CHAPTER 1

Life and the Riddle of Randomness

As biologists our great aim is to find order in all the diversity and complexity of the living world. This is something we all strive for: it is what gives us a feeling of fulfillment and satisfaction. We seek the rules that underlie living phenomena to make ignorance and confusion turn into clarity and order. This is what Linnaeus did by finding a way to classify the vast numbers of different kinds of animals and plants: he brought order out of chaos. And this is what Mendel did with crossing his peas to reveal the basic rules of inheritance, a discovery of such great importance that it provided the basis for the majority of the advances in biology—which have been profound—in the twentieth, and now into the twenty-first century.

The great advance of Charles Darwin in discovering natural selection was another momentous step forward. It explained how organisms could evolve, how they, through successive generations, could become optimally adapted to their environment. There is continual competition between individuals, and the winners are the ones that are successful in producing offspring, thereby passing on the advantageous traits. All biologists today are so in harmony with this idea that it frames all our thoughts, so much so that it has a way of obscuring for us some important and peripheral factors that seem to be less worthy of our attention. But I think they are important, and this book is an attempt to put one of those factors before our eyes.

The most obvious one is randomness. There is something about this idea that is unsettling to many, no doubt because it goes directly against the more comfortable feeling of the order that we all seek. For this reason there is less written on randomness in evolution than on selection, although it is by no means totally absent, as we shall see. Compared to natural selection, it is no great enlightening principle, and therefore it is often relegated to a background noise that really is not doing anything. Natural selection carves out novelties that lead to evolution: randomness seems to go nowhere; it just shuffles things backwards and forwards. While there is some truth to this way of putting the matter, it is fundamentally wrong, as I plan to show in some detail. All of evolutionary change is built on a foundation of randomness. It provides the necessary material for natural selection which then does indeed bring forth the order our inner mind so actively craves.

More than that, we will see examples where randomness is literally put to use as a way of managing a key step in development of an organism (and also in animal societies). In evolution randomness can, in some special circumstances, directly produce order.

The part that randomness plays in evolution differs with the size of the organism. In fact, this is what alerted me to the subject. For many years I have worked with small cellular slime molds, and because of them I have been much concerned in the matter of how size influences both the development and the evolution of organisms. As I bore into this interesting matter I realized that most evolutionary biologists, following the tradition of Darwin, think in terms of large or at least complex plants or animals, and assume that microorganisms are no different despite their small size. There are those who work on the evolution of bacteria and often can distinguish between their characteristics and those of larger eukaryotic organisms, but the prokaryotic world is in some ways a specialized subject, although one of great interest.

An important point should be made right in the beginning. In this book I will be concerned with the variations in morphology. Bacteria, and other prokaryotes, have a very limited morphological variation, and therefore my argument here only concerns eukaryotes, whose cells contain a nucleus and come in a great variety of shapes. Those vast numbers of varieties involve both unicellular and multicellular forms.

Chance in Evolution

The role of chance in evolution has a venerable history, and there has been a recent renewed interest. It was recognized early in the history of genetics that mutations were random. More recently, and for many years, this randomness was understood at the molecular level where one of the bases in a DNA chain substituted for another. There have been many attempts to show that in some circumstances mutation might force change in a particular direction, but these experiments have not stood up with time; the idea that mutations are random has long been generally accepted. It should be noted that this fact has been used by skeptics to doubt Darwin and his natural selection: how can the complexity and the beauty of a bird or a flower be explained by a mechanism rooted in the chaos of randomness! But indeed it can, and we have more and more evidence that there are numerous aspects of evolution besides mutations that involve chance. There is a primaeval notion that one cannot produce order out of chaos despite the fact that it is a common phenomenon.

Not only is mutation random, but the genetic events involved in sexual reproduction are peppered with chance events. Since the egg and the sperm each have half as many chromosomes as the other cells of the body, and they arise with chromosome reshuffling during their formation, during meiosis, the genes any one gamete might possess will vary and the nature of this variation is a matter of chance. So stochastic or random events are very much involved in producing the genetic variation among individuals in a population; they help produce the variation that is the fodder for natural selection that makes evolution possible.

