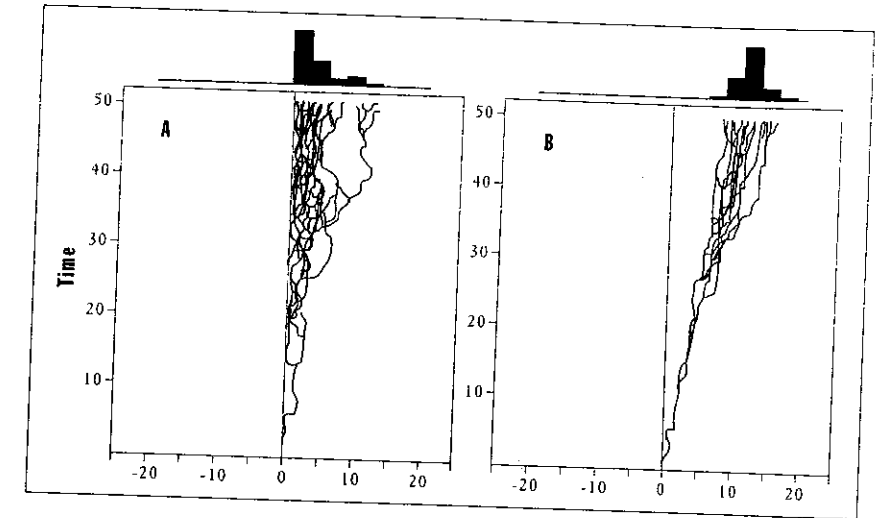


FIGURE 33

Passive and driven trends in McShea's terminology. A passive trend (A) begins near a left wall, retains a constant mode at this beginning position, and expands in the only open direction toward the right. In a driven trend (B), both minimum and maximum values increase through time.

McShea proposes three tests for distinguishing driven from passive trends:

1. **THE TEST OF THE MINIMUM.** In passive systems, minimum values of complexity should be preserved by some species throughout the expanding history of a lineage because no general evolutionary preference for complexity exists, and some species should therefore do best by remaining simple. In driven systems, both minimum and maximum complexity should increase through time because higher complexity confers such general advantages that evolution of all species should be biased in this direction. (The preservation and continuing enhancement of life's bacterial mode strongly points to the passive mode for life as a whole.)

This test, although indicative, does not fully distinguish passive from driven trends because even a driven trend might permit a few species to retain minimal values. (In a driven trend, the minimum might not disappear, but these lowest values should at least become less frequent over time.)

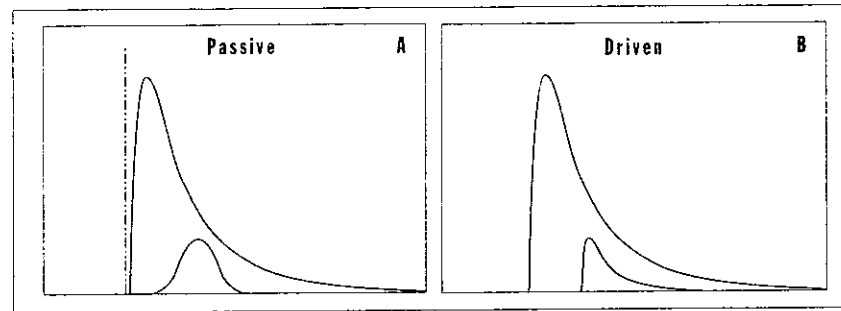


FIGURE 34

A test to distinguish passive from driven trends. The entire distribution for the passive trend should be right skewed, but component lineages that begin far away from the left wall should have normal distributions.

2. THE TEST OF ANCESTOR-DESCENDANT PAIRINGS. This powerful and obvious test identifies an ancestral species for an expanding lineage and then simply tabulates all descendants to judge whether most become more complex, simpler, or stay the same. In principle this is the most decisive test of all. But in practice we cannot always use it because the fossil record is so imperfect. We often do not know the ancestral species, or we do not have enough descendants to make a proper randomized test of subsequent directions.

