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Evolutionary Biology:
THE DARWINIAN REVOLUTIONS
PART ONE

Allen D. MacNeill
Cornell University

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Evolutionary Biology I
The Darwinian Revolutions

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Course Syllabus

Evolutionary Biology I
The Darwinian Revolutions

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About Your Lecturer

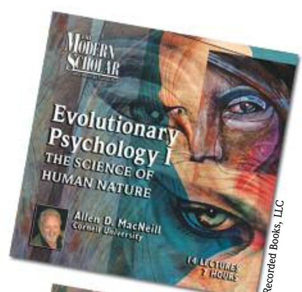
Allen D. MacNeill

Allen MacNeill earned a B.S. in biology in 1974 and an M.A. in science education from Cornell in 1977. He has taught the support course for introductory biology at Cornell University since 1976. As a senior lecturer in the Learning Strategies Center at Cornell, MacNeill works with students taking both majors and non-majors introductory biology. In addition, he organizes and carries out in-service training for teaching assistants in biology and related fields. MacNeill also teaches evolution for the Cornell Summer Session and has taught the introductory evolution course for non-majors at Cornell. He has served as a Faculty Fellow at Ecology House and as an honorary member and faculty advisor for the Cornell chapter of the Golden Key International Honour Society. He has served on numerous advisory committees and editorial boards at Cornell and in the Ithaca community.

Allen MacNeill's *The Evolution List* blog (http://evolutionlist.blogspot.com) is a forum for commentary, discussion, essays, news, and reviews that illuminate the theory of evolution and its implications.

A useful resource for MacNeill's first two Modern Scholar courses, *Evolutionary Psychology I* (2010) and *Evolutionary Psychology II* (2011), is his companion blog *Evolutionary Psychology* (http://evolpsychology.blogspot.com).

Along with his many teaching assignments, MacNeill has appeared in a number of Off-Broadway plays and in other acting venues.



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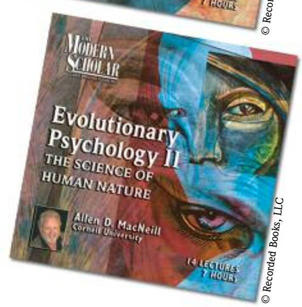

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Introduction

The theory of evolution is one of the most profound ideas ever entertained by the human mind. It fundamentally alters our perception of reality. In profound and unsettling ways, the theory of evolution changes our understanding of who we are, where we come from, why we do the things we do, and where we might be going. It does this by making us look carefully and dispassionately at the world around us, asking questions and seeking answers in the things we can see and hear and smell and taste and touch. It forces us to look beyond ourselves and our immediate surroundings, and to make educated guesses about things that have happened that we cannot directly observe. And it requires us to think long and hard about what is real and what isn't.

Ideas, like species, have origins. Like most profound ideas, the idea that the world has changed, is changing, and will change has very deep roots. In this lecture series we will trace the beginnings of the idea of evolution, from its origins in the thoughts and writings of the philosophers of ancient Greece, through the careful and detailed observations of the great naturalists of the nineteenth century, through the revolutionary theoretical work of the founders of the "modern evolutionary synthesis," to the fascinating discoveries being made every day by experimental scientists and field biologists. As we do so, our emphasis will always be on understanding where the ideas come from and what they imply about our understanding of the natural world—about reality itself.

Daniel Dennett, a historian and philosopher of evolutionary biology, has likened the theory of evolution to a "universal acid" that can dissolve all of the beliefs we hold most dear. In his most famous book, *Darwin's Dangerous Idea*, Dennett argues that the philosophical and religious implications of evolutionary biology fundamentally undermine many of the central principles upon which Western civilization is based. And indeed, evolutionary theory and the philosophical assumptions upon which it is based are largely incompatible with such traditional ideas as universal purpose, benign (or malignant) nature, gods or other supernatural entities that can intervene in human affairs, and human free will.

However, evolutionary theory can also be thought of as a tool, one of the sharpest and most useful tools humans have ever devised. Like any very sharp tool, evolutionary theory is dangerous, and should not be bandied about without training in its use and an appreciation for its uses and abuses. That is what we will cultivate throughout this lecture series: an understanding and appreciation of the power and potential—and beauty—of evolutionary theory.

Lecture 1

Darwin's Revolutionary Idea

The Suggested Reading for this lecture is Ernst Mayr's *What Evolution Is.*

Evolution is *change*. Since the publication of Charles Darwin's *Origin of Species*, the term "evolution" has had a more specific meaning, especially among naturalists and scientists. To a scientist, *evolution* means the process by which biological organisms and their characteristics have changed over time. For this reason, scientists often refer to the evolution of life and living things as *biological evolution*, and the scientific study of biological evolution is usually referred to as *evolutionary biology*.

Evolution is a *process*. The theory of evolution describes the processes whereby organisms (and their various parts) change over time. This process depends on four characteristics of living organisms.

1. *Variety*: structural and functional differences between individuals in populations.
2. *Heredity*: the inheritance of structures and functions from parents to offspring.
3. *Fecundity*: the ability to reproduce, especially at a rate that exceeds replacement.
4. *Demography*: the idea that some individuals survive and reproduce more often than others.

As a result of these four preconditions, the heritable characteristics of some individuals become more common in populations over time. The pattern of changes that occur in the heritable characteristics present among the surviving members of populations is what we call biological evolution.

Evolution is a *theory*. The theory of evolution is a scientific explanation for how living organisms interact with their environment, producing the changes we observe in the characteristics of living organisms in populations, in their genes, and in the fossils of organisms that have died and were preserved. A *scientific theory* is a provisional explanation for a natural phenomenon that is accepted by most scientists as the best explanation for that phenomenon, given the observable evidence available at the time. The theory of evolution has two related parts:

1. An explanation for the mechanisms by which evolutionary change has occurred.
2. An explanation for the patterns of change that we infer from comparative anatomy, comparative genetics, and the fossil record.

Evolution is a *worldview*. The theory of evolution has been formulated, tested, and expanded according to a particular view of reality—a *worldview*—shared by virtually all scientists. There are many distinct and sometimes contradictory worldviews held by people from different backgrounds and traditions. Each of us holds a personal worldview, and groups of people share public worldviews. The public worldview shared by virtually all scientists is called naturalism.

The theory of evolution is an *idea*. As we observe and interact with the world around us, we formulate explanations about what things are, about how things happen, and why they happen. These explanations are *not* the objects and events themselves. Rather, they are *ideas* about those objects and events. The idea that things have changed, are changing, and will continue to change—the *idea* of change—seems simple. Yet, the idea that evolution has occurred, is occurring, and will continue to occur is difficult for many people to even accept, much less understand.

Ideas have *origins*. In this lecture series we will trace the beginnings of the idea of evolution, from its origins in the thoughts and writings of the philosophers of ancient Greece and Rome, through the careful and detailed observations of the great naturalists of the eighteenth and nineteenth centuries, through the revolutionary theoretical work of the founders of the "modern evolutionary synthesis," to the experimental scientists and field biologists of today.

Ideas have *contexts*. Ideas generally don't come out of nowhere. They have a context and arise out of other ideas at particular times and in particular places. Ideas make more sense when we understand where they come from, what other ideas led to them, and the historical and sociological context within which they arose.

Scientific ideas require *evidence*. Ideas are generally about something (even when they are about nothing). That is, we formulate and adopt ideas on the basis of what we know and understand about reality. The theory of evolution is part of the natural sciences. As such, the idea of evolution is ultimately based on observation of nature and natural processes, and it requires evidence.

Ideas have *consequences*. Ideas are born, live, reproduce, and die in our minds, and they can be transmitted to other minds. As they do so, they influence other ideas and thereby shape our understanding of reality. This means that they also change the way we behave. Ideas are encoded in patterns of chemical and electrical activity in our sensory, nervous, and motor systems, and therefore they are causally linked to the things we do, not just to the things we think. Our ability to conform our behavior to our ideas is clearly imperfect, but it exists nonetheless. Therefore, to succeed in conforming our behavior to our ideas, we should make certain that our ideas conform to reality.

FOR GREATER UNDERSTANDING

Questions

1. What are the prerequisites for biological evolution and what is the outcome, given those prerequisites?
2. What is the worldview of most scientists and how does it differ from that of most of the general public?
3. What two main ideas did Darwin present in the *Origin of Species* and how are they related to each other?

Suggested Reading

Mayr, Ernst. *What Evolution Is*. New York: Basic Books, 2002.

Other Books of Interest

Dennett, Daniel C. *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. New York: Simon & Schuster, 1996.

Larson, Edward J. *Evolution: The Remarkable History of a Scientific Theory.* New York: Modern Library, 2006.

Websites of Interest

1. The *Cornell University Cyber Tower* website features a video study room entitled "Darwinian Revolutions," which is a six-part series hosted by Allen MacNeill at the Museum of the Earth at the Paleontological Research Institution in Ithaca, New York. — http://cybertower.cornell.edu/lodetails.cfm?id=421
2. The *Understanding Evolution* website at the University of California Museum of Paleontology (Berkeley, CA) provides fundamental information on evolution, teaching materials, and resources on the topic. — http://evolution.berkeley.edu
3. The PBS *Nova Evolution* website features resources for teachers, students, and the general public from the television series and ongoing research on evolution. — http://www.pbs.org/wgbh/evolution

Lecture 2

Consensus and Controversy

The Suggested Reading for this lecture is Eugenie C. Scott's *Evolution vs. Creationism: An Introduction.*

You're heading down the street, when suddenly you come upon a smoking pile of wreckage—what looks like it was once a house. From the evidence you can see (and hear and smell), there are at least three possibilities:

1. There has been a house fire, which started accidentally.
2. There has been a house fire, which was set on purpose.
3. Someone has staged what looks like the aftermath of a house fire.

How can you tell the difference? Consider the following:

- You did *not* witness a house fire, only what looks like its aftermath.
- All you have available to you to answer this question is what you can see, smell, hear, touch, and so forth.

Now consider your three alternative explanations:

1. Can you be absolutely certain that the house fire (if there was one) happened by accident?
2. Can you be absolutely certain that it didn't happen on purpose?
3. Can you be absolutely certain that it hasn't been staged?

If you answer these questions from the viewpoint of a scientist, your answer to all three must be no. All you have to go on is what you can observe now, and what you observe now is not a house fire, but evidence that one might have happened. So how do you decide which explanation is most likely?

The answer, if you are a scientist, is that you provisionally accept the explanation that best fits what you have observed, along with your knowledge of similar events you have observed in the past.

What you are doing when you make a guess like this is inferring that an event that you have not witnessed has, indeed, taken place. This is precisely what evolutionary biologists do when they study evidence that indicates that evolution has occurred in the past. *Inference* is the basis for almost all reasoning, including scientific reasoning.

Now consider the following:

> In crossing a heath, suppose I pitched my foot against a *stone*, and were asked how the stone came to be there; I might possibly answer, that, for any thing I knew to the contrary, it had lain there for ever: nor would it perhaps be very easy to show the absurdity of this answer.

> But suppose I had found a *watch* upon the ground, and it should be inquired how the watch happened to be in that place; I should hardly think of the answer which I had before given, that, for any thing I knew, the watch might have always been there. Yet why should not this answer serve for the watch as well as for the stone? Why is it not as admissible in the second case, as in the first? For this reason, and for no other, . . . that, when we come to inspect the watch, we perceive (what we could not discover in the stone) that its several parts are framed and put together for a purpose . . . it must have had, for the cause and author of that construction, an artificer, who understood its mechanism, and designed its use. This conclusion is invincible.

This passage is from *Natural Theology: or Evidences of the Existence and Attributes of the Deity*, by William Paley, an Anglican minister and tutor at Christ's College, Cambridge.

As the quotation from Paley's *Natural Theology* indicates, most people have a "feeling" that nature is designed in some deep way. Most religions agree: *The concept of God goes hand-in-hand with the concept of design in nature.* This is even true for most religions that lack a deity.

In addition to an explanation for the "feeling of design" in nature, religions generally provide their believers with a "feeling of hope." Houston Smith, a historian of religion, has said that hope is "our prime resource." He believes that hope is essential to psychological and physiological health. Furthermore, Smith believes that Darwinian evolutionary theory "dashes all such hopes" and that Darwinian evolution is the antithesis of the best that religions have to offer. This viewpoint is echoed by many creationists, who assert that the theory of evolution and the social policies that they believe are derived from it are responsible for most, if not all, of the ills of modern society.

If this were indeed the case, then there should be a correlation between the degree of religious belief in a society and its level of moral behavior, or between the degree of atheism in a society and its degree of moral degradation.

Two international surveys were conducted during 1991 and 1993 by the International Social Survey Program. This is currently located at the National Opinion Research Center at the University of Chicago. Seven "yes" or "no" questions were asked in the survey in 1991:[1]

God:	"I know God exists and I have no doubts about it."
Afterlife:	"I definitely believe in 'life after death.'"
Bible:	"The Bible is the actual word of God and it is to be taken literally, word for word."
Devil:	"I definitely believe in 'the Devil.'"
Hell:	"I definitely believe in 'Hell.'"

1. See Table 2.1 on page 14 for survey results.

Heaven: "I definitely believe in 'Heaven.'"

Miracles: "I definitely believe in 'religious miracles.'"

In the United States, almost 63 percent of respondents indicated that they agree that they "know God exists and . . . have no doubts about it." Only the Philippines and Poland—both predominantly Catholic countries—ranked higher than the United States.

The results of another survey[2] showed the percentage of persons who said "yes" to the following question: "In your opinion, is this statement true: 'Human beings developed from earlier species of animals'?" The results of this survey are a measure of belief in human evolution and, by implication, disbelief in creation science.

In stark contrast to the first survey, the United States ranked *dead last* in this listing, with less than 35 percent of respondents indicating that they agree with the statement "Human beings developed from earlier species of animals." Also, unlike most of the other questions in the first survey, which showed a strong positive correlation between the general belief in God and specific beliefs in such things as the Devil, an afterlife, Heaven, Hell, and miracles, there is no strong correlation between religious belief and disbelief in the theory of evolution. For example, only 9 percent of East Germans had a belief in God, but 82 percent accepted evolution, but 61 percent of Filipinos, 86 percent of whom believed in God, also accepted the theory of evolution.

The United States is often held up as the world leader in science and technology. However, polling data collected by the Gallup organization indicates that Americans do *not* support science and scientific ideas when they have to do with evolution. Beginning in 1982, the Gallup organization has polled Americans on the subject of evolution versus creationism. At Cornell University, we have conducted similar polls in our biology and evolution courses over the same period of time. In both sets of polls, respondents were asked with which of three statements they agreed:[3]

1. God created man pretty much in his present form at one time within the last 10,000 years. This is the position of most "young-Earth creationists."
2. Man developed over millions of years from less advanced forms of life, but God guided this process, including mankind's creation. This is the position of most supporters of "intelligent design."
3. Man developed over millions of years from less developed forms of life. God had no part in this process. This is the position of almost all evolutionary biologists.

2. See Table 2.2 on page 14 for survey results.
3. See Table 2.3 on page 15 for survey results.

The differences could hardly be more stark: 90 percent of Americans believe that God has guided human evolution, with almost half of them agreeing that humans have *not* evolved at all. By contrast, 95 percent of American scientists believe that humans *have* evolved over millions of years by a process in which God played no part (the same percentages hold for students at Cornell). This leads many people to ask the question: Do American scientists believe in God?

James H. Leuba conducted a poll of American scientists in 1914, asking whether they believed, disbelieved, or were agnostics about this statement:

> I believe in a God in intellectual and affective communication with mankind, *i.e.,* a God to whom one may pray in expectation of receiving an answer. By "answer" I do not mean the subjective, psychological effect of prayer.

The results of Leuba's poll indicated that in 1914, the percentage of American scientists who believed in God was 42 percent, while the percentage of American scientists who disbelieved in God was 41 percent, with 17 percent agnostics on the question.

