Taking a Chance on Evolution

Wonderful Life: The Burgess Shale and the Nature of History
by Stephen Jay Gould
Norton, 347 pp., $10.95 (paper)
Bully for Brontosaurus: Reflections in Natural History
by Stephen Jay Gould
Norton, 540 pp., $10.95 (paper)
Toward a New Philosophy of Biology: Observations of an Evolutionist
by Ernst Mayr
Harvard, 564 pp., $14.95 (paper)

By John Maynard Smith

Although very different in style and content, the last two books by Stephen Jay Gould—*Wonderful Life* and *Bully for Brontosaurus*—and Ernst Mayr's *Toward a New Philosophy of Biology* are ultimately about the same questions. Is evolutionary biology a science? If so, what kind of a science is it? Mayr's book is a collection of essays, published over the past thirty years, and addressed both to biologists and philosophers. His aim is to clarify the concepts that underlie evolutionary biology. His central theme is that these concepts make evolutionary biology an autonomous science, and not merely a subbranch of physics. This claim must not be misunderstood. Like all serious biologists, he believes in the unity of science: in particular, he believes that the laws of physics and chemistry are the same in living and inanimate matter. The claim for autonomy rests on the existence of concepts—for example, natural selection, genetic program, species—that are needed if we are to understand biology. These concepts are consistent with physical laws, but could not be deduced from them.

In distinguishing between physics and biology, he points to the different role of laws in the two sciences. In physics, laws are intended to be universal. Popper's falsifiability criterion depends on this: a single case of levitation would be sufficient to falsify Newton's law of universal gravitation. Such laws do exist in some branches of biology. For example, the "central dogma of molecular biology" that information can pass from nucleic acid to nucleic acid, and from nucleic acid to protein, but not from protein to nucleic acid, is intended to be such a law, universal as far as life on earth is concerned. As yet, there is no convincing falsifying evidence. The law is important for evolutionary biology, because it provides one explanation for the noninheritance of acquired characters. In evolution, such laws are hard to come by. Even the "law" that acquired characters are not inherited has exceptions, because not all heredity depends on the sequence of bases in nucleic acids. We do, however, have theories about evolutionary processes, although, as Mayr points out, there is hardly a theory in biology for which some exceptions are not known.

An example will help to make clear the nature of such theories about evolution. It is appropriate to choose a theory for which Mayr himself is largely responsible, that of "allopatric speciation." It holds that when a species divides into two reproductively isolated species, a period is required during which the two populations are spatially separated. The study of the geographical distribution of animals and plants lends empirical support for this view, and there are theoretical reasons, from population genetics, why it should be true. But, as Mayr was well aware, it is not a universal truth. There is at least one process—the formation of a hybrid between two species, followed by a doubling of the number of chromosomes—whereby new species have arisen without spatial isolation. The existence of such exceptions, however, does not make the theory uninteresting or unimportant. Most biologists agree that, at least in animals, speciation did require a period of geographical isolation in the great majority of cases.

Evolutionary biology is full of theories of this kind. The fact that we expect our theories to have exceptions makes it hard to test them. I will return to the problem of testing later. For the moment, let me only say that it is a more serious problem than either Mayr or Gould seems to allow. It makes me envious of my colleagues in molecular biology. They can usually settle their problems by experiment: I seem to live with mine. Of course, my problems are more interesting.

Gould's *Wonderful Life* is an account of the Burgess Shale, and its philosophical implications. As always, he follows the admirable policy of writing at the same time for amateurs and professionals. I envy him his ability to do this, although I think he would find it harder if, like mine, his view of the world was essentially mathematical. First, the story. Fossils of animals with shells and carapaces first appear some 570 million years ago: their rather sudden appearance marks the beginning of the Cambrian. The Burgess Shale in British Columbia is a Cambrian rock formation in which soft-bodied animals are exquisitely preserved. Their fossils were first found by the American paleontologist Charles Doolittle Walcott. He interpreted them as primitive members of groups—jellyfish, crustacea, clams, and so on—that are still with us today. Gould argues that this interpretation, which was certainly mistaken, arose from Walcott's belief that evolution was progressive, from simple beginnings to a complex end.