3. THE TEST OF SKEWING. For life-as-a-whole, both the passive and driven mechanism can produce the same overall result of a right-skewed distribution with an expanding tail at maximal complexity. McShea argues that we might distinguish passive from driven modes by studying the skewness of component lineages that begin far from the wall and can therefore vary in either direction (see Figure 34). In driven systems, the component lineages should also tend to be right skewed because all species experience the bias of progress as a favored direction and should therefore contain more species moving along this preferred pathway, thereby stretching the entire distribution toward the right. But in passive systems, component lineages should develop no skew because increases and decreases in individual species should be equally common—that is, as many species should move leftward to less complexity as rightward to more elaboration.

In his major study, McShea (1993, 1994) has applied these tests to evolution of the vertebral column. A general trend obviously exists for vertebrates as a whole because the first vertebrates were fishes with a backbone built of essentially identical elements, while later mammals evolved considerable variation among vertebrae along the spinal column. But is this trend passive or driven? (Tradition says driven, but one fact certainly leaves maximal “room” for passivity. Much like the initial living thing at the left wall of minimal complexity, or the founding foraminiferal species at the absolute left wall of minimal sieve size [see pages 157–158], vertebrates begin at a theoretically minimal value of complexity by McShea’s measurements. Since the founding fishes tend to have vertebral columns made of identical elements, their measured complexity will be close to flat zero [McShea measures complexity as differences among vertebrae]. There really is no place to go from this initial point but up!)

McShea’s study of sublineages within mammals provides strong quantitative evidence for increasing general complexity in the passive mode—thus supporting the claim of this book that no explicit preference or bias for complexity acts as a driving force in the evolution of life. McShea surveyed five sublineages where he could identify or infer an ancestor, thus permitting him to use the most powerful second test: ruminant mammals (the large group of cud-chewing cattle, deer, etc.); squirrels of the large family *Sciuridae*; the entire order of pangolins (a group of armored anteaters, now represented by the genus *Manis* of Africa and Asia); whales; and camels.

All the tests provide evidence for a passive trend and no drive to complexity. McShea found twenty-four cases of significant increases or decreases in comparing the range of modern descendants with an ancestor (out of a total potential sample of ninety comparisons, or five groups of mammals, each with six variables measured in each of three ways; for the other comparisons, average descendants did not differ significantly from ancestors). Interestingly, thirteen of these significant changes led to *decreases* in complexity, while only nine showed increase. (The difference between thirteen and nine is not statistically significant, but I am still wryly amused, given all traditional expectation in the other direction, that more comparisons show decreasing rather than increasing complexity.)

McShea was then able to apply the third test of skewing to three ver-

tebral dimensions measured in three lineages. The mean skew value for all nine distributions is actually negative (-.19), not significantly so to be sure, but quite a comeuppance for the traditional view of complexity as driven—a conclusion that implies positive (right) skewing for component lineages!

McShea then summarizes his entire study (1994, page 1761):

The minimum complexity of vertebral columns probably did not change (indeed, the actual minimum seems to have remained close to the theoretical minimum), ancestor-descendant comparisons in subclades of mammals revealed no branching bias, and the mean subclade skew was negative, all pointing to a passive system.

One study doesn't prove a generality any more than a single swallow makes a summer, but when our first rigorous data point to a conclusion so at variance with traditional views, we must sit up and take notice, and then go out to make more tests. The few other available studies also support the passive rather than the driven mode. In an interesting report, presented at paleontological sessions at the 1995 annual meeting of the Geological Society of America in New Orleans, McShea provided the first results for a quite different meaning of complexity—developmental rather than morphological, and defined as the number of independent growth factors that build a structure through embryology (practically measured as correlation coefficients between pairs of measures, with perfect positive correlation indicating that the two measures represent only one mode of growth, and zero correlation implying that the two measures indicate different developmental influences).

Working with Benedikt Hallgrímsson and Philip D. Gingerich, McShea applied this method to a large series of classical and excellent data on measurements of fossil teeth, compiled over many years by Gingerich on evolutionary sequences for several mammalian lineages in the Bighorn Basin of Wyoming. They found no trend to increasing complexity and concluded: "Tests detected no bias, no tendency for non-hierarchical developmental complexity either to increase or decrease."