Leuba repeated his poll of American scientists in 1933 and found that the percentage of American scientists who believed in God was 15 percent, while the percentage of American scientists who disbelieved in God was 68 percent, with 17 percent remaining agnostics on the question.

This was a dramatic change. What happened to cause such a change?

One significant event that almost certainly influenced the beliefs of some American scientists was the famous "Scopes monkey trial," which took place in the summer of 1925 in Dayton, Tennessee. John T. Scopes was a high-school biology teacher who was arrested and charged with violating Tennessee's Butler Act.

Scopes was defended by renowned trial lawyer and atheist Clarence Darrow, while the prosecution was assisted by populist and former presidential candidate William Jennings Bryan. While Scopes was found guilty of violating the law, the trial created a sensation in the press, with H.L. Menken portraying the people of Tennessee and the supporters of the Butler Act as uneducated, illiterate, anti-science rubes. Scientists, and especially evolutionary biologists, followed the trial and its outcome closely and could not help but notice that their own discipline was under attack. By 1933, the average American scientist had become an atheist.

What about today? In 1998, Edward J. Larson and Larry Witham conducted a poll similar to the one conducted by the Gallup organization, this time focusing on members of the National Academy of Sciences. They found that the percentage of members of the National Academy of Sciences who believed in God was 7 percent, while the percentage of members of the National Academy of Sciences who disbelieved in God was 73 percent, with 20 percent remaining agnostics on the question.

In 2004, Gregory Graffin, a PhD graduate student in evolutionary biology at Cornell University under Professor William Provine, conducted a similar study, this time polling evolutionary biologists who were members of the national academies of sciences in countries throughout the world.

The percentage of members of the national academies of sciences of twenty-three major countries who believed in God was 5 percent, while the percentage of members of the national academies of sciences who disbelieved in God was 87 percent, with 8 percent agnostics.

The overwhelming majority of scientists, then, and especially evolutionary biologists, do *not* believe in God, especially a God who is in personal contact with us and who has created humans or guided our evolution.

What is the connection between the concept of design in nature and the theory of evolution by natural selection?

While there may have been be a place for a supernatural deity at the beginning of time, to establish the laws of nature and set them in motion, that would be the first and last time that such an entity intervened in natural processes. If those laws were sufficiently comprehensive, then further intervention in nature by its creator would be unnecessary. As many theologians, along with Cornell evolutionary biologist and historian of science William Provine, have pointed out, such a deity would not in any way be contradicted by the theory of evolution.

This has led to a perennial controversy in American public policy, in which creationists demand that laws be passed to either prohibit the teaching of evolutionary theory in the public schools or, if it is allowed, to require that the religious creation story from the Bible be taught along with it. However, the United States Constitution has been interpreted in multiple civil court decisions, including a series of Supreme Court decisions, to prohibit the teaching of creationism or “intelligent design” in American public schools (as constituting an “establishment of religion”) and to allow the teaching of the theory of evolution as accepted by scientists.

This situation is almost unique to the theory of evolution by natural selection. No other scientific theory, with the possible exception of Einstein’s theory of relativity, has met with such intense and sustained opposition. And, as the survey results outlined earlier indicate, there is a greater disconnect between the public perception and acceptance of a scientific theory and its acceptance by the scientific community. Clearly, something about the theory of evolution by natural selection repels nonscientists as much as it appeals to scientists.

Table 2.1

Descending Order by Percent of Belief In

Country	God	Afterlife	Bible	Devil	Hell	Heaven	Miracles	Evolution
Philippines	86.2	35.2	53.7	28.3	29.6	41.9	27.7	60.9
Poland	66.3	37.8	37.4	15.4	21.4	38.6	22.7	35.4
United States	62.8	55.0	33.5	45.4	49.6	63.1	45.6	<35.4
N. Ireland	61.4	53.5	32.7	43.1	47.9	63.7	44.2	51.5
Ireland	58.7	45.9	24.9	24.8	25.9	51.8	36.9	60.1
Italy	51.4	34.8	27.0	20.4	21.7	27.9	32.9	65.2
Israel	43.0	21.9	26.7	12.6	22.5	24.0	26.4	56.9
Hungary	30.1	10.6	19.2	4.2	5.8	9.4	8.2	62.8
New Zealand	29.3	35.5	9.4	21.4	18.7	32.2	23.1	66.3
W. Germany	27.3	24.4	12.5	9.5	9.3	18.2	22.7	72.7
Netherlands	24.7	26.7	8.4	13.3	11.1	21.1	10.2	58.6
Great Britain	23.8	26.5	7.0	12.7	12.8	24.6	15.3	76.7
Slovenia	21.9	11.6	22.3	6.9	8.3	9.5	13.4	60.7
Norway	20.1	31.6	11.2	13.1	11.4	23.0	17.8	65.0
Russia	12.4	16.8	9.9	12.5	13.0	14.7	18.7	41.4
E. Germany	9.2	6.1	7.5	3.6	2.6	10.2	11.8	81.6

Table 2.2

Descending Order by Percent of Belief In

Country	God	Afterlife	Bible	Devil	Hell	Heaven	Miracles	Evolution
E. Germany	9.2	6.1	7.5	3.6	2.6	10.2	11.8	81.6
Great Britain	23.8	26.5	7.0	12.7	12.8	24.6	15.3	76.7
W. Germany	27.3	24.4	12.5	9.5	9.3	18.2	22.7	72.7
New Zealand	29.3	35.5	9.4	21.4	18.7	32.2	23.1	66.3
Italy	51.4	34.8	27.0	20.4	21.7	27.9	32.9	65.2
Norway	20.1	31.6	11.2	13.1	11.4	23.0	17.8	65.0
Hungary	30.1	10.6	19.2	4.2	5.8	9.4	8.2	62.8
Philippines	86.2	35.2	53.7	28.3	29.6	41.9	27.7	60.9
Slovenia	21.9	11.6	22.3	6.9	8.3	9.5	13.4	60.7
Ireland	58.7	45.9	24.9	24.8	25.9	51.8	36.9	60.1
Netherlands	24.7	26.7	8.4	13.3	11.1	21.1	10.2	58.6
Israel	43.0	21.9	26.7	12.6	22.5	24.0	26.4	56.9
N. Ireland	61.4	53.5	32.7	43.1	47.9	63.7	44.2	51.5
Russia	12.4	16.8	9.9	12.5	13.0	14.7	18.7	41.4
Poland	66.3	37.8	37.4	15.4	21.4	38.6	22.7	35.4
United States	62.8	55.0	33.5	45.4	49.6	63.1	45.6	<35.4

Table 2.3

Evolution Poll Results
(expressed as percents)

	Gallup Poll: General Public	Gallup Poll: College Graduates	Gallup Poll: American Scientists	Cornell Evolution Course 2001–2009
Young Earth Creationist	44	24	5	5
God-Guided Evolution	46	59	40	41
Unguided Evolution	10	17	55	54

FOR GREATER UNDERSTANDING

Questions

1. Why are design or purpose excluded from scientific explanations, especially the theory of evolution?
2. Some supporters of "intelligent design" assert that it is not an inherently religious concept and therefore can be legally taught in the public schools. Is this assertion valid and, if so, on what grounds? If not, why not?
3. Does the training that accompanies becoming an evolutionary biologist cause one to become an atheist or agnostic, or are atheists and agnostics predisposed toward pursuing a career in the science of evolutionary biology, or both?

Suggested Reading

Scott, Eugenie C. *Evolution vs. Creationism: An Introduction.* 2nd ed. Berkeley: University of California Press, 2009.

Other Books of Interest

Larson, Edward J. *The Creation-Evolution Debate: Historical Perspectives.* Athens, GA: University of Georgia Press, 2007.

National Academy of Sciences. *Teaching about Evolution and the Nature of Science*. Washington, DC: National Academies Press, 1998.

Websites of Interest

1. The *National Academy of Sciences* website provides its publication *Science and Creationism*, 2nd ed. (1999). — http://www.nap.edu/openbook.php?record_id=6024
2. The *National Center for Science Education* website provides an article by Peter M. J. Hess, Director, Religious Community Outreach (2009), entitled "Science and Religion. — http://ncse.com/religion
3. The *TalkOrigins Archive* website is devoted to the discussion and debate of biological and physical origins. — http://www.talkorigins.org/origins/faqs.html
4. The *Complete Work of Charles Darwin Online* website features William Paley's *Natural Theology, or Evidences of the Existence and Attributes of the Deity, Collected from the Appearances of Nature* (1802). — http://darwin-online.org.uk/content/frameset?viewtype=text&itemID=A142&pageseq=1

Lecture 3

Doing Science

The Suggested Reading for this lecture is Karl R. Popper's *The Logic of Scientific Discovery.*

Imagine that you are an alien explorer from a planet that does not have fruit trees. As you leave your spacecraft, you walk through an apple orchard and a green apple falls from a tree and bounces off your head.

You could ask, "*What* is this object that just bounced off my head? "What" questions ask for a *description*. Scientists often ask "what" questions about things in the world around us. The answers to such questions collectively constitute what could be called *descriptive science*. Until the twentieth century, much of biology was primarily descriptive.

Another question you could ask about the apple is, "*How* did this object fall from the tree and hit my head? "How" questions ask for an *analysis*. Scientific analysis often involves "taking apart" something to better understand the interactions and relationships between its constituent parts. This process is often called *scientific reductionism*, which means that the phenomenon is analyzed by "reducing" it to some simpler or more basic parts or principles.

Scientific analyses often focus on causes. In our apple example, you could say that the force of gravity *caused* the green apple to fall to the ground. Implicit in this analysis is the flow of time. When something *causes* something else, an event has occurred in time, with the cause *preceding* the effect that it brings about. One of the most basic principles of natural science is that *effects cannot precede causes*.

There are at least four major causes of evolutionary change:

1. mutation
2. genetic drift
3. natural selection
4. sexual selection

All four of these processes cause observable changes in the structural, functional, and genetic characteristics of populations of living organisms. Two of these processes—mutation and genetic drift—are random as far as we can tell, while two of them—natural selection and sexual selection—are not. All of these changes happen over time (often very long periods of time). As in all natural processes, the causes of evolutionary change precede their effects.

Scientists often ask "how" questions about events in the world around us. The answers to such questions constitute what could be called *analytical science*. Biology didn't become a fully analytical science until the twentieth century.

"Why" questions ask for an *explanation*. Traditionally, "why" questions focus on the "reasons" for events; that is, the details and dimensions of the "plans" for the events that resulted in their occurrence.

Asking for an explanation (as opposed to an analysis) is appropriate when you are interested in the reason why a person does something. A simple answer to the question "Why are you listening to this lecture?" might be "In order to learn more about evolution." Humans can "reason" about things: we can think about reality, make plans for the future, and conform our behavior to those plans (more or less).

Notice the phrase "in order to." Why do we say that we are doing something "in order to" accomplish some end? Because *time order* is central to such explanations: you are listening to this lecture *in order to* learn more about evolution. That is, we perform some action *first* "in order to" bring about some result *afterward*.

This is essentially the same time order as causes and effects; causes precede their effects in the same way that means precede ends. However, there is a crucial difference: *causes and effects do not require intentions or plans, but means and ends do*.

Intentional processes, in other words, seem to involve an inversion of the relationship between causes and effects as observed in nature. We know this because if we are prevented from accomplishing our goal—learning about evolution—we can still accomplish it by coming back to this lecture or by listening to another lecture or reading a book on the subject. Goal-oriented behavior involves compensation for deflection from the goal in such a way that if one is deflected from one's goal, it is still possible to accomplish it by shifting to alternative means.

This does not happen in purely natural, nonintentional processes. If an apple falls from a tree and a table intervenes, the apple does not dodge the table "in order to" reach the ground. The natural sciences are founded on this principle: *natural causes do not include intentions, purposes, or plans*.

In the natural sciences, "how" questions and "why" questions have the same answer. To a scientist, the analysis of a natural event and its explanation are exactly the same. That this is the case is virtually universally accepted by all natural scientists. It is, however, the source of much misunderstanding about science and scientific reasoning, and a source of much of the uneasiness people feel when they are first exposed to the theory of evolution by natural selection.

Science

The word *science* by itself simply means "knowledge," which can come in an almost infinite variety of forms, only some of which are what we would commonly recognize as "science." Furthermore, there is more than one kind of knowledge that can be called "science." To simplify somewhat, there are at least two kinds of "science": empirical and nonempirical.

Empirical sciences are ultimately based on the observation of nature and natural processes. Most people use the term *science* to refer to the various empirical sciences, such as astronomy, biology, chemistry, geology, physics, and so forth. In all of these empirical sciences, the various scientific principles, laws, and theories are ultimately based on observation of nature and natural processes. For this reason, the empirical sciences are often called the *natural sciences*.

Scientists working in the natural sciences assume that only those objects and processes that can be either directly or indirectly observed should be used to formulate scientific descriptions, analyses, and explanations: *Only nature matters* when doing science.

To a scientist, all natural objects and processes can, and therefore should, be completely understood and explained simply by referring to other natural objects and processes, without reference to supernatural entities or forces. This assumption, which is shared by virtually all scientists, is often referred to as *naturalism*. Because empirical scientists study nature, the common assumption that determines the methods they use to study nature is called *methodological naturalism*. Virtually all natural scientists who have thought about these issues agree that methodological naturalism is the absolute foundation of all of the natural sciences.

Like all natural sciences, the theory of evolution has been formulated based on methodological naturalism. Evolutionary biologists, like all empirical scientists, assume that the only valid scientific principles are those that have been formulated on the basis of empirical observation of nature and natural processes.

Scientific explanation involves several types of logical reasoning. Let's assume that you've never tasted a green apple before. It's sour and you might be tempted to conclude that "green *apples* are sour." However, you've only tasted *one* green apple. Therefore, the only thing that you can legitimately conclude is that this particular green apple is sour.

Having tasted one green apple, you sample another. The first thing you need to verify is that you are sampling the same thing—that the second object you sampled is the same as the first. To do this, you use what is perhaps the most widely used (but least widely recognized) form of logical reasoning: reasoning by analogy.

An *analogy* is a perceived similarity between two or more objects or processes. When you sample your second green apple, you logically assume that it has properties that are similar enough to those of the first that you can come to valid conclusions about green apples as a class of similar objects.

The kind of logic you use to make statements about classes of similar objects or processes is sometimes called *transductive reasoning*, which is the simplest form of logical reasoning. It is also absolutely necessary for all other forms of logical reasoning. Without the ability to recognize similarities between distinct objects and processes, it would be impossible to say anything about collective classes or groups of objects, and therefore to formulate generalizations (and to use generalizations to formulate specific examples).

However, transductive reasoning by itself is the weakest form of logical argument. Analogies, by definition, are not "true" statements. An analogy is *not* a statement of an observable *fact*; it is simply a statement of logical relationship.

You've now tasted two green apples. You can therefore conclude that the second green apple is similar enough to the first to come to a conclusion about the two apples as an identifiable class of similar objects. And then you sample another green apple, and another, and yet another. Eventually you sample enough that turn out to be sour that you can formulate a general statement (a "generalization") about green apples as a collective group or class: you conclude, on the basis of repeated observations, that *green apples are sour*.

How confident can you be that your generalization is valid? If you think back on the series of observations you made, you should realize that your generalization is only as good as the number and consistency of the observations you made. The more observations you make, the more confident you can be that any conclusions are valid. Logical reasoning that conforms to this pattern of repeated observation, followed by an inferred generalization, is called *inductive reasoning* (also called *induction*).

First, *inductive reasoning can never prove any generalization with absolute certainty*. No matter how many similar observations one has made, this does not absolutely guarantee that every possible observation about every single member of a logical class will turn out the same.

Second, *all conclusions based on inductive reasoning are provisional*. They are only valid up to the moment of the most recent observation. As implied in the first statement, it may turn out that the next observation will contradict any prior generalization.