It was first pointed out by Sewall Wright, a pioneer of the surge in population genetics in the 1930s, that because of random events, such as the ones just described, the genetic makeup of a population could change simply because of those random events.[1] He called this stochastic evolutionary change "drift." It follows that this might be particularly important if a population was very small at one point in its history, for the variant genes it possessed would be the ones that remained when the population subsequently expanded. The whole genetic constitution of that population was founded on the genes that just happened by chance to be present when the population consisted of few individuals. It is obvious why such a bottleneck in population size would allow the chance event of "drift" to produce evolutionary change. This bottleneck phenomenon has also been called the "founder effect" because it might lead to the invention of a new species. It has also been called the "Adam and Eve effect," the ultimate in narrowness of a bottleneck. The important lesson from all this is that changes in the genetic constitution of a population can be determined by chance; chance plays an important role in evolution.

[1] For a review see V. Grant, 1977.

Another foray into the role of chance in evolution was made by C. E. Finch and T.B.L. Kirkwood.[2] They begin by taking note of the fact the duration of the life span of any animal is, within limits, entirely random. It is the result of an accumulation of accidents and not something that is consistent and controlled. Even genetically identical twins will show differences, not only in their life span, but in other characteristics as well. Furthermore, Finch and Kirkwood point out in great detail that many events during development are random and leave their imprint on the resulting adult. C. H. Waddington called this "developmental noise."[3]

One of the most important advocates for the role of random events in evolution is Michael Lynch.[4] He deplores the idea that natural selection accounts for everything and argues that random events play a significant role in evolutionary change, particularly in the evolution of complexity. His main concern is the evolution of the genome; he emphasizes that not only is the randomness of mutation key, but also the shuffling of the genome in recombination. He argues that, as in the drift of Sewall Wright, random molecular changes could give a directional push over time that does not involve natural selection.

The idea that chance plays a role in evolution has a venerable past and has been promoted by a number of individuals; it may therefore be considered an

[2] Finch and Kirkwood 2000.
[3] Waddington 1957.
[4] Lynch 2007a,b.

accepted notion. What might be new in my discussion will be the point that the effect of randomness differs for organisms of different sizes. This is the major argument I wish to pursue.

Size and Randomness

Evolution has been from small to big, from simple to complex. Besides this obvious point, there has been another neglected but equally important trend in the control—or suppression—of the effect of randomness. In microorganisms, random events are common, but with the increase in size and complexity there has been a corresponding decrease in the role of chance. So there are three phenomena: (1) the increase in size, (2) the increase in complexity, and (3) the decrease in the part played by randomness: all three go together during the course of evolution. And clearly they are interrelated.

While it is true that compared to small organisms, large organisms are protected to a considerable degree from the vagaries of chance, they nevertheless cling to some randomness; in fact, randomness is essential to their very existence. One need only remember that all novelty is founded on the generation of new genes, which arise from the directionless, random appearance of new mutations. So while large animals and plants, by a vast array of mechanisms, limit chance, they do so within a well-defined boundary: not too much, and not too little—something that is so admirably managed through the sexual system, which in turn is ruled, and created, by natural selection.

There is a danger in following this line of thought, i.e., that all organisms, over geological time, have pursued the same path; and if they have, why do any of those simple, primitive microorganisms still exist today?

Natural selection could not have it otherwise. The progression over many millions of years has not meant the elimination of simple, smaller organisms, but they also have been continuously maintained by selection or the lack of selection. So the role of selection in the great evolutionary history of life on Earth not only is responsible for the progressive changes in any one group of organisms, but also takes cognizance of the interdependence of organisms. The whole community is continuously under the stern eye of natural selection. To make the point by giving a simple-minded example, animals could not exist without plants, the ultimate suppliers of the energy for life through the process of photosynthesis. The role of any organism in the size-complexity-randomness spectrum exists because it fits in, and is part of the whole fabric of a community, all the result of natural selection. So, still existing today we have prokaryotes, protozoa, a great plethora of invertebrates, fungi, and lower plants, all of which joined the world eons ago. They have not been abandoned, and although they are continuously evolving, they remain within the group in which they originated. They are a permanent part of all evolution on Earth.