In the only other comprehensive study, using an interesting metric for

complexity applied to a very different group of organisms, Boyajian and Lutz (1992 and personal communication) studied one of the classic examples of supposedly driven evolution toward greater complexity—and again found evidence only for the passive mode!

Ammonites are extinct relatives of the modern chambered nautilus—coiled cephalopod shells housing animals related to modern squid and octopuses. Internal chambers meet the external shell at a boundary known as a "suture line." In nautiloids the suture line is usually straight or mildly wavy, but in ammonites the suture line can become intricately sinuous and digitated. In the everyday sense that sinuous and digitated looks more complicated than straight or mildly wavy, an old paleontological truism asserts that ammonite sutures become more complex through time. Ever since the earliest days of paleontology, increasing complexity of the ammonite suture has ranked among the two or three "classic" trends that "everybody knows" in the fossil record of invertebrates.

Boyajian and Lutz used a clever measure of "fractal dimension" to assess the complexity of ammonite sutures. (Heretofore, the trend has merely been asserted subjectively, rather than proven quantitatively, because no one could figure out a rigorous way to measure the complexity of such a twisty line.) Fractals have become a hot topic of popular culture, but in a technical sense, fractals are curves and surfaces that exist between ordinary dimensions. Since a straight line has a fractal dimension of one, and a plane a fractal dimension of two, twisty lines must measure between one and two—that is, between a minimum of one for the straight line between two points, and the unattainable maximum of two for a line that twists and turns so much that it fills an entire plane between the two points at opposite edges. The higher the fractal dimension, the more "complex" the suture in our visceral and traditional sense that the squiggliest lines are most elaborate. Boyajian and Lutz measured the fractal dimension of a suture in each of 615 genera of ammonites spanning the full range of their history. The measured scope of fractal dimensions runs from just a tad over 1.0 (very simple sutures are close to straight lines) to just over 1.6 for the most complex.

All early ammonites grew fairly simple sutures, and some measure near the theoretical minimum of 1.0 for a straight line. Thus, as in McShea's vertebrae, where founders showed minimal complexity, any move-

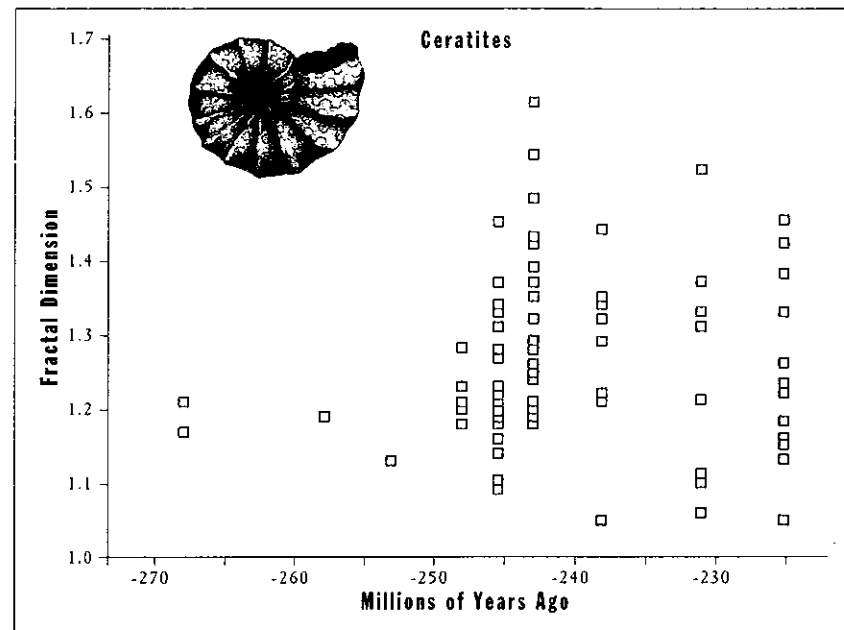


FIGURE 35

Evolution of complexity as measured by fractal dimension in a group of ammonites (the ceratites). The first species (left) have simple sutures near the left wall. Low values persist and even decrease through the group's history, but variation also expands into the only open direction of higher fractal dimension.

ment away from initial values could only be upward! This origin at a true left wall set the supposedly driven trend to increasing sutural complexity—for many later ammonites have very complex sutures, and scientific imagination can always drum up some putative adaptive reason for why complex sutures should be better, and therefore favored by natural selection (greater shell strength against hydrostatic pressure, and increasing area for attachment of muscles, have been favored).