Finally, all scientific reasoning begins with, and is ultimately based on, inductive reasoning. Therefore, all scientific descriptions, principles, theories, and laws have the characteristics listed above.

In many cases, scientists are unwilling to base their conclusions on a relatively small number of simple observations. Instead, most scientists attempt to further validate their conclusions by making one or more predictions based on their original generalizations, and then testing those predictions using further observations. This process—arguing from a generalization to specific cases—is known as *deductive reasoning* (also called *deduction*).

A classical example of deductive reasoning is called a *syllogism*. Here's an example:

- Scientists wear white lab coats.
- Jane is a scientist.
- Therefore, Jane wears a white lab coat.

Is this true? No; Jane Goodall is a famous scientist, but, as far as I am aware, she has never worn a white lab coat.

What this example demonstrates is that the "truth" of any syllogism absolutely depends on the validity of its beginning generalization. Therefore, although the conclusion in the syllogism listed above—that Jane wears a white lab coat—follows logically from the starting generalization (and is therefore deductively valid), since the starting generalization is clearly not valid, the syllogism as a whole is also invalid as an accurate depiction of reality.

The *scientific method* usually involves induction, followed by deduction, followed by empirical testing, followed by statistical verification, repeated indefinitely.

When a scientist has either formulated a generalization or cited a generalization that already exists, that generalization is usually called a hypothesis:

> A hypothesis is a generalization about some observable pattern in objects or events.

A hypothesis can be used to make a prediction that can be used to further test the validity of that hypothesis. A hypothesis can be tested in one of two ways: by further simple observation or by experiment. An *experiment* usually involves performing and comparing the results of two sets of observations: an *experimental test* in which you manipulate the variable that you are testing and a *control test* in which you do not manipulate the same variable. In many tests of biological hypotheses, control tests are used to determine if the variable being manipulated actually affects the outcome. This kind of investigation is sometimes called *experimental science*.

In biology in general, and especially in evolutionary biology, many investigations are essentially discovery science, rather than experimental science. As we will see, conducting simple observations, without deliberately manipulating some variable, is still a very powerful method for studying evolution.

Regardless of whether you have tested your hypothesis by simple observation or by experiment, you aren't really finished. The next step is to compare your test results with the prediction that you made using your hypothesis. If the results are close to the ones predicted, then you have confirmed (or "validated") your hypothesis. However, if the results are significantly different from the ones you predicted, you take the next (and in many ways the most important) step: you modify (or completely reformulate) your hypothesis and repeat all of the steps described above.

In science, a hypothesis that has been repeatedly tested and has not *yet* been contradicted by the available evidence is referred to as a *theory*. A hypothesis is a *tentative* guess about the way the world works. When a scientist uses the word *theory*, he or she is generally referring to what a nonscientist would call a *scientific law*, and the forces and relationships causing the phenomena described by scientific laws are sometimes referred to as *laws of nature*. Notice that although there is no real difference between a scientific theory and a scientific law, there is a fundamental difference between a *scientific* law and the law of nature it describes. The law of nature is the actual process in physical reality that causes the regularities in the phenomena under investigation.

A scientific theory is only as reliable as the observations and experiments that have been done so far to formulate and test it. This means that what scientists refer to as "theories" generally have a great deal of evidence backing them up, more than alternative explanations.

Nothing is really "true" in science, using the commonly accepted definition of "truth"—always and absolutely "true." All scientific theories are open to revision, and even a cursory look at the history of science indicates that theories that were once considered "true" are now either highly modified or have been thrown out altogether.

Much of evolutionary theory is based on logical inference:

> You make your best guess, based on the information available and what you know from past experience.

A common misunderstanding of science is that it can "prove" things. It can't, at least not in the sense of "absolute proof." However, using the scientific method one can *disprove* things. If you have formulated a hypothesis, made a prediction based on it, tested that prediction, and found it to *not* hold for a significant number of samples, then your hypothesis must either be significantly altered or thrown out entirely.

Karl Popper, possibly the greatest philosopher of science of the twentieth century, argued that to be considered scientific, a hypothesis must be *falsifiable*. It must be possible to observe evidence that would contradict, and therefore falsify, that hypothesis.

Popper's definition of what is and isn't scientific makes it seem like doing science is a smooth progression from initial observations to formulating a hypothesis to prediction to testing to statistical verification to either confirmation of the original hypothesis as a theory or disconfirmation and formulation of new hypotheses. But an examination of the actual history of science presents a different picture. Instead of smooth and steady "progress," what often happens is that theories remain relatively unchanged for a period of time, and then are relatively suddenly overturned during what historian and philosopher of science, Thomas Kuhn, has called a *scientific revolution*.

According to Kuhn's model of the evolution of science, theories (or "laws") are used by scientists to do what he called *normal science*. This is the collection of data and observations that confirm and extend already widely accepted theoretical models of nature and physical reality. However, as scientists practice normal science, they encounter anomalies: that is, observations that do not fit the already established model, which Kuhn referred to as a *scientific paradigm*. Eventually, enough anomalous evidence has accumulated that one or more scientists formulate a revolutionary hypothesis. This sets in motion a scientific revolution—what Kuhn called a *paradigm shift*—in which the old theories or laws are modified or replaced by new theories.

Charles Darwin's publication of the *Origin of Species* in 1859 is one of the clearest examples of such a paradigm shift. Prior to 1859, the predominant theory for the origin of life and living organisms was that "God did it." But, during the nineteenth century, an avalanche of new observations of fossils and living organisms from around the world provided the anomalies that Darwin used to formulate his theory of evolution by natural selection. In so doing, Darwin set in motion what would eventually be called the science of biology as we know it today.

Another way to lend confidence to a hypothesis is to show that it is part of a larger theory that already has considerable empirical support. This is a form of logical reasoning known as *abductive reasoning* (also called *abduction*). As the name implies, a tentative idea can be abducted into a larger set of ideas that already have stronger support. When this happens, the tentative idea gains considerably in credibility, even if it has little direct support.

A similar form of validation is called *consilience*. According to Edward O. Wilson, *consilience* happens when multiple, independent sources of validation all point to the same conclusion. Consilience is similar to abduction, in that it tends to strengthen hypotheses and theories without requiring as much testing and verification as new, untested ideas.

Consilience, like abduction, has played an important part in the establishment and expansion of the concept of evolution in science. As we will see (and as Wilson and others have pointed out), there are many lines of investigation in what once appeared to be widely separated fields of knowledge, all of which are now converging on what could be called a "grand unified theory of evolution" in the natural and social sciences.

FOR GREATER UNDERSTANDING

Questions

1. Since inductive reasoning cannot produce absolute certainty, is there any such thing as "truth" in science?
2. It is sometimes asserted that the validity of inferential reasoning increases from transduction through induction, deduction, and abduction, with consilience providing the greatest degree of confidence in the validity of one's generalizations. Is this hierarchy of increasing validity itself valid, and why (or why not)?

Suggested Reading

Popper, Karl R. *The Logic of Scientific Discovery*. 2nd ed. New York: Routledge, 2002.

Other Books of Interest

Feyerabend, Paul. *Against Method*. 4th ed. New York: Verso Books, 2010.

Kuhn, Thomas S. *The Structure of Scientific Revolutions*. 3rd ed. Chicago: University of Chicago Press, 1996.

Wilson, Edward O. *Consilience: The Unity of Knowledge*. New York: Vintage, 1999.

Websites of Interest

1. Allen MacNeill provides an article entitled "TIDAC: Identity, Analogy, and Logical Argument in Science" on the *Evolutionary List* blog. — http://evolutionlist.blogspot.com/2009/01/tidac-identity-analogy-and-logical.html
2. An article in pdf format by William F. McComas (University of Southern California) entitled "The Principal Elements of the Nature of Science: Dispelling the Myths." — http://coehp.uark.edu/pase/TheMythsOfScience.pdf
3. The University of Rochester (New York) features an article entitled "Introduction to the Scientific Method" by Professor Frank L.H. Wolfs of the Department of Physics and Astronomy. — http://teacher.nsrl.rochester.edu/phy_labs/AppendixE/AppendixE.html

Lecture 4

Chance and Necessity

The Suggested Reading for this lecture is Edwin Arthur Burtt's *The Metaphysical Foundations of Modern Physical Science: A Historical and Critical Essay.*

The idea of change in nature is not new or unusual. Evolution *is* change, but as anyone can observe, change happens all the time in nature.

Evolutionary change is not cyclic, like the precession of the seasons or the development of an individual organism. Evolutionary change, like the flow of time itself, is unidirectional and irreversible. Even so-called evolutionary reversions are not really cyclic, as the evolving organisms change over time into something like (but not the same as) they were before.

The idea of fundamental, irreversible change in nature is deeply unsettling to many people. On a personal level, most of us are frightened of our inevitable descent into death, and that fear encourages us to believe that death is not permanent, but only a transition to something else, something permanent and unchanging, or at least recurring, cycle after cycle. But evolution, like death, is irreversible and permanent, as far as we can tell. Natural selection, the process that Darwin proposed as the engine of evolution, depends on the birth and death of uncountable living organisms.

The idea of evolution is not new, but it has been a minority view in Western culture. What we now think of as science began in a place called Ionia: the coastline of what is now western Turkey (also called Anatolia) and the islands between it and the Greek mainland. The Ionians were originally from Greece and settled the Anatolian shore around 3,000 years ago. In the Ionian cities of Abderra, Colophon, Ephesus, and Miletus, a group of philosophers laid the foundations for the Western intellectual tradition.

Thales of Miletus (ca. 625–546 BCE) formulated a naturalistic explanation for natural phenomena. Thales is generally recognized as the founder of Western philosophy and science. In his scientific investigations, Thales was a true naturalist, asserting that natural phenomena could be studied using observation and explained with reference to natural, not supernatural, causes.

Anaximander of Miletus described the Earth as being suspended in space and proposed that humans developed from fish. Anaximander was a contemporary of Thales, but unlike him, Anaximander traveled widely throughout the Mediterranean world. Anaximander is credited with writing the first scientific treatise, usually referred to by the title *On Nature*. Also like Thales, Anaximander asserted that it was possible to explain natural phenomena without invoking the gods. He proposed that "all the heavens and the worlds within them" have sprung from "some boundless nature," an idea that is surprisingly similar to the modern theory of the origin of the universe. Anaximander, like Thales, believed that the Earth was a sphere, and that it was suspended in empty space, again anticipating basic principles of modern astronomy.

Most remarkable of Anaximander's ideas was the proposal that humans had developed (that is, evolved) from a lower form of life—fish, to be specific. He drew analogies between infant humans and infant sharks, some of which are born alive (rather than from eggs), and argued that humans must have developed from something like them.

Heraclitus of Ephesus (ca. 535–475 BCE) is most famous for asserting that "all things go and nothing stays . . . you cannot step twice into the same river." Even more than Anaximander, Heraclitus was a proponent of change in the universe. His most famous assertion states that everything in nature changes in law-like ways. The changes Heraclitus described, in other words, were not random, but rather followed patterns that could be discerned through observation and logic. He also asserted that the Earth was not created, but rather has always existed as part of what he called the *cosmos*. Like Thales and Anaximander, Heraclitus believed in natural laws and creative processes, rather than supernatural intervention into nature. However, Heraclitus went beyond Thales and Anaximander in proposing a linkage between natural laws and human ethics, a linkage that several evolutionary biologists have drawn more recently.

Democritus of Abderra (ca. 460–370 BCE) asserted that "nothing exists except atoms and the void" and that "all things are the fruit of chance and necessity."

Democritus is best known as one of the founders of the atomic theory. Long before the invention of chemistry, Democritus proposed that all matter in the universe is composed of atoms. He described atoms as tiny, hard, "uncuttable," massy objects of different composition and weight, which combine to form all material objects. Democritus explained that all of the characteristics of material objects are the result of the combination and interaction of different atoms.

Even more radical than his idea of atoms was Democritus's assertion that between the atoms in matter there is absolutely nothing—the "void." This means that all of nature consists solely of atoms, separated by nothingness. This is precisely the model of reality that is the basis of modern physics.

The idea that "nothing exists except atoms and the void" is radical because it rules out any interference or intervention into reality by supernatural entities or forces. From this, Democritus proposed an even more radical idea: that "all things are the fruit of chance and necessity." By this he meant that all events and the objects that participate in them, including ourselves, are the result of either chance (that is, random, accidental interactions) or natural (and therefore "necessary" or inescapable) causes. Taken to its logical conclusion, Democritus's model of reality rules out the intervention into nature by God or gods, and any possibility of "free will" in the universe, including human free will.

Epicurus (ca. 341–270 BCE) expanded Democritus's atomic theory, using it to provide a logical basis for naturalism and to deduce a comprehensive system of aesthetics—why we find things beautiful/pleasing and ugly/disgusting—and ethics—why actions and the thoughts that motivate them are right or wrong. Absolutely central to Epicurus's philosophy was the idea that all knowledge ultimately comes from sensory perception, and therefore from experience. According to this outlook, sense data are the basis for all generalizations about the nature of reality. The concepts we form as the result of such generalizations we then relate to each other, and ultimately we build a consistent worldview from them. Like Democritus's atomic theory, the Epicurian worldview does not require, and therefore does not include, any reference to supernatural causes for natural processes. Indeed, according to Epicurus, the gods are natural phenomena, just like anything else we observe. The only difference is that we "observe" the gods as entities in our minds, rather than as entities that live somehow outside of us and outside of nature.

Epicurus greatly extended Democritus's atomic theory, showing how atoms could be combined to form combinations like molecules, with properties that combined and went beyond the simple properties of their constituent atoms. He also proposed that atoms could "swerve" in an undetermined way, and that this "undetermined movement" could explain the existence of human "free will."

The Roman poet Lucretius (99–55 BCE) reinforced and extended Epicurus's theories about nature in a long poem entitled *De Rerum Natura*, or "On the Nature of Things." *De Rerum Natura* is a detailed explanation of how the philosophy of Epicurus (and his predecessor, Democritus of Abderra) can be applied to an understanding of nature and natural processes.

Like Epicurus, Lucretius asserted that everything we know about the universe around us we know because of observations of that universe: sense data is the basis of all knowledge. This idea, now called empiricism, is the basis for all of the natural sciences. Also like Epicurus and most modern scientists, Lucretius explained that it is possible to use logical inference to learn about events one has not observed directly or personally.

Furthermore, Lucretius made it very clear throughout his great poem that the Earth and all of the things on it had come about by chance and necessity, rather than by design. Lucretius based this assertion on the observation that many things we observe in the natural world are imperfect and therefore clearly not the result of intelligent design.

Lucretius proposed a theory of evolution by natural selection twenty centuries before Darwin. In Book 5 of *De Rerum Natura*, he proposed that the Earth (and the moon and stars) were all formed from atoms that had clumped together as a result of their "natural tendency" to combine. He then explained how plants and animals had formed from the material of which the Earth was composed, and that there was a period of time when this process produced "monsters" composed of mismatched parts. Finally, he explained why the animals we see around us today still exist: they essentially evolved by natural selection, with the well-formed animals surviving and the poorly formed ones dying off.

The philosophers of Ionia laid the groundwork for what would eventually become the modern natural sciences. But something happened between the fourth century BC and today, something that would in many ways retard the progress of science and set the stage for the current warfare between evolutionary theory and religion. That "something" was the development of Platonic philosophy.

Plato, who lived from about 428 to 347 BCE, believed that ideal forms, not natural ones, are the ultimate reality. These were essentially ideas or concepts that were related to actual, natural objects, but they existed in the mind rather than in nature. Whose mind? To Plato, the ideal forms ultimately existed in the mind of a supernatural entity or entities, which he often equated with the Greek gods or with a creator he referred to as the "demiurge."

This philosophical worldview has been called *essentialism*, because it emphasizes the "essences" of things, rather than their differences. Central to this worldview is the idea that such "essences," including the human soul, are eternal and unchanging. The most "real" things—the "essences"—cannot be perceived with the senses at all, but only with the mind, imperfect as it might be in any individual person.