Recent work by Harry Whittington, and his colleagues Derek Briggs and Simon Conway Morris, of the University of Cambridge, has shown that the fauna were far more diverse than Walcott supposed. Early in the Cambrian, a wider range of body plans existed than is present today. Animals are built on a number of different plans, but those with the same body plan may live very different lives. Thus sharks, snakes, vultures, and humans all have the same body plan—they are all vertebrates—despite their different ways of life. Similarly, squids, snails, and clams have the same body plan—they are mollusks. It seems that, early in the Cambrian, all the currently existing body plans already existed: a few have not been observed, but this may be an imperfection of the record. In addition, there are animals that appear not to belong to any existing plan. The extent of this early diversity may have been overestimated. For example, it turns out that the strangest of them all, *Hallucigenia*, was restored the wrong way up: properly inverted, it turns out to be a relative of the existing segmented worm, *Peripatus*. As it happens, Gould is cautious about *Hallucigenia*. In any case, I do not doubt that he is right in thinking that the animals were immensely diverse. Subsequent evolution has reduced the number of body plans, not increased it, even if it has given rise to ways of life—for example, life on land, flight, tool-making—that did not then exist.

The message that Gould draws from this is that evolution is contingent. It is not the case that, initially, there were a few simple organisms, and that, as time passed, there was a steady increase in diversity and complexity, leading inevitably to the emergence of an intelligent, tool-using, talking animal—ourselves. If one was able to replay the whole evolution of animals, starting at the bottom of the Cambrian (and, to satisfy Laplace, moving one of the individual animals two feet to its left), there is no guarantee—indeed, no likelihood—that the result would be the same. There might be no conquest of the land, no emergence of mammals, and certainly no human beings. It may have been a matter of chance which body plans, or "phyla," survived: for example, there might have been no vertebrates.

The book reflects two themes that run through all that Gould has written. First, science is done by individuals, whose conclusions are influenced by the beliefs they bring with them. Second, evolution is contingent: it is not a stately law-governed progression, leading inevitably to human intelligence. To say that an event is contingent is not the same as saying that it is random. Chance events can lead to predictable outcomes. For example, the decay of a single radioactive atom is the paradigm of randomness, but the behavior of a large lump of radioactive material can be accurately predicted. Hence the contingency of evolution does not depend merely on the random nature of genetic mutation. It arises because mutations have qualitatively different effects, and because these effects can be amplified. Thus a chance change in a single molecule can, if present in a fertilized egg, alter the nature of the individual that develops: natural selection can then amplify a change in an individual to a change in a whole population. This amplification of quantum events, combined with the unpredictability of the environment, makes it impossible to foretell the longterm future, although it may still be possible to explain evolution in retrospect.

I agree with Gould that evolution is not in general predictable. I am willing to predict that, if the chemical companies introduce a new insecticide, the whitefly in my greenhouse will be resistant to it in ten years or less. In Gould's "replay from the Cambrian" experiment, I would predict that many animals would evolve eyes, because eyes have in fact evolved many times, in many kinds of animal. I would bet that some would evolve powered flight, because flight has evolved four times, in two different phyla; but I would not be certain, because animals might never get out on the land. But I agree with Gould that one could not predict which phyla would survive and inherit the earth.

In the replay experiment, what can one say of the emergence of human beings? Clearly, it is enormously unlikely that human beings indistinguishable from ourselves could have evolved. But what of intelligent, tool-using, talking animals? In an article on "the probability of intelligent extra-terrestrial life," Mayr argues that such life is infinitely unlikely. His argument seems to run as follows. Life has existed on earth for some five thousand million years, during which time many hundreds of millions of species have evolved: of these, only one is intelligent and technological; therefore, the chance of such life existing elsewhere is vanishingly small. This argument seems to me so manifestly false that I fear I must have misunderstood it. After all, life on any other planet could also exist for thousands of millions of years, and produce hundreds of millions of species, so why should it not also give rise to one intelligent species? Given that intelligence emerged here, I do not think one can say more than that it is a possibility. (There is an ingenious but difficult argument, based on the anthropic principle, showing that extra-terrestrial life is very unlikely, but I think it is based on an assumption—Bayes's postulate—that I find unacceptable.)