My friend V. Nanjundiah has pointed out to me that this very matter is discussed in Darwin's *On the Origin of Species* in an intriguing passage:

> Why have not the more highly developed forms everywhere supplanted and exterminated the lower? Lamarck, who believed in an innate and inevitable tendency towards perfection in all organic beings, seems to have felt this difficulty so strongly, that he was led to suppose that new and simple forms were continually being produced by spontaneous generation. I need hardly say that Science in her present state does not countenance the belief that living creatures are now ever produced from inorganic matter. . . . If it were no advantage, these forms would be left by natural selection unimproved or but little improved; and might remain for indefinite ages in their present little advanced condition. And geology tells us that some of the lowest forms, as the infusoria and rhizopods, have remained for an enormous period in nearly their present state.[5]

As we shall see, his answer to the question is not all that different from mine. In fact it looks very much as though he (and not Lamarck!) scooped me!

If we concentrate on the third major evolutionary trend—randomness and its progressively decreasing role—an unnoticed phenomenon is revealed.

[5] 3rd edition et seq., John Murray (1861) p. 135.

Eukaryotic microorganisms, in contrast to larger, more complex forms might have a greater prevalence of morphological variation, that is, they might be relatively untouched by natural selection (as Darwin suggests). This could possibly hold for numerous small organisms. As we will see, the great difficulty is that it cannot be proved, but it is a hypothesis that cannot be ruled out, either. This raises a very interesting point concerning the psychology of biologists.

Ever since I started to pursue these ideas some six years ago, I have been burdening respected friends and divers first-rate evolutionary biologists with early (and admittedly wanting) versions of this idea, and their criticisms have been enormously helpful. But as the process went on I began to realize that there was a bigger issue than correcting my bent sentences: the idea that biological diversity could be explained by something other than natural selection approaches heresy. The dogma, often stated explicitly, is that for any character in an organism for which its selective advantage may not be apparent, the safest assumption is that it is an adaptation and some day the reason for its selection will be revealed. This is so engrained in our thinking about evolution that the idea that stable morphological traits could be established during the course of evolution by chance is often dismissed without a thought. This is by no means universally true, and, as we have seen, there are some authors who, like me, bemoan the neglect of considering randomness's role in evolution. A good example was the publication of Stephen Jay Gould and Richard Lewontin's *Spandrels of San Marco,*[6] in which they argue that many of the justifications of calling something an adaptation is totally absent: they were *Just So Stories,* like those of Kipling. This was met with a deluge of counter-criticism, and it is clear to me that this outburst took place because the tradition of always assuming adaptation is so deeply embedded in our psyche. It is difficult to turn the page. I urge the reader to stay calm: I am not going to throw Darwin out with the bathwater.

One further point. The great difficulty in dealing with adaptations, or lack of adaptations, is that it involves a large share of speculation. It is an easy matter to make hypotheses and argue forcefully on either side. One way to deal with this problem is the use of mathematics. A reasonable mathematical model can often be very helpful, but all too often the model is substituted for reality. It may provide the perfect, satisfying solution, but in itself it usually involves assumptions, that is, hypotheses. Such a model certainly can be a very useful approach, but it may not contain the whole answer. At least in the best of circumstances it leads one in a helpful direction.

Using mathematics has been enormously effective in population biology, and indeed the great advances

[6] Gould and Lewontin 1979.

of R. A. Fisher, J.B.S. Haldane, and Sewall Wright are all the product of skillful mathematics. A while ago, when I was trying to convince a friend who is a population geneticist in the mathematical tradition that small organisms may be relatively unaffected by natural selection, he found the idea totally unacceptable. When I asked him if the difficulty was that he could not see how to put the matter mathematically, his immediate answer was yes. Mathematics in biology has tremendous power, but it cannot do everything.