Notice here, too, the emphasis on the unchanging, eternal quality of the "essences," as opposed to natural objects and processes. Natural phenomena (that is, the nonessential) are always changing, but "real" phenomena are not. Here we see the root of the opposition between the evolutionary worldview and the Platonic worldview.

Most of Plato's followers agreed wholeheartedly with these teachings and carried his ideas throughout the Mediterranean world. However, this was not entirely the case with Plato's most illustrious pupil, Aristotle.

Aristotle (384–322 BCE) taught that all natural phenomena have four causes, of which the most important were intentions or purposes. Aristotle is often credited with being the first great naturalist, in the sense of being a person who studies nature directly and for its own sake, rather than studying abstract concepts such as mathematics. Yet, for all of his careful study of the natural world, Aristotle was not an evolutionist. On the contrary, he formulated and taught a set of ideas that fundamentally contradict the basic principles of evolutionary biology. Because his writings were so influential, and because so much of medieval Christian theology was based on his ideas, Aristotle can be both credited for establishing the discipline of natural history and blamed for retarding a naturalistic model of evolutionary biology for more than two thousand years.

Central to Aristotle's worldview was the idea that everything, both objects and processes, have causes. This is part of the naturalist worldview. However, to Aristotle, intentions or purposes were always part of every cause. He argued that all objects and processes have four causes:

1. A *material cause*, by which Aristotle meant the "stuff" of which an object is composed.
2. An *efficient cause*, by which Aristotle meant the immediate producer of the object or process.
3. A *formal cause*, by which Aristotle meant the category in which an object may be classified.
4. A *final cause*, by which Aristotle meant the purpose for which the object or process is intended.

To Aristotle, all things—objects and processes—have all four causes. This means that everything has a purpose; all things exist for a reason. This is one of the two fundamental problems with Aristotle's worldview from the standpoint of evolutionary biology. To a natural scientist (and indeed, to almost anyone living in the modern world), there are many natural objects and processes that we understand to have no purpose or intentions at all. Rocks, water, air, fire, stars—the list includes most nonliving things—all have no purposes or intentions *in and of themselves*. A living organism may use one of these things and thereby give it a purpose, but otherwise a rock (falling or sitting still), water (solid, liquid, or gas), air (moving or not), fire (a rapid chemical reaction between oxygen and some other material), and so forth have no preexisting purposes that cause them to exist or do what they do.

Aristotle also believed that the many and varied types of living organisms that he had described and classified (what would later be called "species") were not only well-defined, but were also permanent and unchanging. He recognized that change occurs, but he believed that all change in nature was essentially cyclic, and that therefore no real permanent change occurs. In this view, Aristotle reverted to the idealism of his teacher, Plato, and in so doing promulgated a doctrine that made the idea of evolution virtually unthinkable for two millennia.

FOR GREATER UNDERSTANDING

Questions

1. What was so revolutionary about the ancient Ionian "enlightenment"?
2. Aristotle has often been called "the first naturalist." However, it is clear from most of his work that he opposed the worldview known as ontological naturalism. Why is this, and is this a contradiction in Aristotle's thinking or not?
3. Do Plato's and Aristotle's philosophical ideas resonate with modern evolutionary biology or with modern creationism, including "intelligent design," or both (or neither) and why?

Suggested Reading

Burtt, Edwin Arthur. *The Metaphysical Foundations of Modern Physical Science: A Historical and Critical Essay*. Charleston, SC: BiblioBazaar, 2010 (1924).

Other Books of Interest

Pirsig, Robert M. *Zen and the Art of Motorcycle Maintenance: An Inquiry into Values*. New York: Harper Perennial, 2008.

Popper, Karl. *The Open Society and Its Enemies: Volume One: The Spell of Plato*. 7th ed. New York: Routledge, 2002 (1971).

Schrödinger, Erwin. "The Ionian Enlightenment." Pp. 53–68. *Nature and the Greeks* and *Science and Humanism*. Cambridge: Cambridge University Press, 1996.

Websites of Interest

Allen MacNeill provides an article entitled "Incommensurate Worldviews" on the *Evolutionary List* blog. —
http://evolutionlist.blogspot.com/2006/02/incommensurate-worldviews.html

Lecture 5

The Origin of the *Origin*

The Suggested Readings for this lecture are Edward J. Larson's *Evolution: The Remarkable History of a Scientific Theory,* chapter 1: "Bursting the Limits of Time" and chapter 2: "A Growing Sense of Progress."

To understand why modern biologists, and especially evolutionary biologists, assume the revolutionary and controversial idea that purpose plays no more part in evolution than it does in physics or chemistry, we need to look at the historical changes in the ideas of the origin of life. In European culture, the predominant explanation of the origin of life was originally provided by the Judeo-Christian Bible:

- All life was created by God approximately 6,000 years ago in a single act of creation that took place over four days.
- All forms of life were created in essentially their present form out of nothing.
- Since that first creation, none of these specially created "kinds" of living things have changed fundamentally from their originally created "kinds."

This creation myth was combined during the Middle Ages with Plato and Aristotle's ideas about "ideal forms" and purposeful causation in nature, producing a system of beliefs in which the direct intervention by God in natural processes was necessary for anything to happen anywhere.

During the Scientific Revolution, which began in the sixteenth century and continues to the present, this situation finally began to change:

- In 1632, Galileo Galilei, in his *Dialog Concerning the Two World Systems*, undermined the biblical story of creation by showing that the Sun, not the Earth, is the center of the universe, an idea that had first been proposed by Copernicus.
- In 1687, Isaac Newton published *Philosophiae Naturalis Principia Mathematica*, now usually called simply the *Principia*). In it, he laid out a system of physical laws by which motion could be analyzed, based on the assumption that all physical motion is the result of purposeless mechanical forces. This idea—that purpose was unnecessary for the explanation of physical phenomena—became a universal standard in all of the physical sciences within the century following the publication of Newton's *Principia*.
- In 1789, Antoine Laurent Lavoisier published his *Elementary Treatise of Chemistry*. In it, he presented the basic principles of modern chemistry, including the conservation of mass and an

explanation of how combustion, photosynthesis, and respiration were related chemical processes, none of which required supernatural explanations. Again, Lavoisier's explanations for chemical reactions did not require any assumption of preexisting purpose or design in nature.

The idea of evolution has existed as a minority view within Western culture since the dawn of recorded history. However, it was not until the eighteenth century that the groundwork for a fully scientific theory of evolution was laid. Ironically, the cornerstone of such a theory was based on the idea that all life and living organisms were created by God relatively recently.

As the title of Darwin's *Origin of Species* implies, the concept of species is central to the concept of evolution. People have recognized the existence of what could be called "species" since prehistoric times, but it wasn't until the eighteenth century that the concept of species was systematically defined and recognized by naturalists.

The person who deserves much of the credit for this recognition was Karl Linnaeus. A Swedish naturalist, Linnaeus is best remembered for his introduction of the system of classification known as binomial nomenclature, by which every living organism can be classified as a member of a particular genus and species.

Linnaeus proposed a systematic classification system for plants in his *Systema Naturae*, first published in 1735 as a pamphlet of eleven pages. In it, he proposed that every species of plant could be classified using a two-part name consisting of a genus and species name. Linnaeus followed common practice at the time by using Latin as the language in which all plants would be named and classified.

Linnaeus's classification scheme was immediately popular with other naturalists, for several reasons:

- First, it allowed all plants, including newly discovered ones, to be classified relatively quickly and easily on the basis of their reproductive anatomy.
- Second, Linnaeus's *Systema Naturae* classified all plants within a hierarchical scheme, thereby allowing naturalists to relate species to each other and to their habitats. This dramatically reduced ambiguity in identification and classification, and set the stage for Darwin's revolutionary classification system based on descent.
- Linnaeus's classification scheme was also useful because it was written in Latin, the universal language of science at the time. As a "dead" language, its grammar and vocabulary were fixed and unchanging, thereby allowing all scientists in all countries to use it without confusion.

At about the same time that Linnaeus was developing his classification system in Sweden, a Frenchman named Georges-Louis Leclerc was writing a massive "natural history"—that is, an encyclopedia of all that was known about the natural world at the time.

Like the philosophers of ancient Ionia, Leclerc suggested that all material objects were composed of particles, and that in particular living organisms were composed of "organic particles." These could aggregate to form living things and could also reaggregate to form other living things at other times. This simple form of evolution was not far from that proposed by Lucretius, but like those earlier theories, Leclerc's was purely descriptive. He did not suggest an actual mechanism for how such changes could come about, nor did he suggest any way in which his ideas could be tested.

An aspect of Leclerc's natural history that would be expanded later by several geologists, and would eventually provide a crucial foundation for Darwin's theory of evolution, is that things that are happening now can be assumed to have been happening in the past and to have produced the world that we see around us today: "The present is the key to the past." This idea would by formalized into the principle of uniformitarianism, first by the geologists James Hutton and later by Charles Lyell, who was to have an extraordinarily important influence on the young Charles Darwin.

One of the intellectuals who had a profound, though often overlooked, influence on subsequent developments was Erasmus Darwin, the grandfather of Charles Darwin. In 1803, Erasmus Darwin published a long prose-poem entitled *Zoonomia*, or the *Laws of Organic Life*. In it, the elder Darwin speculated on the origin of living things.

When Charles was working on the *Origin of Species* he considered using some of his grandfather's ideas in his own theory of evolution. However, he eventually concluded that Erasmus Darwin's ideas about "organic change" owed more to the revolutionary temper of the times and could not be considered to be scientific.

As the director of the Musée National d'Histoire Naturelle, Leclerc arranged to have fellow naturalist Jean-Baptiste Lamarck appointed as curator of invertebrates.

Lamarck's study of the mollusks of the Paris basin indicated that many species had changed over time, with new species arising and others disappearing. He summarized his ideas in his most important book, *Philosophie Zoologique*, first published in 1809. In it, Lamarck presented the first logically reasoned scientific theory for the origin of species. He proposed two laws, as follows:

- Use and disuse: "In every animal which has not passed the limit of its development, a more frequent and continuous use of any organ gradually strengthens, develops and enlarges that organ, and gives it a power proportional to the length of time it has been so used;

while the permanent disuse of any organ imperceptibly weakens and deteriorates it, and progressively diminishes its functional capacity, until it finally disappears."

- Inheritance of acquired characteristics: "All the acquisitions or losses wrought by nature on individuals, through the influence of the environment in which their race has long been placed, and hence through the influence of the predominant use or permanent disuse of any organ; all these are preserved by reproduction to the new individuals which arise, provided that the acquired modifications are common to both sexes, or at least to the individuals which produce the young."
- Lamarck also proposed that new living forms arose continuously through a kind of spontaneous generation, so that independent lines of evolving organisms are constantly being added to living systems.

A further aspect of Lamarck's evolutionary theory, which Darwin would directly oppose, was that as a result of their activities, species are constantly "improving," that is, becoming more complex and better adapted over time. In other words, Lamarck believed that evolution had a purpose, which was to produce more and more complex and highly adapted living organisms, with the ultimate goal of bringing about the evolution of humans.

All the major features of Lamarck's evolutionary theory have since been shown to be either false or unnecessary for a scientific explanation of evolutionary change. However, at the time, they were considered revolutionary, and their importance to Darwin's later theory has often been ignored. Lamarck not only proposed that species could evolve, he was the first to propose a law-like explanation for how such changes could take place, explanations that could then be tested by empirical observation. Unfortunately for Lamarck's career, however, his ideas ran directly counter to those of the most widely respected and politically powerful naturalist in France: Georges Cuvier.

Jean Léopold Nicolas Frédéric Cuvier published his *Discourse on the Revolutionary Upheavals on the Surface of the Globe* in 1825, proposing that many species had gone extinct in the distant past as the result of worldwide catastrophes. Cuvier's ideas were extraordinarily influential and we will briefly focus on four of them:

1. *Extinction has happened*. Cuvier believed in a version of deism in which God intervened periodically in life on Earth by causing the catastrophes that resulted in mass extinctions. However, the idea that extinction had occurred undermined a basic principle of Christian creationism: that God had created all forms of life all at once about 6,000 years ago and that since that time no significant changes have happened to the originally created kinds. By legitimizing the idea of extinction for scientists and undermining the concept of unchangeable "originally

created kinds," Cuvier unintentionally set the stage for Darwin's theory of evolution by natural selection.

2. *Comparative anatomy can be used to show relationships between extinct and still-living forms*. Under the tenets of biblical creationism, there are no necessary relationships between extinct and still-living organisms. Indeed, the former are assumed for doctrinal reasons to be impossible. Cuvier made it possible to believe that extinct organisms were related to still-living ones, and that the way to explain those relationships was through the comparative study of the anatomy of extinct and still-living forms. Darwin used these same principles in the *Origin of Species*, but he proposed a revolutionary explanation for the relationships both he and Cuvier had observed.

3. *The history of life on Earth can be inferred from the fossils and other remains found in the layers of rock found around the world*. According to the most widespread interpretation of the biblical creation story, the fossils and rock layers that Cuvier studied were deposited by a single worldwide flood that happened only a few thousand years before and lasted for only forty days and nights. However, as Cuvier pointed out, the rapidly accumulating weight of the geological evidence was for multiple extinction events, taking place over a very long period of time, and followed each time by the repopulation of the world by new species of animals and plants.

4. *The Earth must be very, very old*. The age of the Earth according to the biblical account is approximately 6,000 years. This is nowhere near enough time for evolution to have occurred, and so even if it were possible for the "original created kinds" to have evolved (an idea rejected by most biblical creationists), not enough time would have elapsed for any significant evolutionary change to have happened.

The application of naturalistic explanations to the living world that was begun by Lamarck and Cuvier reached its climax in the work of Charles Darwin. His ideas have had an enormous impact on society, perhaps more than those of any other single person. His books changed the world and will continue to change it for the foreseeable future.

Darwin's only formal training and his only formal academic degree was in Anglican theology. How could he have written the most important book in biology, if not all of science? There are several aspects of Darwin's character that could explain this apparent contradiction:

- He was an extraordinarily avid collector, especially of natural objects.
- He was very deeply interested in geology.
- He was fascinated by botany and "natural history." His botany teacher, Professor Henslow, thought so much of his talents that he recommended that Darwin be appointed as ship's naturalist for the

> voyage of HMS *Beagle*, a royal navy survey ship, scheduled for a three-year around-the-world voyage.

The *Beagle*'s captain, Robert Fitzroy, felt that Darwin was insufficiently qualified for the post, but he offered Darwin the position of "gentleman's companion." While voyaging on the *Beagle*, Darwin read Charles Lyell's multivolume text, *Principles of Geology*, which convinced him of Lyell's principle of uniformitarianism.

From a reading of his journals and notebooks, it is clear that Darwin was not convinced of the reality of evolution while on the voyage of the *Beagle*. However, Darwin's voyage aboard the *Beagle* transformed him from an indifferent student to a passionate and highly skilled naturalist. He had a natural talent for collecting specimens and recording his observations. He wrote volumes of notes and sent thousands of specimens back to museums in England. His notes eventually became the basis for his first book, *A Journal of the Voyages of HMS Beagle*.

The crucial turning point in Darwin's thinking came on the evening of 28 September 1838—two years after his return to England—when (according to his autobiography),

> . . . I happened to read for amusement "Malthus on Population," and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species. Here then I had at last got a theory by which to work . . .

FOR GREATER UNDERSTANDING

Questions

1. Linnaeus, author of *Systema Naturae*, was a Christian creationist, yet his work set the stage for Darwin's theory of the origin of species. How and why was this the case?
2. What aspects of Lamarck's theory of evolution did Darwin accept and which ones did he deny and replace?
3. Why was Darwin so impressed with Reverend Paley's books on natural theology, and why did he eventually publish a book that undermined Paley's arguments?