But Boyajian and Lutz could find no evidence for a driven trend; all data identify the trend as probably passive—an incidental effect of minimally simple beginnings at a left wall, followed by no bias whatever for increasing complexity in individual lineages thereafter. Most lineages of ammonoids maintain species of low complexity throughout their history (see Figure 35 for an example). Most important, Boyajian and Lutz found no bias for increasing complexity among all the ancestor-descendant pairs

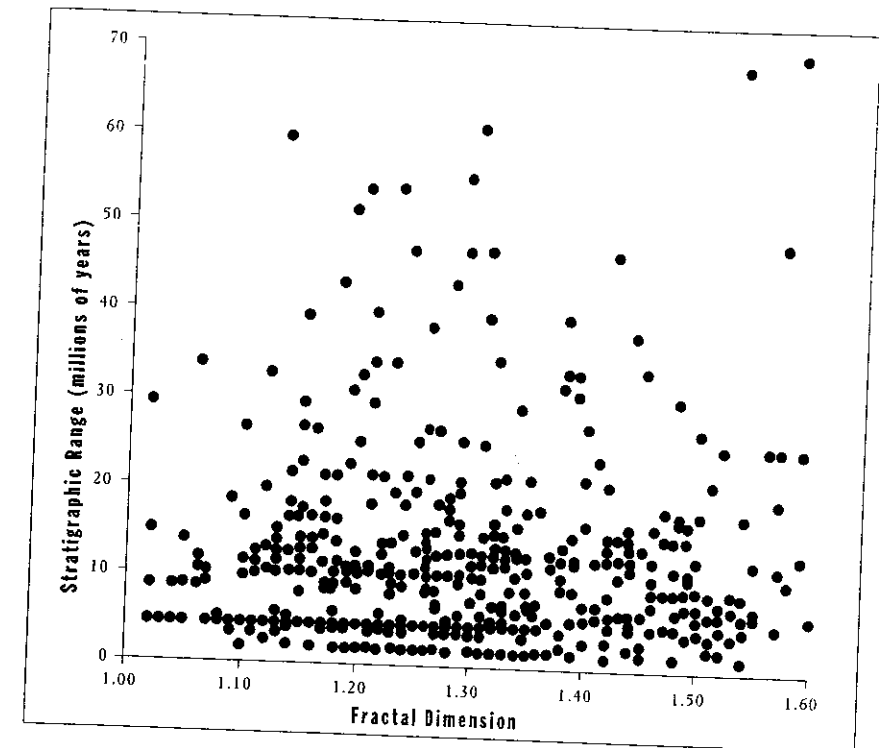


FIGURE 36

Longevity (in millions of years) for ammonite genera on the vertical axis plotted against fractal dimension on the horizontal axis. There is no correlation between complexity and success as measured by longevity.

they could specify (note the similarity to Arnold et al.'s discovery of no bias for increasing size in ancestor-descendant pairs of forams—see page 161). Finally, if complexity is such a good thing, then genera with more complex sutures should live longer. But Boyajian and Lutz found no correlation between sutural complexity and geological longevity (see Figure 36).

Only the most minuscule proportion of scientific studies ever gets reported in the press, and these decisions often bear little correlation with the importance of such studies for professionals. Better relationships can be found between the decision to report and the degree to which a conclusion disturbs conventional notions (often misconceptions) about the nature of things. The research of McShea and Boyajian is important to professionals, but their studies also received rare and extensive coverage



## FULL HOUSE

in the popular press because they challenged something that "everybody knows"—and that turns out to be probably wrong: the supposed drive to increasing complexity as the defining feature of life's evolutionary thrust. Consider the leads to the two major press accounts. Carol K. Yoon in *The New York Times* (March 30, 1993):

Surveying life's rich parade from the first single-celled beings in the primordial soup to the diverse array of organisms into which they developed, evolutionary biologists have marveled at the ever more complex cast of creatures that has continued to grace the planet. The evolution of larger brains, more efficient metabolisms and more elaborate social systems all seem to support the conventional wisdom that complexity increases during evolution. So clear is the trend that some biologists suggest that the evolutionary process is actually driving the increase in complexity. . . . But in two of the first studies to measure these trends, based on mammals' backbones and fossil shells, researchers say they have been unable to detect any overall evolutionary drive toward greater complexity.