Although I agree with Gould about contingency, I find the problem of progress harder. I agree with him in rejecting the Victorian notion of a stately and inevitable progress toward the omega point. Empirically, individual lineages do not necessarily progress: they are as likely to lead to tapeworms, or to nothing at all, as to lead to man. As Darwin understood, there is nothing in the theory of natural selection that predicts progress in any global sense: only a tendency to get better at whatever you happen to be doing. But if we concentrate only on the most complex entities present in the biosphere at any moment, we can identify the following stages: replicating RNA molecules; simple bacterium-like cells ("prokaryotes"); cells with a nucleus and internal structure ("eukaryotes"); eukaryotes with sex; multicellular animals and plants; social animals; animals with language. This looks like progress, if only in the sense of an increase in the amount of information transmitted between generations. The series could only occur in this order. Some of the transitions have occurred just once (as with the origin of eukaryotes, or of language), others several times. I think Gould would say that all of them are contingent, not inevitable: if so, I agree. But I do think that progress has happened, although I find it hard to define precisely what I mean.

Gould's *Bully for Brontosaurus* is a collection of essays that first appeared in *Natural History*. He displays his usual gift for arguing from the particular to the general, and from the peculiarities of the individual scientist to the content of the science. His interests are catholic. How far does a classification of human populations on the basis of the languages they speak correspond to one based on their genes? How did the typewriter keyboard become fixed in a manifestly suboptimal arrangement? Are flamingoes pink because it makes them less visible against the sunset? What really happened in the debate between T. H. Huxley and "Soapy Sam" Wilberforce at the 1860 meeting of the British Association? One thing I find impressive about Gould's essays is that they often tell me something that I ought to have known but didn't. I have space to dwell on only one of them, which is relevant to the topic of this review. I'm afraid I had never heard of N.S.

Shaler, professor of geology at Harvard during the latter part of the last century. Gould tells us that Shaler puts forward a version of the fallacy which, earlier in this review, I ascribed to Mayr. Shaler argued that it is infinitely improbable that, without divine guidance, evolution should have led to the appearance of human beings. Hence our existence demonstrates the presence of "the guidance of a controlling power intent on the end." His friend and contemporary William James pointed out his mistake, concluding, "Where only one fact is in question, there is no relation of probability at all." Of course, Shaler's argument and Mayr's are different: Shaler argued that, because the evolution of man was exceedingly unlikely, there must have been divine guidance, and Mayr that, because it was unlikely, no comparable and equally unlikely event has happened elsewhere. Although different, both arguments draw unjustified conclusions from a single unlikely event, observed only after it had happened. I plan to spend this evening playing bridge. Each hand I am dealt will be exceedingly unlikely, in the sense that it could not have been predicted, but none of them will surprise me. Of course, if someone correctly predicts, before the deal, which cards I will be dealt, I will be very surprised—or, perhaps, very suspicious. There is an amusing final twist to Gould's essay on Shaler. After it was published, he received a letter from Jimmy Carter apparently defending Shaler's position. But in fact Carter's position may not be quite the same. He wrote, "You seem to be straining mightily to prove that—it is unlikely that cognitive creatures would have been created or evolved." I'm not sure that this is what Gould argued, or would agree to. Both of us, I think, agree that it is exceedingly unlikely that, in the "rerun" experiment, exactly the same cognitive creatures—with five fingers on each hand, a vermiform appendix, thirty-two teeth, and so on—would have evolved. But I do not agree that it is unlikely that "cognitive creatures" of some kind would have evolved. I just don't know.