Suggested Reading

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Other Books of Interest

Ruse, Michael. *The Darwinian Revolution: Science Red in Tooth and Claw.* Chicago: University of Chicago Press, 1979.

Thompson, Keith Stewart. *Before Darwin: Reconciling God and Nature.* New Haven: Yale University Press, 2005.

Websites of Interest

1. Project Gutenberg provides the text of Erasmus Darwin's *Zoonomia, or the Laws of Organic Life* (1796). — http://www.gutenberg.org/etext/15707
2. The *Complete Work of Charles Darwin Online* website features Charles Darwin's *Journal of Researches into the Geology and Natural History of the Various Countries Visited by* HMS *Beagle* (1839). — http://darwin-online.org.uk/EditorialIntroductions/Freeman_JournalofResearches.html
3. The University of Colorado at Boulder's *Charles Darwin: Early Evolutionists* website provides Jean-Baptiste Lamarck's *Zoological Philosophy* (1809, reprinted in 1914). — http://spot.colorado.edu/~friedmaw/Early_Evolution/Lamarck.html

Lecture 6

The Darwinian Manifesto: Natural Selection

The Suggested Reading for this lecture is Daniel C. Dennett's *Darwin's Dangerous Idea: Evolution and the Meanings of Life.*

Most revolutions, including most scientific revolutions, begin with a manifesto of some sort. The opening salvo in the Darwinian revolutions was the publication of Darwin's most important (and controversial) book, the *Origin of Species*, in 1859. In it, Darwin drew together the multiple threads of nineteenth-century natural history and wove them into what he himself called "one long argument." Like any good argument, it was buttressed by evidence, which Darwin marshaled to support his revolutionary (and deeply disturbing) ideas.

But Darwin did not start out as a revolutionary. He was still a creationist when, in 1836, he returned to England after the five-year voyage of the *Beagle*. Upon his return, he pondered the things he had observed. In particular, he considered three sets of observations that were eventually to lead him to the idea of evolution by natural selection:

1. The patterns he observed in the geographic distribution of animals and plants as the *Beagle* circumnavigated South America. Darwin observed that similar habitats in widely separated locations were inhabited by similar (but not the same) species; he eventually concluded that this indicated that such species had descended from common ancestors.
2. The fossils of extinct animals he observed and collected from all over South America. His careful observations of these fossils convinced him that they were the remains of species no longer present in South America, but which were related to species that still existed. Like the geographical distributions described above, these observations suggested that modern species had descended from other, similar species now extinct.
3. The distribution of species he observed on volcanic islands in the Atlantic and Pacific oceans. He noticed that although these islands were located in the same types of habitat, they were inhabited by different species. Furthermore, although these species were not at all related to each other, they were related to species located on the nearby mainland, suggesting again that the island species and the nearby mainland species had descended from common ancestors.

According to Darwin, natural selection is the outcome of a process that has four prerequisites:

1. Variety: There are significant variations in the characteristics of the members of populations.

2. Heredity: The distinct variations noted above must be heritable from parents to offspring.
3. Fecundity: Living organisms have a tendency to produce more offspring than can possibly survive. Among those individuals that do survive, those that also reproduce pass on to their offspring whatever heritable characteristics made it possible for them to survive and reproduce.
4. Demography: Some individuals survive and reproduce more often than others. Individuals survive and successfully reproduce because of their physical and behavioral characteristics, which are the basis for evolutionary adaptations.

In about 1854, Darwin began working on the manuscript of what he called his "big species book," to be titled *Natural Selection*. He toyed with the idea of having it published after his death, so as to avoid the controversy that he knew it would generate.

Darwin never published *Natural Selection*. Instead, he rushed a brief "abstract" of his "big species book" into print in the fall of 1859. The reason for this sudden rush to publication is well known: Darwin had been scooped on his theory of natural selection by a fellow English naturalist, Alfred Russell Wallace. Anxious to preserve his priority as the discoverer of natural selection, Darwin rushed what he considered to be an "abstract" of his ideas into print in November 1859. This "brief abstract," published without footnotes, illustrations, or bibliography, was the first edition of the *Origin of Species by Means of Natural Selection*.

In it, Darwin began by pointing to the various breeds of domesticated animals and plants as being analogous to the products of natural selection. He then launched into an extended discussion of domesticated pigeon breeds, which he concluded are descendants of the wild rock dove.

Although these breeds are startlingly diverse, they are not separate species. Darwin asserted that all seven-hundred-plus breeds of pigeons had been bred from the wild rock dove by means of artificial selection and that most of the artificial selection done by animal and plant breeders was probably done unconsciously, by breeders choosing desirable traits among their domesticated animals and plants.

Darwin had two aims in writing the *Origin of Species*:

1. To convince his readers of the reality of "descent with modification" from common ancestors; he was largely successful in this aim.
2. To convince his readers that natural selection was the cause of the "beautiful adaptations" that define species; he was largely unsuccessful in this aim.

To accomplish the second aim, Darwin was forced to use an "argument from analogy," because he could not point to any real-world examples. He essentially argued that "breeds" under domestication are analogous to "species" in the wild insofar as both are shaped by selection. The animal and plant breeders that Darwin consulted believed that their breeds were derived from separate species of pigeons in the wild. Darwin pointed out that they were all derived from one "wild type" ancestor, which had been modified by artificial selection. In other words, natural selection is analogous to artificial selection.

After reading Malthus's essay on population growth, Darwin realized that the excess population growth that Malthus described would result in a "struggle for existence" that he would later call "natural selection." Malthus's *Essay on the Principle of Population* included two ideas that were crucial for Darwin's theory:

1. That the food supply in any area increases only linearly, whereas the population increases exponentially.
2. That because of this every natural population will eventually outstrip its food supply, leading to widespread starvation.

Darwin proposed that species in nature were subject to a "struggle for existence" caused by the enormous reproductive potential of living organisms. As Malthus pointed out, if a population is not limited by food, space, or other resources, it will rapidly increase. In the *Origin of Species*, Darwin pointed out that unchecked populations could easily cover the surface of the Earth.

The "struggle for existence" proposed by Darwin is a struggle to leave the most offspring, which over time will result in the offspring of the more successful individuals becoming more common among the members of their populations.

Central to Darwin's theory was the idea that, contrary to the biblical account of creation and history, the Earth was very old—indeed, many millions of years old. Darwin argued that natural selection acts too slowly to be observed.

If this is the case, then how did Darwin go about proving to the reader that natural selection occurs, and that it is the "engine" of "descent with modification"? Darwin drew analogies to artificial selection in the breeding of domesticated animals and plants. He also provided two examples of natural selection in action: wolves preying on deer, and plant-insect coevolution. However, it is important to note that both of these examples are imaginary. Darwin had no direct observable examples of natural selection.

Natural selection doesn't depend upon survival alone. Indeed, only individuals who reproduce pass on their heritable characteristics to their offspring. This means that successful reproduction is at least as important, if not more important, than survival alone. Darwin stated that mating among most animals is based on "female choice." That is, females are "choosy" about who they will mate with, while males are generally "ready and waiting" for females to allow them to mate. Darwin pointed out that this will cause females to shape the adaptations of males by choosing mates based on their characteristics. He called this process sexual selection.

Darwin implied that sexual selection can have effects that are separate from those due to natural selection (some evolutionary biologists agree, but others argue that sexual selection is merely a special form of natural selection). Darwin based most of his second-most-famous book, *The Descent of Man and Selection in Relation to Sex*, on the concept of sexual selection, especially as the result of female choice. Darwin believed that female choice could explain the evolution of the various races of humans, as well as the more obvious differences between females and males in other species.

Recall that according to Darwin, variation among the heritable characteristics of individuals in populations is one of the most important prerequisites for evolution.

Neither Darwin nor any of his contemporaries (that he knew of) had a coherent theory of heredity or variation. In a coincidence of history, Gregor Mendel had published his theory of heredity at about the same time, but Darwin either never read it or didn't understand its importance to his own work. Consequently Darwin could propose no theory of heredity or variation in the *Origin of Species*, nor could he suggest how it might affect his conclusions.

However, instead of giving up his argument, he simply accepted as a given that many important traits of animals and plants are heritable. He also proposed that, although he had no explanation of how they arose, variations among the members of a species do indeed occur and can provide the raw material for natural selection.

Darwin also asserted that use and disuse could produce characteristics that were inherited. This assertion is surprisingly close to that of Lamarck's idea of inheritance of acquired characteristics. Although Darwin returned to this idea several times in the *Origin*, he concluded that such changes do not account for most of the variation we observe among the members of most species.

Criticisms

Darwin's imagination (and his faith in natural selection alone) sometimes seemed to fail him. Speaking of blind cave fish, he wrote:

> [It] is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, I attribute their loss wholly to disuse.

Actually, it is relatively easy to explain the evolution by natural selection of eyelessness in cave fish. Eyes, especially those of fish (which have no eyelids) are a common site of infection and injury. Natural selection is essentially a balance between positive and negative aspects of any trait.

If the positive aspects outweigh the negative, the trait will persist; otherwise it will eventually disappear. In the case of eyes, as long as the positive benefit of sight outweighs the probability of infection or injury, eyes will persist. However, without any positive benefit from having eyes, natural selection will eventually cause their disappearance.

Darwin also stressed that "correlation of growth" could produce peculiar side effects when only certain traits were subjected to selection.

Selection for traits controlled by genes that have more than one phenotypic effect can produce considerable variation between the individuals in populations, which may serve as raw material for selection. Darwin seemed to be asserting that because of correlation of growth, there are limits on how much change can take place in any organism (or part of an organism) as the result of natural selection. However, later in the same chapter he wrote

> I believe . . . natural selection will always succeed in the long run in reducing and saving every part of the organization . . . without by any means causing some other part to be largely developed in a corresponding degree. And, conversely, that natural selection may perfectly well succeed in largely developing any organ, without requiring as a necessary compensation the reduction of some adjoining part.

As he stated in both the *Origin of Species* and his autobiography, Darwin used a powerful technique to deal with his critics: he listened very carefully to their criticisms and objections and addressed these directly in his presentations of his theories. For example, he anticipated that some readers would disbelieve his assertion that the wings of bats are descended from a common ancestor of the hands of humans. He countered this by pointing out that it is possible to imagine how bats might have evolved from something like a flying squirrel.

In so doing, Darwin committed a serious fallacy: implying that a species living today is descended from another species living today. Creationists gleefully jump on such assertions, because they are in nearly all cases egregiously false. What Darwin should have said is that flying squirrels and bats are both descended from a squirrel-like common ancestor.

Darwin pointed out that convergent evolution (that is, adaptation to similar environmental pressures) could result in traits that appeared very similar in unrelated organisms. This could lead observers to false assumptions about common ancestry and phylogenetic lineages. He suggested that it would be more useful to focus attention on nonadaptive characteristics, especially when determining phylogenetic relationships (that is, constructing evolutionary "family trees" of descent with modification).

Darwin concluded that evolution, like all of nature, does not act by sudden jumps. However, as we will see later in this series of lectures, on this point at least, one hundred fifty years of paleontology have tended to point to a very different conclusion.

Many of Darwin's critics pointed out the inconceivability of the idea that an organ such as the vertebrate eye, so complex and well-adapted, could have arisen without some kind of design or purpose in mind. Darwin countered this argument—often referred to as an "argument from incredulity"—by pointing out that it is possible to imagine how such an organ arose, not from a sudden creation, but rather from a series of gradual steps.

Darwin therefore asserted the following:

> If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down. But I can find out no such case.

Darwin himself pointed out another potential fatal argument against his theory: if any species could be shown to have evolved a trait exclusively for the benefit of another species, it could not have done so by natural selection. The only logical alternative is design by a benevolent deity. Darwin pointed out that in many cases, what seem to be adaptations that benefit other species (such as the flowers that provide nectar and excess pollen to pollinating insects) actually benefit both species, and so natural selection is not undermined. Indeed, Darwin took pains several times in the *Origin* to point out that natural selection generally results in adaptations that are far less than perfect. His point in doing so was to imply that an omnipotent supernatural creator would not have created such "imperfect adaptations."

Darwin was very interested in the behaviors of nonhuman animals, especially those that were commonly referred to as "instincts." He analyzed instinctive behaviors in much the same way as he wrote about the anatomical characteristics of organisms:

> The canon of *Natura non facit saltum* applies with almost equal force to instincts as to bodily organs.

He then launched into a discussion of the evolution of the fascinating behavior of two groups of social insects: honey bees and ants.

> Thus, as I believe, the most wonderful of all known instincts, that of the hive-bee, can be explained by natural selection having taken advantage of numerous, successive, slight modifications of simpler instincts.

But then, immediately following this statement, Darwin pointed out that the existence of sterile castes in social insects could present a "fatal flaw to the theory" of evolution if he could not explain them as just another case of natural selection in action.

Members of neuter castes (such as "worker ants") have instincts and anatomical features that are different from those of reproductive individuals (such as "queen ants"). The question Darwin confronted was, how can a characteristic of a neuter (that is, sterile) individual be passed on?

Darwin answered:

> This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end.

Darwin's argument was this:

- Neuter castes show adaptive variation, just like individual organisms.
- Neuter caste members are directly (and closely) related to reproductive individuals.
- Therefore, selection acting on fertile individuals can produce adaptations in their closely related sterile "family members."

FOR GREATER UNDERSTANDING

Questions

1. What was it about Darwin's theory of evolution by natural selection that made it convincing for scientists in a way that Lamarck's theory was not?
2. What is the importance of variation to Darwin's theory of natural selection?
3. The prevailing theory of inheritance at the time of Darwin's *Origin* was that the characteristics of living organisms were blended during mating, like different colors of paint. If this were the case, would Darwin's theory of natural selection be viable?

Suggested Reading

Dennett, Daniel C. *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. New York: Simon & Schuster, 1996.

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Lecture 7

The Darwinian Manifesto: Descent with Modification

The Suggested Reading for this lecture is Daniel C. Dennett's *Darwin's Dangerous Idea: Evolution and the Meanings of Life.*

Darwin included an entire chapter on hybridization in the *Origin of Species*. This is because the theory of special creation, which Darwin directly opposed, implies that species are created separately and that there are "unbreakable barriers" between species that prevent real hybridization. Darwin attacked this idea on three fronts:

1. He pointed out that there are viable hybrids between many species in nature, thereby undermining the "unbreakable barrier" argument.
2. He also pointed out that natural selection itself could not erect any such barriers, because natural selection cannot possibly select for any form of sterility. How can a tendency toward sterility possibly be inherited?
3. Finally, he pointed out that within species there is nearly as much sterility as exists between species. This implies that sterility per se is neither a necessary nor a sufficient condition for defining species, nor does it necessarily imply anything about the supposedly "unbreakable" barriers between species.

Darwin asserted that hybrid sterility or inviability must be side effects of the divergence of species. Essentially, once one species has diverged into two separate species, random changes in the hereditary makeup of the members of the separate species will eventually result in their being unable to interbreed and produce viable offspring.

The Fossil Record

During the late seventeenth and early eighteenth centuries, geologists codified several principles that correlated rock formations with the passage of time and distribution in space. These principles are the basis for the science of stratigraphy, which is the study of the pattern of layering in sedimentary rocks.

The principles of stratigraphy, when combined with Lyell's principle of uniformitarianism, implied that the Earth was much older than the biblical account of creation. Geologists and evolutionary biologists have used several techniques to provide dates for geological processes:

- Relative dating: Relative dates are usually based on stratigraphic position; that is, deeper strata are considered older, whereas more superficial strata are considered newer (that is, more recently deposited). Fossil inclusions are very often used to identify and correlate stratigraphic sequences, and as a consequence are central to the process of relative dating.

- Absolute dating: Several techniques have been developed to allow geologists to infer absolute (that is, chronological) dates for different rock layers. Each of these techniques depends upon a physical or chemical process that changes over a known rate of time, such as the decay of radioactive isotopes in igneous rock intrusions.