And Lori Oliwenstein in *Discover* (June 1993):

Everybody knows that organisms get better as they evolve. They get more advanced, more modern, and less primitive. And everybody knows, according to Dan McShea (who has written a paper called "Complexity and Evolution: What Everybody Knows"), that organisms get more complex as they evolve. From the first cell that coalesced in the primordial soup to the magnificent intricacies of *Homo sapiens*, the evolution of life—as everybody knows—has been one long drive toward greater complexity. The only trouble with what everybody knows . . . is that there is no evidence it's true.

Few intellectual tyrannies can be more recalcitrant than the truths that everybody knows and nearly no one can defend with any decent data (for

## *The Power of the Modal Bacter*

who needs proof of anything so obvious). And few intellectual activities can be more salutary than attempts to find out whether these rocks of ages might crumble at the slightest tap of an informational hammer. I love the wry motto of the Paleontological Society (meant both literally and figuratively, for hammers are the main tool of our trade): *Frango ut patefaciam*—I break in order to reveal.

## A Note on the Fatal Weakness of the Last Straw

People under assault, and hopelessly overmatched, often do the opposite of what propriety might suggest: they dig in when they ought to accommodate. We call this behavior "siege mentality." Davy Crockett, Jim Bowie, and Co. won posthumous immortality by their intransigence at the Alamo, but an honorable surrender (given their hopeless situation and the certainty of carnage with continued fighting) might have secured the more worldly privilege of telling good war stories over a beer at a Texan bar (for independence from Mexico would have been won in any case) some twenty years later.

I believe that the power of arguments against inherent progress as a driving force of evolution, and the strength of data on the modal bacter and the passive character of trends to the right tail, must now evoke something like a siege mentality among those who still wish to maintain that evolution validates the primacy and domination of human life on our planet. To what may such people now turn as a source of natural solace? The modal bacter must be acknowledged as dominant by any reasonable criterion. The right tail exists, but only as a little appendage that cannot wag the dog of life's full house. Moreover, the right tail arose as an incidental consequence, in a passive trend powered by constraints of life's origin next to the left wall—and not by any cause or bias that favored increasing complexity as a natural good, and a driving thrust of evolution.

The embattled traditionalist must therefore stand his ground on the right tail of his natural habitat. He must adopt a siege mentality and dig in to protect his own restricted turf. The right tail, he must now admit, may be small and merely consequential. But grant me, he pleads, this last

potential natural comfort: "May I not at least be a king in my own restricted castle? I once thought that my domain extended over all nature—that all else must be viewed as predictably preparatory to my eventual origin. I am now prepared to admit the hubris and falsity of this view. I reside on a small and incidental tail. But I am, at least, the creature of maximal complexity ('properly' defined by neural elaboration) on this tail, which I therefore dominate by right. This right tail, however passively fashioned, still had to develop and, ultimately, had to spawn a creature like me. Give me, then, at least, this one remaining solace in a parody of a fine old song: 'It had to be me, wonderful me; it had to be me.'

"Let me, in short, live like Pio Nono (the nineteenth-century Pope Pius IX). My predecessors held temporal power over much of Europe. I once ruled a good part of Italy, though I am now confined to a tiny principality—Vatican City—within Rome. But at least my rule here is absolute—and I can proclaim my infallibility!"

But even this reverie—a bit manic to be sure, for embattlement tends to inspire paranoia and delusions of limited grandeur—cannot be sustained. The claim that a conscious creature like us must evolve because we can predict the development of an expanding right tail for all of life represents a classic "category mistake"—in this case, the false inference of a particular from a valid generality. The right tail did predictably arise (if only as a passive consequence), but any individual creature on the right tail of earthly life at this particular time represents a fortuitous and improbable result, one actualization among a hundred million unrealized alternatives. Wind back the tape of life to the origin of modern multicellular animals in the Cambrian explosion, let the tape play again from this identical starting point, and the replay will populate the earth (and generate a right tail of life) with a radically different set of creatures. The chance that this alternative set will contain anything remotely like a human being must be effectively nil, while the probability of any kind of creature endowed with self-consciousness must also be extremely small.