I'm not sure where Gould stands on this. The question is important, not so much because of its possible theological relevance as because it raises questions about prediction in biology. Richard Lewontin discussed the question in a review of *Wonderful Life* in these pages.[1] Can we predict what biological forms are likely, or even possible? He concluded his review as follows:

> *We cannot know the answer unless we have a theory of biological form that is deduced from some general principles of biological organization, rather than inferred from the collection of objects. Or it may be that no such principles exist, and that in this broadest sense, life has no meaning.*

In seeking a theory of biological form, I would probably place greater emphasis than Lewontin on the principles of engineering design. I suspect that there are only a limited number of ways in which eyes can possibly work, and, maybe, only a limited number of ways in which brains can work. But I agree that it would be good to know whether such principles exist, and, if so, what they are. I also agree that, in his words, "a description of all the organisms that have ever been cannot decide the issue."

For me, the hard question raised by these books is the matter of testability. One does not have to be a hard-nosed Popperian to think that the progress of science—and I do think that science progresses—depends on the possibility of testing theories by observations, experimental or otherwise. If, as Mayr suggests, our theories always have exceptions, and if, as Gould argues, evolution is contingent and unpredictable, how can we test our ideas? Gould's answer is interesting. He argues that Darwin developed a method of testing that is appropriate for historical science, a method which is as rigorous as the experimental testing of a universal physical law. This is to require that our theory can explain data from different sources, for example,

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from embryology, biogeography, the fossil record, vestigial organs, taxonomic relationships, and so on. He quotes Darwin's words:

> *Now this hypothesis may be tested . . . by trying whether it explains several large and independent classes of facts, such as the geological succession of organic beings, their distribution in past and present times, and their mutual affinities and homologies. If the principle of natural selection does explain these and other bodies of facts, it ought to be received.*

This is fine, but we must be clear what it does for us. It provides a method of testing theories about the mechanisms of evolution which we believe to apply in a wide range of cases: in the quote from Darwin, it is the theory of natural selection, which we believe to apply in all evolutionary events. Sometimes we have other ways of testing such theories. For example, the theory that predicts the relative numbers of males and females can be tested qualitatively for all sexual species. The neutral theory of molecular evolution can be tested quantitatively by any molecular sequence data. More specific theories relevant to particular groups—for example, concerning why some monkeys are monogamous, or why some plants are self-fertile—can be tested by comparative methods. As Mayr implies, the most we can hope for in such cases is a theory that explains most of the observations. The important point, however, is that these are theories intended to explain a class of events by a common mechanism; they are not intended to explain unique events.

We can sometimes hope to explain unique events. For example, Gould discusses the suggestion of the physicist Luis Alvarez that the extinction of the dinosaurs, and of many other taxa, was caused by a meteorite collision. Although the matter is still controversial, the effects of such a collision would have been so extensive that it should be possible, in time, to establish its truth or falsehood beyond reasonable doubt. Evolutionary origins are usually more difficult. For example, I have for many years been interested in the origin of sex. This was, in all probability, a unique event: it happened in an unknown species. Although I can think up plausible scenarios, it is hard to see how they can be tested. It is equally hard to test ideas about the origin of language. It is easier to test ideas about why sex has been retained by most species, but lost by some, or about how and why human languages have subsequently diverged. In these cases, we are studying events that occur repeatedly.

Finally, although theories about origins are hard to test, it may be easier to test ideas about the origin of life, because this may have been an inevitable, non-contingent event, given conditions on the primitive earth. I am interested to find that Gould also thinks that contingency may have entered the scene after the origin of life.

Gould tells us that, at Harvard, they have divided the sciences according to procedural style and not conventional discipline: that is, not into physical and biological, but into "experimental-predictive" and "historical." I hope they will not make the division too deep. Evolution may be a historical science, but it differs from the study of human history in having a theory about the mechanism of change, based on the laws of inheritance, the concept of natural selection, and the theory of population genetics. Only an unusually dogmatic Marxist, or perhaps an equally dogmatic Thatcherite, would claim that there is any comparable body of theory concerning the mechanisms of historical change. This difference has important implications for how evolution should be studied, and how it should be taught. If they are not careful at Harvard, they will finish up training a lot of molecular biologists who do not know what the right questions are, and a smaller number of evolutionary biologists who know the questions, but have not the knowledge to answer them.