Relative and absolute dating scales have been combined to produce the geological time scale. The order of layers in this column (which are generally named after the geographical region from which they were first described) are the same the world over, although the entire column is not known from any single location. There are very large gaps in most of these layers, and in many places whole layers are entirely missing.

Darwin described this situation by saying that the fossil record (the collection of fossils that might confirm the theory of evolution) is everywhere incomplete. We do not have a continuous, unbroken fossil record of the evolution of any living thing, and certainly not for life on Earth as a whole.

In particular, Darwin pointed out that intermediate forms are almost entirely missing from the fossil record. He wrote that this is to be expected, for two reasons:

1. The process of natural selection itself generally eliminates the intermediate forms, as the more recent forms are better adapted and have replaced the older ones.
2. There is a very low probability of finding a complete record, plus the difficulty of finding a transitional form among all of the other forms in the geological column.

That was the situation in Darwin's time. Today, we have the opposite problem: There are literally millions of fossils in collections around the world, most of which have never been carefully analyzed.

The geographical distribution of animals and plants around the world provided Darwin with a powerful argument against the theory of special creation: Why would a deity create unrelated, but very similar, organisms at the same latitude but on different continents, when they had the same climate, geology, and so forth, but create different, yet closely related, organisms at the same latitude on the same continents?

Darwin pointed out that if one travels up or down the coast of nearly any continent, one "never fails to be struck by the manner in which successive groups of beings, specifically distinct, yet clearly related, replace each other."

Finally, Darwin pointed out that the inhabitants of islands lying at about the same latitudes worldwide were also populated by animals and plants that were not at all related to each other. Instead, they were closely related to organisms located on the nearby mainland, providing strong evidence that they had been derived from those organisms, rather than having been created in place. Taken together, these correlations present some of the strongest evidence for descent with modification and were crucial to Darwin's eventual success in convincing most biologists that evolution had happened.

The distribution of several species of fossil animals and plants at the end of the Permian period (approximately 245 million years ago) was puzzling to Darwin. Fossils of extinct animals and plants, such as Cynognathus, Lystrosaurus, and Glossopteris from South America, Africa, India, and Australia, were similar enough to be classified in the same species (or at least the same genus). Yet, they were so widely separated as to require Darwin to propose complex explanations, such as land bridges and transoceanic floating mats of vegetation.

Now we know that these fossils are explainable with reference to a much broader explanation. All of the continents (including Antarctica) were once connected in a giant continent, called Pangea, which later split apart into six pieces and "drifted" to their current locations. The theory of continental drift (with its underlying geological theory, called plate tectonics) provides the explanation that Darwin missed.

There is also very strong evidence that sudden, drastic changes can alter not only the course of evolution, but the geological features of the Earth itself. For example, there is increasing evidence that the extinction of the dinosaurs at the end of the Cretaceous period was caused by an asteroid collision.

Darwin completely overturned the previous system of taxonomy, which was based on the underlying assumption that all living things had been created by God in essentially their present form, and that species boundaries were fixed and unbreakable.

Darwin proposed descent as the basis for a more "scientific" systematic classification and pointed out that basing a new system of classification on descent (that is, evolution) was prone to error in the case of convergent organisms (that is, organisms that appear superficially similar as the result of adaptation to similar environmental conditions).

This caveat has caused problems for systematists right up to the present day. An important point to note in this context is that acceptance of natural selection as the primary "engine" of evolutionary descent is not necessary for the construction of a taxonomy based on descent. On the contrary, evolutionary systematics is concerned only with the outcome of evolution, not with its mechanism.

For this reason, and to compensate for the pitfalls of convergent adaptations, systematists have generally followed Darwin's lead and used non-adaptive characters as the basis for taxonomic groupings.

Systems of evolutionary classification are often confounded because of confusion between homology and analogy. Homology (in evolutionary biology) is the existence of similar (or modified) characteristics as the result of descent from a common ancestor. Examples of homology are the wings of bats and the hands of humans. Although these structures appear quite different at first glance, a more detailed examination of the bone structure of both indicates that the same bones are located in the same relationships with each other.

Analogy (in evolutionary biology) is the existence of similar characteristics as the result of convergent evolution. Examples of analogy are the wings of insects and the wings of birds. They both appear superficially similar in some respects, and both perform the same functions for the animals that have them, but they are not derived from a common ancestor. That is, the common ancestor of insects and birds (a very primitive animal indeed) did not have wings, which evolved independently in insects and birds.

Recent genetic analysis of many structures in many species of animals has indicated that what were once thought to be the result of homology actually are not; in many cases, structures that appear to have been derived from a common ancestor actually evolved independently in separate lines of descent.

There are several objections that have been raised to the use of evolutionary descent as the basis for a comprehensive system of taxonomic classification. Beside the obvious objections of creationists, there are some problems with using descent for classification, even among scientists.

The prevailing "biological species concept" (which is based on the ability of members of the same species to interbreed and produce fertile offspring under natural conditions) is not applicable to several important groups of organisms:

- Extinct organisms (known only from fossils or preserved specimens)
- Organisms whose reproductive capacity in the wild is unknown
- Organisms that can be forced to hybridize under laboratory conditions, but do not do so under natural conditions
- Asexually reproducing organisms

Evidence of descent with modification from common ancestors is useful in applying the currently most favored kind of classification scheme, called cladistics. Cladistics is a system of classification based on shared derived characteristics (that is, characteristics that have changed over time and are therefore shared by the descendants of a common ancestor).

The remarkable complexity and similarity of the embryos of widely separated vertebrate groups (such as fish, amphibians, reptiles, birds, and mammals), plus the tendency of developing embryos to survive rather drastic shocks without lasting damage, has often been cited as evidence of intelligent design. However, Darwin pointed out that these same similarities could be viewed as evidence for descent with modification from common ancestors sharing similar early embryonic stages.

Several qualities of the *Origin* made its reception by scientists and lay people alike controversial:

- Only blind and purposeless natural forces (that is, heredity, variation, and natural selection) were needed to explain the extraordinary diversity and adaptive perfection of living systems.
- There was no reference to supernatural forces whatsoever, especially in the first edition of the *Origin*.
- Darwin implied (but did not explicitly state) that humans had evolved from lower forms of life.
- The diversity of living organisms was explained as the result of descent with modification (Darwin's term for "evolution"), which Darwin suggested could be used to extensively revise the taxonomy of life on Earth.
- Natural selection doesn't, and almost certainly can't, produce perfect adaptations. All adaptations are, of necessity, compromises.
- Natural selection, in the long run, virtually guarantees extinction. Indeed, the more "perfectly adapted" a species is to its environment, the more likely it is to go extinct if that environment changes significantly.
- Life almost certainly arose on Earth only once; since then, all living organisms are the descendants of that most ancient of ancestors.

Darwin concluded the *Origin* with these paragraphs:

> It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us.
>
> Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

FOR GREATER UNDERSTANDING

Questions

1. Why was the question of hybridism crucial to Darwin's theory of descent with modification?
2. What does the fossil record show us about the pattern of evolution over time, and how do we know?
3. Darwin's arguments for the biogeographic distribution of species around the world have never been directly addressed by creationists. Why is this, and why do most evolutionary biologists consider that Darwin's arguments for biogeographical distribution constitute his strongest argument for descent with modification (and against creationism)?

Suggested Reading

Dennett, Daniel C. *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. New York: Simon & Schuster, 1996.

Other Books of Interest

Futuyma, Douglas. *Evolution*. 2nd ed. Sunderland, MA: Sinauer Associates, 2009.

Larson, Edward J. *Evolution: The Remarkable History of a Scientific Theory*. New York: Modern Library, 2006.

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Websites of Interest

The *Complete Work of Charles Darwin Online* website features Charles Darwin's *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (1859). — http://darwin-online.org.uk/content/frameset?itemID=F373&viewtype=side&pageseq=1

Lecture 8

Mendel's Dangerous Idea

The Suggested Reading for this lecture is Peter J. Bowler's *The Eclipse of Darwin: Anti-Darwinian Evolution Theories in the Decades Around 1900.*

Darwin began his summary of his views on variation with this statement:

> Our ignorance of the laws of variation is profound.

Neither Darwin nor any of his contemporaries (that he knew of) had a coherent theory of heredity or variation. However, this was not an insuperable obstacle to Darwin. Instead of giving up his argument, he simply accepted as a given that many important traits of animals and plants are heritable, pointing to the observable facts of inheritance in domesticated animals and plants. He also proposed that, although he had no explanation of how they arose, variations among the members of a species do indeed occur and can provide the raw material for natural selection.

This tactic on Darwin's part was largely successful, for a while. His assertion that the huge diversity of living forms and their exquisite adaptations had evolved by "descent with modification from common ancestors" was largely accepted by his scientific contemporaries. However, his assertion that natural selection was the mechanism by which this process had occurred was not nearly as widely accepted.

There were two reasons for this lack of acceptance:

1. Many of Darwin's contemporaries (and, in fact, Darwin himself) believed in Lamarck's assertion that acquired characteristics could be inherited. This process directly contradicts the blind and purposeless process of natural selection, and therefore "holds the door open" for purpose in evolution.
2. The consensus among naturalists was that inheritance worked by "blending" the characteristics of parents, which would cause any incipient adaptations to be diluted out of existence.

This second objection was in many ways the more worrisome to Darwin. In an influential review of the *Origin*, Fleeming Jenkin in 1867 pointed out that blending inheritance would eliminate variation within a few generations.

The variations that provide the raw material for natural selection must be "real"—that is, they must have significant effects on survival and reproduction, and they must persist from one generation to the next. However, if all traits are blended from generation to generation, all of the distinctiveness of each variation would be lost and the population would remain essentially unchanged in the long run. This was what most naturalists of Darwin's time believed. Darwin got around this objection by proposing that large numbers of new variations (what we would now call "mutations") occur with each new generation. He called these changes "continuous variations" and eventually proposed a theory of genetic inheritance called pangenesis.

In *The Variation of Animals and Plants Under Domestication* (1868), Darwin proposed that all of the traits of organisms produced "particles" of inheritance, called "pangenes," which could travel from the anatomical locations of the traits to the sex cells, where they could be passed on to the organism's offspring. He proposed that the pangenes would probably travel through the circulatory system and that they could somehow enter the sex cells in the gonads prior to mating and reproduction.

The problem was that neither of these assertions matched what naturalists observed. The amount of variation that appeared with each generation, while significant, was not sufficient to explain why such variations would not eventually disappear as they were blended with other traits. Furthermore, Darwin's "pangenes" could not be detected, only inferred, nor could their observable effects be separated from the effects predicted by the theory of blending inheritance (not to mention that they would produce a form of inheritance indistinguishable from Lamarck's inheritance of acquired characteristics). Several experiments by Darwin's contemporaries produced results that contradicted Darwin's theory, and consequently it was not widely accepted, even by his closest colleagues. Therefore, although most naturalists accepted that descent with modification had occurred, they did not agree that it had occurred by natural selection.

At about the same time that Darwin was working out his ideas on natural selection and evolution, an Augustinian monk named Gregor Mendel was working out a revolutionary new theory of genetics.

Mendel observed that some offspring of some organisms had traits that were similar to only one parent, rather than being intermediate between both. He explained this phenomenon by assuming that heredity was determined by tiny, indivisible bodies that were passed from the parents to the offspring via the reproductive cells. This would explain how some traits could remain unblended in the next generation.

In his most famous set of experiments, Mendel studied twenty-two varieties of pea plants of the same species (Pisum sativum). He studied a total of seven different traits:

1. Seed shape.
2. Seed color.
3. Seed coat color.
4. Ripe pod shape.
5. Unripe pod color.
6. Flower position on the stem.
7. Stem height.

Mendel always began with plants that were true-breeding. That is, the forms of each trait were passed from parent to offspring without significant changes. Mendel then performed a series of controlled fertilizations, which geneticists and plant breeders call crosses. Some of these crosses were self-crosses, that is, fertilization of a plant using its own pollen. Other crosses were cross-fertilizations—fertilization using pollen from another plant. In each cross-fertilization, Mendel placed pollen from specific individual plants on the egg-containing parts of specific individual plants.

Consider Mendel's results for seed shape. Mendel took pollen from plants that produced smooth seeds and fertilized the flowers of plants that produced wrinkled seeds. He also did the reciprocal cross, taking pollen from plants that produced wrinkled seeds and fertilizing the flowers of plants that produced smooth seeds.

The original true-breeding plants were the parental generation. The offspring obtained from a cross are called the first filial generation (usually referred to as the F_1 generation). All of the F_1 seeds obtained from this cross were smooth, regardless of which plant provided the egg and which plant provided the pollen. Notice that this means that the characteristics of the two parents were not blended in the F_1 generation. Rather, one of the two characteristics—in this case smooth seeds—completely masked the other characteristic (that is, wrinkled seeds).

In the next growing season, Mendel planted the smooth seeds obtained from the first cross. He then allowed the plants produced from these F_1 seeds to self-fertilize, producing the second filial generation (usually referred to as the F_2 generation). Because these plants were self-fertilized, this was essentially a cross between two smooth-seeded F_1 plants. Such a cross appears to be a cross between two true-breeding individuals, which most breeders at the time would probably assume would produce an F_2 generation in which all the pea plants also had smooth seeds.

But this isn't what happened. Instead, in this F_2 generation, Mendel obtained 5,474 plants that yielded smooth seeds and 1,850 plants that yielded wrinkled seeds. The trait of wrinkled seeds had disappeared for one generation (the F_1) but had reappeared unblended in the next generation (the F_2). To most plant breeders at the time, this outcome would have seemed outlandish, even annoying. But to Mendel, it confirmed his theory of unblending "particulate" inheritance.

In his other experiments investigating the inheritance of the other six traits, Mendel recorded similar proportions in all of the F_2 generations. In every case, the F_2 offspring were distributed in approximately a 3:1 ratio. Clearly, the two forms of these traits did not blend with each other, and so Mendel's hypothesis concerning particulate inheritance was verified. On the basis of the numerical analysis of his results, he concluded that discrete units of heredity are transferred unblended from parent to offspring.

Mendel explained this result by saying that the lost form of each trait was actually latent or "masked" by the expressed form. He called the prevailing form of a trait "dominant" and the latent form of a trait "recessive."

Mendel's definitions of dominance and recessiveness are sometimes called Mendel's law of dominance.

In the example just considered, the gene for seed shape has two different forms. One form—the dominant form—produces smooth seeds. The other form—the recessive form—produces wrinkled seeds. Different gene forms that produce different forms of a trait are called alleles.

Following Mendel's lead, geneticists observe an organism's phenotype, the physical appearance of an organism that is the result of the way in which its genes are expressed. For example, the phenotype of our pea plant would be described as having smooth seeds.

Most large organisms, including nearly all plants, have two sets of genetic material, one set received from each parent during fertilization. Therefore, such organisms can have two alleles for each gene. If the two alleles are the same (whether dominant or recessive), then the organism is said to be homozygous for that gene. If the two alleles are different, then the organism is heterozygous, and the dominant allele determines the phenotypic expression of that gene by masking the expression of the recessive allele.

Mendel could not observe directly whether a pea plant was homozygous dominant, homozygous recessive, or heterozygous for any of the traits he was studying. He could only infer the pea plants' genotype, the underlying set of alleles that produced the organism's phenotype. An organism's genotype consists of all of its alleles. The effects of dominant alleles are usually visible in the phenotype. However, the effects of recessive alleles are expressed only when no dominant alleles for that trait are present, a condition usually referred to as homozygous recessive.

Mendel observed that dominant and recessive forms of a trait did not become blended. Instead, the recessive form of the trait reappeared in an unaltered form in the F_2 generation. Based on this observation, Mendel formulated his law of segregation, which states that the different forms of a trait remain separate and unblended from generation to generation.