This theme of radical contingency and improbability for particulars, whatever the predictability of general patterns (with humans clearly defined as an improbable particular, not part of any expected generality), does not fall under the scope of this book. But I do need to epitomize the ar-

gument at this point (as abstracted from my previous book *Wonderful Life*) because the traditional view, challenged and upended by contingency, forms the last refuge for a hope that we might validate human supremacy as an expected result of general evolutionary principles.

Under the traditional model of evolutionary history as a "cone of increasing diversity," life moves ever upward to greater progress, and outward to a larger number of species—from simple Cambrian beginnings for multicellular animals to our modern levels of progress and range of diversity. Under this iconography, pathways actually followed run along predictable courses that would be at least roughly repeated in any replay. But a radically different view, suggested by a thorough restudy of soft-bodied fossils in the Burgess Shale and other Cambrian faunas, indicates that an inverted iconography may be more appropriate—with maximal anatomical range of disparity reached early in life's history, followed by the extinction of most initial experiments and the "settling down" of life's diversity to just a few of the original possibilities. Moreover, we have strong reason to suspect that the loss of most, and survival of just a few, occurred more through a distribution of lottery tickets than by victories for predictable cause based on higher levels of progress among winners. In the "pure" lottery model, "tickets" are distributed at random and few initial lineages receive such a blessing. Any replay distributes the tickets to another random set, and leads to a radically different group of survivors. Since our own lineage of vertebrates held a tenuous position among these initial experiments—with only two early Cambrian precursors known as fossils, *Pikaia* from the Burgess Shale, and *Yunnanozoon* recently described from Chengjiang in China (see Chen et al., 1995, and Gould, 1995)—we must assume that most replays would not include the survival and flourishing of vertebrates. All of us—from sharks to rhinos to humans—would then have been excluded from the history of life.

If this good fortune of radical contingency occurred but once, with predictability based on progress prevailing thereafter, then we might view human emergence as close to inevitable following one lucky spin of fortune's wheel. But radical contingency is a fractal principle, prevailing at all scales with great force. At any of a hundred thousand steps in the particular sequence that actually led to modern humans, a tiny and perfectly

## FULL HOUSE

plausible variation would have produced a different outcome, making history cascade down another pathway that could never have led to *Homo sapiens*, or to any self-conscious creature.

If one small and odd lineage of fishes had not evolved fins capable of bearing weight on land (though evolved for different reasons in lakes and seas), terrestrial vertebrates would never have arisen. If a large extraterrestrial object—the ultimate random bolt from the blue—had not triggered the extinction of dinosaurs 65 million years ago, mammals would still be small creatures, confined to the nooks and crannies of a dinosaur's world, and incapable of evolving the larger size that brains big enough for self-consciousness require. If a small and tenuous population of protohumans had not survived a hundred slings and arrows of outrageous fortune (and potential extinction) on the savannas of Africa, then *Homo sapiens* would never have emerged to spread throughout the globe. We are glorious accidents of an unpredictable process with no drive to complexity, not the expected results of evolutionary principles that yearn to produce a creature capable of understanding the mode of its own necessary construction.

•15•

## *An Epilog on Human Culture*

Most of this chapter has focused on constraints imposed by life's origin at a left wall of minimal complexity, followed by a passive trend to the right as life diversified. As in all other examples for this book, I emphasized how explicit consideration of all the variation (the "full house") can engender proper understanding, while the old Platonic strategy of abstracting the full house as a single figure (an average construed as an archetype, or an extreme example to excite our wonder or horror), and then tracing the pathway of this single figure through time, usually leads to error and confusion.

My two major examples in this book—the extinction of 0.400 hitting in baseball and the absence of a driven trend to complexity in the history of life—consider different sides of the same analytical strategy (studying the full house rather than the abstracted essence). The baseball example speaks of encroachment upon a right wall of human limitations; the his-