As the upper size limit increases over geological time, there is a corresponding increase in the period of development that produces the mature morphology. This involves a great increase in the complexity and effectiveness of the mechanisms of control, and one result is a progressive stifling of the influence of randomness. The role played by randomness is significantly different between micro and macro organisms.

In large organisms there are many sequential steps in their extended development, each of which is under genetic control. If there is an unfavorable mutation in one of those steps, it will simply block any further development, and the embryo dies. This is what Lancelot Law Whyte called "internal selection."[7] The chances that any such mutation could be beneficial are extremely unlikely because all the steps that follow will be totally dependent upon

[7] Whyte 1965.

that previous step, so any change is very likely to be deleterious. Development has a built-in mechanism to eliminate undesirable random mutations. The larger the organism, the longer the sequence of developmental steps, and the greater the possibilities of internal selection.

In small organisms, with few developmental steps, one random change might not only affect the morphology of the organism, but often the whole organism. In this way it is possible to generate masses of different whole-organism forms, many of which might be unaffected by natural selection; one shape will do as well as another.

The key is the number of developmental steps: many, and randomness is suppressed; few, and the effect of randomness can come to the surface and bloom.

Sex

As I already indicated, randomness is the backbone of Darwinian evolution in the form of variation, in particular variation that is inherited. And the amount of such variation must be carefully controlled: too little means that selection does not have enough material to work with; too much means no change because of a glut of variants. And the sexual mechanism is a remarkably effective way of providing just the right amount of variation. Furthermore, this mechanism that makes evolution by natural selection possible is itself the product of selection. Having the right amount of variation leads to greater reproductive success. Sexuality is such an important element in natural selection that, not surprisingly, it is essentially ubiquitous. It has been pointed out by many that sexual reproduction, which yields fewer offspring per parent, is far more costly than asexual reproduction. But if that cost were not paid, there would be no evolution. Sex is the golden key to evolutionary progress. Evolution starts off on a foundation of randomness followed by the natural selection of a mechanism to control it.

In organisms that arose early in Earth history (invertebrates from protozoa to sponges, cnidarians and upwards; lower plants from algae to mosses and in between; and let us not forget fungi), there is a great variety of ways in which sex appears in their life histories. In the simpler forms, asexual cycles are often interspersed with sexual ones: the former are clones and generally have no variants and are present in a benign environment where they can multiply rapidly, while the latter characteristically appear in a changing environment where variation might produce some individuals that are more likely to be able to cope successfully with a change. At a later time in Earth history, when the larger and more complex animals and plants appear, there is no longer this switching back and forth of sexual and asexual phases: the asexual phase disappears almost completely. With a few exceptions, large animals and higher plants have lost the ability to have an asexual cycle.

This is the apex of control in the great sweep of organic evolution, but not everything is rigidly controlled; in fact, there is an underlying foundation of all of Darwinian evolution for organisms of all sizes, and that is a randomness. Without it there would be no evolution. Mutations are random, and without mutation there could be no change. So we see that while many of the stochastic processes found in small organisms have been diluted and to some degree silenced in the larger ones, the randomness of mutation is retained and is essential at all levels or stages of evolutionary progress.

In the pages that follow, the points made in this brief abstract will be greatly amplified. Chapter 2 begins with a description of the increase in size and complexity over geological time, from multicellularity (cell societies) to animal societies, with an attempt to understand the periods of little change with those of relatively rapid change. Next, in chapter 3, I will review how morphological randomness is dealt with at different size levels, beginning with eukaryotic microorganisms, where we see the greatest amount of morphological randomness in both aquatic and terrestrial forms. Chapter 4 will explain why randomness is curtailed in larger forms. Chapter 5 discusses how the sexual cycle also varies in a general way depending on the size and complexity of organisms. A partial reversal of my main contention that randomness is more prevalent in microorganisms is found in some smaller forms, for periodically in their life cycle some species suppress randomness by turning to asexual reproduction. Finally, I discuss two cases of great interest in chapter 6 where, in cell and insect societies, there is a small reversal, and randomness is brought back to the fore to play a key role in their respective developments.