A shorthand technique for predicting the outcomes of genetic crosses, developed by the English geneticist R.C. Punnett, is the Punnett square method. In this method, the alleles of one parent are listed down the left side of a four-by-four matrix (a "Punnett square"), and the alleles of the other parent are listed across the top of the four-by-four matrix. The genotypes of the fertilized zygotes that can result from the combining of these alleles are indicated within the four cells of the Punnett square.

Because Mendel's major work was done with garden peas, which exhibit simple patterns of inheritance, Mendel could clearly and convincingly validate his hypothesis concerning the units of heredity. Indeed, he was so convinced of the validity of his conclusions that his subsequent work with other plants, some of which failed to support his hypothesis, did not discourage him. He persisted in his studies, although his contemporaries believed in a completely different theory of inheritance. Understanding how inheritance works and seeing that it could be explained by a few simple mathematical laws was sufficient for him.

Mendel's belief that his work would eventually be recognized was not mistaken. In 1900, only fourteen years after his death, his work was simultaneously rediscovered by three different geneticists—Carl Correns, Erich Tschermak, and Hugo de Vries—working independently in three different countries. They each realized that Mendel's particulate theory of inheritance fit the patterns of inheritance they were observing in the organisms they were studying.

It is interesting to speculate what Darwin would have thought had he known about Mendel's work. Genes that did not blend in each generation were the answer to Darwin's dilemma and could have put him onto the right track as early as 1866, the year Mendel's most important paper was published. A copy of the journal containing Mendel's paper was found in Darwin's library at Down House, but it had not been opened or read.

There is an even deeper irony: the rediscovery of Mendel's work led geneticists to reject natural selection as the mechanism for evolution, in favor of mutations. Hugo de Vries, one of the rediscoverers of Mendel's work, proposed that "mutations" (that is, changes in the phenotype of an organism, occurring in just one generation) were the primary "engine" of evolutionary change, not natural selection.

De Vries did his pioneering work in genetics studying the evening primrose (Oenothera biennis), which is known for having sudden, large mutations in its overall phenotype. De Vries argued that these kinds of mutations were the basis for the changes in phenotype to which Darwin referred in the *Origin of Species*, and that therefore natural selection was neither necessary nor likely as a cause of evolutionary change. So convinced was de Vries that the mutant forms of primrose constituted a new species arising from mutation alone that he proposed a new scientific name for them, classifying them as Oenothera lamarkiana, in honor of Jean-Baptiste Lamarck (and, perhaps, in a not-so-subtle dismissal of Darwin).

By the turn of the twentieth century, the rise of what is now called Mendelian genetics seemed to have completely replaced Darwin's theory of evolution by natural selection—not that evolution itself had been undermined. On the contrary, de Vries and the other Mendelian geneticists firmly believed in radical, fundamental change in the underlying genetic characteristics of living organisms by means of sudden genetic mutations. What they believed they had proven false and replaced was Darwin's proposed mechanism of evolution, natural selection. In the *Origin of Species*, Darwin had made it very clear that the kinds of changes he envisioned as the basis of natural selection were so slight as to be almost unnoticeable. Darwin wrote several times in the *Origin* that "nature does not make jumps," by which he clearly meant that evolutionary change was gradual, not sudden.

The early Mendelian geneticists did not agree. Their analysis, which they took directly from Mendel, indicated that the traits of living organisms were discrete and unblending and appeared all at once in a single generation. In 1894, William Bateson, one of the founders of Mendelian genetics in England and coiner of the term "genetics," published a huge compendium of such "sudden" mutations. Entitled *Materials for the Study of Variation: Treated with Special Regard to Discontinuity in the* Origin of Species, it was a copiously illustrated encyclopedia of peculiar, even bizarre mutations, from whales with legs to flowers like something out of a fever dream, all illustrated in living black and white.

The new geneticists, using Mendel's revolutionary theory of inheritance, were on the march, clearing the way to an entirely new view of the origin and evolution of the characteristics of living organisms. So convincing was their mathematical and empirical theory of inheritance that the mutational theory of evolution was accepted by most prominent geneticists at the turn of the century, which led to multiple public testimonials that "Darwinism was dead." But, as will be seen, the reports of the death of Darwinism were greatly exaggerated.

FOR GREATER UNDERSTANDING

Questions

1. Why did many of Darwin's contemporaries reject his theory of natural selection, while retaining his theory of descent with modification?
2. Why is it likely that Mendel's training in Newtonian physics was important in his development of the theory of unblending "particulate" inheritance?
3. Why did their research into the genetics of mutations lead the early Mendelian geneticists to reject Darwin's mechanism of natural selection in favor of the origin of species by means of genetic mutations?

Suggested Reading

Bowler, Peter J. *The Eclipse of Darwin: Anti-Darwinian Evolution Theories in the Decades Around 1900*. Baltimore: The Johns Hopkins University Press, 1992 (1983).

Recorded Books

Dyer, Betsey Dexter. *The Basics of Genetics*. The Modern Scholar Series. Prince Frederick, MD: Recorded Books, LLC, 2009.

Websites of Interest

1. The *Internet Archive* website provides William Bateson's *Materials for the Study of Variation: Treated with Especial Regard to Discontinuity in the Origin of Species* (1894). — http://www.archive.org/stream/materialsforstud00bate/materialsforstud00bate_djvu.txt
2. The *Complete Work of Charles Darwin Online* website features Charles Darwin's *The Variation of Animals and Plants Under Domestication* (1868). — http://darwin-online.org.uk/content/frameset?itemID=F880.1&viewtype=side&pageseq=1
3. The Christ's College Cambridge (UK) *Charles Darwin & Evolution* website provides an article entitled "The Eclipse of Darwin." — http://www.christs.cam.ac.uk/darwin200/pages/index.php?page_id=f2

Lecture 9

Equilibrium Violated: The Hardy-Weinberg Law

The Suggested Reading for this lecture is William B. Provine's *The Origins of Theoretical Population Genetics*, chapter 5, "Mathematical Consequences of Mendelian Heredity."

Darwin's theory of evolution by natural selection was truly revolutionary and represented a fundamental break from the ancient tradition of natural history. That tradition, which can be traced back over twenty centuries to the Greek philosopher Aristotle, had as one of its central concepts the idea of design and purpose in nature.

What made Darwin's theory so revolutionary was that it explained the origin of species and of adaptations without reference to any design or purpose in nature. Darwin proposed that there are a set of natural laws that bring about objects and processes in living organisms without anyone or anything *necessarily* intending that they do so. Just as a dropped rock falls to the ground because of the physical *law* of gravity (but *not* "in order to" reach the ground), living organisms have the characteristics that they have because of what could be called the *law* of evolution by natural selection.

Darwin didn't call his revolutionary explanation the "law" of evolution for historical and philosophical reasons. During the first few centuries of the Scientific Revolution, the explanations that were formulated to describe and predict the behavior of physical and chemical processes were usually referred to as "laws of nature." However, by the time Darwin wrote the *Origin of Species*, the term "law" had come to be replaced in many uses by the word "theory." As learned, scientific theories are explanations for observable natural phenomena that have been thoroughly tested and for which no invalidating evidence has yet been observed. According to the scientific use of these terms, a "theory" is much broader and more comprehensive than a law, and in general has much more observational and experimental evidence supporting it. And, in most cases, a scientific theory has an underlying mathematical form, which can often be succinctly stated in the form of a mathematical equation or set of related equations.

Furthermore, virtually all scientists agree that natural phenomena can, and therefore should, be completely understood and explained simply by referring to other natural objects and processes, without reference to supernatural entities or forces, and without requiring that there be any design or purpose in nature. These criteria, which are often referred to as the principles of "methodological naturalism," were generally *not* a part of natural history until Darwin proposed his theory of evolution by natural selection. For this reason, most historians of science agree that Darwin's theory was the first and most important step in the reformulation of "natural history" as the *science* of biology.

But what about the commonly accepted criterion that a comprehensive scientific theory must be formulated in the language of mathematics? Although Darwin's theory was clearly formulated according to the principles of methodological naturalism, it just as clearly was *not* formulated in explicitly mathematical terms. Darwin's argument was essentially logical and empirical, not mathematical. He asserted that there were four preconditions for natural selection—variety, heredity, fecundity, and demography—and that if these four preconditions are met, there is an inevitable outcome: the heritable characteristics of those individuals who survive and reproduce more often than other individuals with different characteristics will become more common in their populations over time. One can easily imagine that a mathematical reformulation of these conditions might be possible—indeed, Darwin himself thought so. However, Darwin was (by his own rueful admission) not a mathematician, nor were most of his contemporary supporters.

This situation changed dramatically with the rediscovery of Mendel's laws of genetic inheritance and the rise of the new science of genetics. Mendel himself was trained as a physicist, and his theories were explicitly mathematical in form. Mendel's laws of segregation and independent assortment were essentially mathematical models of how the "particles" of inheritance—what we now call "genes"—were assorted and recombined in the process of mating.

In other words, the "language" of genetics, like the "language" of physics and chemistry, is essentially mathematical as well as logical. This emphasis on mathematical rigor was almost certainly one of the reasons why the early Mendelian geneticists and their supporters considered their theory of the origin of species by means of mutations (rather than natural selection) as a more rigorous and "scientific" theory of such origins.

As a consequence, the theory of evolution by means of genetic mutation proposed by de Vries, Bateson, and their contemporaries was accepted by most of the prominent geneticists at the turn of the century, and this led to public testimonials that "Darwinism was dead." But less than a decade after the rediscovery of Mendel's laws, two researchers, working separately and mostly unbeknownst to each other, proposed a mathematical theory of evolution that would eventually lead to the reestablishment of natural selection as the prime mover of evolution.

During the first decade of the twentieth century, Godfrey H. Hardy, an English mathematician, and Wilhelm Weinberg, a German physician, both proposed a mathematical theory that describes in detail the conditions that must be met for evolution to *not* occur. This theory, now often called the Hardy-Weinberg equilibrium law, lays out the conditions that must be met for there to be *no* changes in the allele frequencies in a population of interbreeding organisms over time. By systematically laying out these conditions, the Hardy-Weinberg equilibrium law also makes it possible to show how evolution *does* occur, by showing how and under what circumstances one or more of these conditions can be violated, and what the consequences of such violations would be.

In the context of evolution, alleles are what code for the characteristics of organisms—that is, their phenotypes—that change over time in an evolving population. Therefore, changes in the *alleles* present in a population will produce changes over time in the *phenotypes* present in that population. According to the Hardy-Weinberg equilibrium law,

Evolution is changes in allele frequency in populations over time.

Notice both the similarities and differences between this definition and the one Darwin proposed in the *Origin of Species*. Darwin defined "descent with modification" (what we call "evolution") as changes in the *characteristics* (that is, "traits") in a population over time. Hardy, Weinberg, and the other early geneticists changed one crucial term: they defined evolution as changes in the *allele frequencies* in a population over time. This made sense, given the definition of alleles, which was those "particles" of inheritance that produced the traits of living organisms. This seemingly minor (and eminently justifiable) substitution of "alleles" for "traits" made possible the mathematical analysis of the genetics of populations, a new branch of the natural sciences now known as *theoretical population genetics*.

What Hardy and Weinberg realized is that for allele frequencies to *not* change in a population, five conditions *must* be met:

1. There can be *no* mutations (that is, alleles cannot change into other, different alleles).
2. There can be *no* gene flow (that is, individuals cannot enter or leave the population).
3. The population must be *very* large (that is, random accidents cannot alter allele frequencies).
4. Survival must be *random* (that is, there can be no natural selection).
5. Reproduction must also be random (that is, there can be no sexual selection).

The Hardy-Weinberg equilibrium law outlines exactly what processes are essential to prevent evolution, and therefore by negation it shows how evolution *can* happen. If any of the five conditions for maintaining a Hardy-Weinberg equilibrium are violated, then evolution *must* be occurring. And, of course, virtually none of these conditions is ever permanently met in any known natural population of organisms.

Therefore, according to the Hardy-Weinberg equilibrium law, evolution *must* be occurring in virtually every population of living organisms. The law also helps to show which of the factors listed is the most important in causing evolutionary change in which groups of organisms.

- Although they are always occurring, mutations do not occur often enough to cause the kinds of changes that characterize most observed evolutionary change. Mutations, in other words, provide the raw material (that is, the "fuel") for the engine of evolution but are not the primary engine itself.
- Gene flow is often restricted in organisms that cannot move around, such as fungi and plants. However, even among them, genetic material gets moved from place to place. And, of course, in animals gene flow is almost always a significant cause of deviations from previous allele frequencies.
- As for population size, most actual breeding populations of organisms are not large enough to ensure that there will be no changes in allele frequencies as the result of purely random accidents (that is, "sampling error"). Indeed, a previously unrecognized form of evolution, called genetic drift, was proposed to occur whenever populations are small enough for random accidents to cause changes in allele frequencies.
- Survival is virtually never random, and nonrandom survival is just another name for natural selection, Darwin's proposed "engine" of descent with modification. As a result of the formulation and widespread acceptance of the Hardy-Weinberg equilibrium law and its mathematical implications, natural selection eventually was once again proclaimed the primary engine of evolution.
- However, there is another engine of evolution, at least among animals. Like survival, reproduction is also virtually never random among animals, especially land animals who can choose who they mate with. Therefore, sexual selection is also an important engine of evolution in animals (and even in some plants).

The Hardy-Weinberg equilibrium law established the precedent that evolution could be conceived of and mathematically modeled by reducing whole organisms to single traits, coded for by combinations of single alleles. This radical reduction of complex concrete entities into simple abstract mathematical relationships formed the foundation of the "modern evolutionary synthesis." The next lecture shows how three of the founders of the new science of theoretical population genetics worked out most of the mathematical equations that were used as the foundation of the "modern synthesis" and how their theoretical work set the stage for the resurrection of Darwin's revolutionary theory.

FOR GREATER UNDERSTANDING

Questions

1. Why was the Hardy-Weinberg Equilibrium Law so important to the development of a mathematical theory of evolution?
2. What simplifying assumptions did Hardy and Weinberg have to make to formulate their theory of genetic equilibrium?
3. What consequences, both intended and unintended, flow from these simplifying assumptions?

Suggested Reading

Provine, William B. *The Origins of Theoretical Population Genetics*. Chicago: University of Chicago Press, 2001 (1971).

Other Books of Interest

Larson, Edward J. *Evolution: The Remarkable History of a Scientific Theory*. New York: Modern Library, 2006.

Mayr, Ernst. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Belknap Press of Harvard University Press, 1985.

Ruse, Michael. *Darwin and Design: Does Evolution Have a Purpose?* Cambridge, MA: Harvard University Press, 2004.

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1. The University of Alberta (Canada) provides a pdf of G.H. Hardy's *A Mathematician's Apology* (1940). — www.math.ualberta.ca/~mss/misc/A%20Mathematician's%20Apology.pdf
2. The *Secular Web* features a paper from 2000 by Barbara Forrest entitled "Methodological Naturalism and Philosophical Naturalism: Clarifying the Connection." — http://www.infidels.org/library/modern/barbara_forrest/naturalism.html
3. The *Stanford Encyclopedia of Philosophy* features "Laws of Nature," written in 2003 and revised in 2010 by John W. Carroll and edited by Edward N. Zalta. — http://plato.stanford.edu/entries/laws-of-nature

Lecture 10

Fisher, Haldane, and Wright

The Suggested Readings for this lecture are Ronald Aylmer Fisher's *The Genetical Theory of Natural Selection* and J.B.S. Haldane's *The Causes of Evolution.*

The Hardy-Weinberg equilibrium law provided a mathematical basis for the founders of theoretical population genetics—principally R.A. Fisher, J.B.S. Haldane, and Sewall Wright—to develop mathematical models for fitness, selection, and other evolutionary processes. These models could then be applied to demographic data derived from artificial and natural populations of organisms in a rigorous and ongoing test of the validity of a neo-darwinian model for genetic evolution.

They also provided the basis for what would eventually come to be known as the "modern evolutionary synthesis," in which Darwin's theories of natural and sexual selection were combined with Mendelian genetics, biometry and statistics, demography, paleontology, comparative anatomy, botany, and (more recently) molecular genetics and ethology to produce a "grand unified theory" of the origin and evolution of life on Earth.

The work of English population geneticist and statistician Ronald Aylmer Fisher further undermined the Mendelian theory of evolution via macromutation by showing that the kind of continuous variation first proposed by Darwin could provide the basis for natural selection.

In his most important work, *The Genetical Theory of Natural Selection*, published in 1930, Fisher showed that traits characterized by continuous variation (that is, traits that approximate a normal, or bell-shaped, distribution) were both common and could provide all the raw material necessary for Darwinian natural selection. This is because such traits, although being continuous in populations, do not blend from parents to offspring because they are produced by unblending "particles" of inheritance (that is, Mendelian "genes"). In other words, Mendelian inheritance conserves, rather than eventually destroying, the genetic variation that exists in natural populations.

Fisher then proposed his fundamental theorem of natural selection:

> The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.

Essentially, Fisher's theorem says that the degree of change that can result from natural selection depends fundamentally on the amount of genetic variation present in the population undergoing selection.

- If there is little variation, then natural selection cannot change the characteristics of the members of the population much at all.

- Conversely, if there is a lot of genetic variation, this can form the basis for considerable evolutionary change as the result of natural selection.

This theorem, although modified somewhat today, forms the basis for most of modern evolutionary theory. It also parallels an observation made by Darwin in the *Origin of Species*: the more widespread and variable a species is, the greater the effects of natural selection will be in that species. Fisher's theorem is a mathematical explanation of Darwin's observation about the variability of organisms in natural populations.

John Burdon Sanderson Haldane (usually referred to as J.B.S. Haldane) furthered the revolution in theoretical population genetics begun by Hardy, Weinberg, and Fisher. In his most important book, *The Causes of Evolution* (1932), he showed that genetic mutations such as those observed by de Vries and the early Mendelians could provide the raw material for Darwinian natural selection. Furthermore, he showed mathematically that such mutations could do this even when their frequency in a population was initially so low that they would be "invisible" to statistical analysis. He also showed how dominance could evolve in populations by means of natural selection, even when the original expression of an allele was initially recessive.

Although Haldane did not propose any single theory in evolutionary biology that could be called revolutionary, his approach, like Fisher's, was. In particular, Haldane stated the following:

> The permeation of biology by mathematics is only beginning, but unless the history of science is an inadequate guide, it will continue, and the investigations here summarized represent the beginning of a new branch of applied mathematics.

In *The Causes of Evolution*, Haldane developed a comprehensive mathematical theory of genetic evolution based on Fisher's pioneering work in population genetics. Although much of the mathematics he presented was based on Fisher's original ideas, Haldane was able to apply them to very practical problems, showing natural selection could produce many of the outcomes originally proposed in nonmathematical form by Darwin. In particular, Haldane was able to show that natural selection could cause a trait that was present in almost vanishingly low frequency in a population (so small that it couldn't be detected by normal statistical means) to become overwhelmingly common in as few as 10,000 generations. While this may seem like a long time, in geological terms it is almost a blink of an eye, and in something like bacteria (which reproduce every twenty minutes or so), it would be less than six months.

Haldane is also remembered for two quips that are often repeated by evolutionary biologists. The first concerns a question posed to him by an Anglican minister, who asked him (supposedly at a dinner party) what his study of nature had led him to conclude about the principal concern of the

Creator. Without batting an eyelash, Haldane replied, "An inordinate fondness for beetles," referring to the fact that there are more species of beetles on Earth than any other kind of organism).

During another conversation (supposedly in a pub), Haldane was confronted with the observation that natural selection should result in pure selfishness on the part of individuals, and therefore no one should be willing to risk his own life to save another. To this Haldane replied, "I would be willing to risk my life to save two brothers or eight cousins." This quip is based on the observation that brothers share an average of one-half of their genetic material, whereas first cousins share an average of one-eighth. Therefore, saving two brothers or eight cousins would result in the same genetic contribution to the next generation as that represented by one's own genome. This quip was later cited by one of the founders of what is now known as the theory of kin selection, in which natural selection is considered to act at the level of genes, rather than individuals.

R.A. Fisher pointed out several times that the mathematics of natural selection were similar in many ways to such physical models as the ideal gas laws and the second law of thermodynamics. According to his mathematical models, alleles that were positively selected would increase in frequency in populations in much the same way that gas molecules spread out in an expanding balloon.

To many evolutionary biologists, this meant that natural selection would inevitably result in "fixation" of alleles that were not selected against. That is, any allele that resulted in increased survival and reproduction should, if given enough time, inevitably become the only allele for that particular trait. This presented a problem to evolutionary biologists by implying that the inevitable result of natural selection would be the eventual elimination of all nonadaptive variation in natural populations. This would then cause natural selection to grind to a halt (or to become reduced to essentially the rate of production of new genetic mutations, which is much slower than the observed rate of evolution).

A solution to the problem was provided by Sewall Wright, who discovered a process that has eventually become known as random genetic drift (or simply genetic drift). Wright proposed that in small populations of organisms, random sampling errors could cause significant changes in allele frequencies in such small populations. He showed mathematically that the smaller a population was, the greater the effect of such random events on its allele frequencies. In other words, evolution could proceed by at least two primary mechanisms: Darwinian natural selection and random genetic drift.

Wright then went on to develop a formal model for genetic evolution in which the allele frequencies present in a population were visualized as forming an adaptive landscape. In Wright's model, the allele frequencies present in a population were visualized as elevations in a topographical surface.

According to the prevailing theory at the time, selection could only cause allele frequencies to ascend adaptive "peaks" in such a landscape, never descend into the "valleys" of maladaptation. This meant that selection alone could only result in fixation and eventual genetic stagnation, just as Fisher's equations for natural selection implied.

What Wright showed is that random drift could, in small populations, cause allele frequencies to drift from one adaptive peak to another, and in this way could keep evolution by natural selection moving. He called this theory the "shifting balance theory of evolution," as it emphasized the shift from one adaptive peak to another by means of random genetic drift.

Wright carried out a long professional correspondence with Fisher, in which the two agreed on the reality of genetic drift but disagreed on its importance to evolution in general. Fisher was committed to natural selection as the principal "engine" of evolution. He argued that natural selection would work fastest in large populations, in which there would be a reservoir of "hidden" genetic variation, in the form of recessive alleles in heterozygotes. This hidden variation could be brought out by changes in the environment, when a recessive allele that was formerly deleterious could become advantageous. Fisher pointed out that once the frequency of such an advantageous recessive allele reached a level at which significant numbers of homozygous recessive individuals would be produced, the frequency of the recessive allele would increase swiftly until reaching fixation. At that point, with the formerly dominant allele then extinct, the formerly recessive allele would become the new dominant allele and remain so until this process repeated.

Wright, by contrast, believed that genetic drift played a very important part in many populations. He argued that what might appear to be a large breeding population was in many cases a mosaic of small breeding populations, within which the actual "effective" breeding population was low enough for random sampling error to produce the kind of genetic drift that he believed could compensate for the tendency of natural selection to reduce the amount of potentially adaptive variation in populations.

Wright also differed from Fisher and Haldane in his view of how individual alleles affected the phenotypes of organisms. In the mathematical models developed by Fisher and Haldane there was an essentially one-to-one relationship between individual genes and individual traits. Wright, by contrast, believed that most phenotypic traits were the result of multiple genes interacting with each other in complex ways. Wright pointed out that inbreeding could expose such deleterious alleles relatively quickly, allowing them to be weeded out of populations. He also became convinced that most evolutionarily significant phenotypic traits were the result of multiple genes interacting with each other, rather than the single genes rising and falling in frequency that formed the basis of Fisher's models of evolution.

FOR GREATER UNDERSTANDING

Questions

1. What is R.A. Fisher's fundamental theorem of natural selection, and what does it imply about the ultimate outcome of natural selection?
2. What did J.B.S. Haldane demonstrate concerning the ability of natural selection to change the frequency of rare alleles in populations and the tendency for recessive alleles to eventually become dominant as the result of natural selection?
3. Why was Sewall Wright's theory of random genetic drift so important to his theory of adaptive landscapes?

Suggested Reading

Fisher, Ronald Aylmer. *The Genetical Theory of Natural Selection*. Charleston, SC: Nabu Press, 2010.

Haldane, J.B.S. *The Causes of Evolution*. Princeton: Princeton Science Library, 1990.

Other Books of Interest

Larson, Edward J. *Evolution: The Remarkable History of a Scientific Theory*. New York: Modern Library, 2006.

Mayr, Ernst. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Belknap Press of Harvard University Press, 1985.

Ruse, Michael. *Darwin and Design: Does Evolution Have a Purpose?* Cambridge, MA: Harvard University Press, 2004.

Websites of Interest

1. The *Wikipedia* entry on the Price Equation cites a number of authoritative sources for the information. — http://en.wikipedia.org/wiki/Price_equation
2. The University of Southampton (UK) School of Social Sciences provides *A Guide to R.A. Fisher*. — http://www.economics.soton.ac.uk/staff/aldrich/fisherguide/rafframe.htm

Lecture 11

Natural Selection and Speciation

The Suggested Reading for this lecture is Ernst Mayr's *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, chapter 12, "Diversity and Synthesis of Evolutionary Thought."

R.A. Fisher, J.B.S. Haldane, and Sewall Wright are usually recognized as having laid the theoretical foundation for modern evolutionary theory. However, many evolutionary biologists and historians of science consider that the "modern evolutionary synthesis" was initiated by Theodosius Dobzhansky with the publication of his most famous book, *Genetics and the Origin of Species* (1937). Dobzhansky combined Mendelian genetics, the mathematical models of Fisher, Haldane, and Wright, and empirical observations of evolution and natural selection in the wild in a theory that reinstated natural selection as the primary engine of evolution.

Perhaps Dobzhansky's most important contribution to the "modern synthesis" was his confirmation of Fisher's assertion that there is an immense amount of "hidden" variation in most populations, in the form of recessive alleles. By collecting fruit flies of several different species from different field and laboratory populations, crossing them under controlled conditions in the laboratory, and then analyzing the results of such crosses, Dobzhansky found that even populations that appeared to be almost completely homogenous (at the level of phenotypes) had a surprising amount of genetic heterogeneity at the level of genotypes). This finding confirmed Fisher's theoretical model that such "hidden" variation could supply the "continuous variation" that Darwin believed would be necessary for natural selection to proceed, but for which Darwin had no mechanistic explanation.

This, in turn, added powerful empirical support to Fisher's assertion that natural selection alone could lead to the kind of large-scale evolutionary changes visible in the fossil record. Rather than relying on the "saltational" models of the early Mendelian geneticists, Fisher's model could be called "gradualist" and relied not on macromutations but rather on very small, almost undetectable "micromutations," spreading gradually through populations as recessive alleles in heterozygotes.

Dobzhansky's field and laboratory studies also confirmed that Sewall Wright's newly discovered, but until then largely theoretical, process of random genetic drift also happened in real populations. Again, by matching the results of his crosses of small populations of fruit flies from relatively isolated populations, Dobzhansky was able to show that his results generally conformed to Wright's predictions.

Among Dobzhansky's other important contributions to the modern theory of evolution by natural selection was his analysis of the three different patterns of evolutionary change that can result from natural selection: directional selection, stabilizing selection, and disruptive selection.

To visualize each type, begin by considering the pattern of variation in a typical trait, such as beak length in Darwin's finches. In such a population, there is a natural (that is, random) variation in this trait, which is arrayed along the X axis. The number of individuals showing a particular value of this trait is entered along the Y axis. The result approximates a bell-shaped curve (that is, a "normal distribution") in which finches with intermediate-sized beaks—what we could refer to as the "average" beak size—are the most common in the population, while finches with very small or very large beaks are much less common. Normal distributions of traits were central to R.A. Fisher's mathematical models of "continuous variation" of multigenic traits.

Consider the effect on the average value of this trait in the population if individuals at one or the other (but not both) extreme of expression of this trait are selected against (that is, have relatively lower survival and/or reproductive success). The result would be a shift in the average value for the trait in this population. For example, if finches with smaller beaks survive less often or have fewer offspring, then finches with larger beaks would have relatively higher reproductive success, and the average beak size for the population as a whole would increase. Such a shift in the average value for a particular trait in any population is a tip-off that selection is occurring in that population. Since the overall effect of such selection is to cause a unidirectional shift in the average value for a trait in a population, this kind of selection is called directional selection. This is essentially the kind of natural selection that Darwin proposed in the *Origin of Species*.

An example of directional selection is the increase in mean beak size among Galapagos finches as the result of prolonged drought, as studied by Peter and Rosemary Grant. The Grants and their student assistants have studied the population of the medium ground finch (Geospiza fortis) on the island of Daphne Major in the Galapagos archipelago since 1973. They observed the following in this intensively studied population of finches:

- Despite similar appearance, there is considerable variation among these finches, especially with regard to the size of their beaks.
- There is also considerable variation in the relative survival and reproductive rates of these finches, which can be correlated with the changing ecology of the island.
- During periods of drought, there is a significant increase in the average beak size in the population, corresponding to an increase in the size and toughness of the seed food supply available to the finches, and a corresponding decrease in the availability of smaller, softer seeds.
- Developmental geneticists determined that the changes observed in the relative sizes of the beaks of the finches can also be correlated

with variations in the underlying genes that regulate the size of the finches' beaks.

In other words, there was a significant shift in the average size of the finches' beaks, correlated with an underlying genetic change, precisely the kind of shift predicted by Dobzhansky's model of directional selection, and confirming Darwin's original hypothesis for the evolution of adaptations by means of natural selection.

Now consider a population in which selection is exerted most strongly against individuals at both extremes of the range of variation in a particular trait. The result of such selection would be no change in the average value for the trait in the population, along with a noticeable decrease in the overall range of variation for the trait in the population. Since the effect of such selection is to maintain the trait in question at or around the previously existing population average, this kind of selection is called stabilizing selection (or "normalizing selection," as Dobzhansky originally referred to it).

Stabilizing selection can have important implications for later evolutionary change, as the decrease in overall variation in the trait in question can limit the amount of change that can occur later if selection is relaxed. In essence, once a population has been subjected to intense stabilizing selection, it is much less likely to shift later as the result of a change in the environment, as there is less potential variation available for such a response.

Finally, consider a population in which selection is exerted most strongly against individuals in the middle of the range of variation, which is usually the largest fraction of the population. The effects of such selection would be the production of a bimodal distribution of the trait under selection—two bell-shaped curves, with a deep valley in between where the average value for the trait used to be. The result of such selection would be a dramatic increase in the amount of variation in the trait in the population, and the splitting of the population into two distinct subpopulations, each with its own characteristic average value for the trait in question. Because the original average population value is eliminated and replaced by two different averages, this kind of selection is called disruptive selection.

Disruptive selection is often called diversifying selection, as it results in the production of increased diversity of traits in populations. As such, diversifying selection has been implicated in evolutionary divergence and may be a primary cause of speciation (that is, the origin of new species from existing ones). Dobzhansky proposed that this would be the case, asserting that diversifying selection could explain the origin of new species from existing species by means of natural selection alone.

And so, having considered Dobzhansky's model for diversifying selection, we come to what Darwin called the "mystery of mysteries"—the origin of species. According to Darwin and all of his intellectual descendents, speciation is the source of all of the diversity in life on Earth. It is also the biggest mystery in evolutionary biology.

As the title of his most famous book suggests, Darwin supposedly wrote about the origin of species in the *Origin of Species*. However, he didn't really write much about speciation, except to suggest that it might be caused by natural selection. Darwin's main focus in the *Origin* (especially the first half) was on the origin of adaptations by means of natural selection. Darwin believed that he had discovered a mechanism by which the apparently purposeful characteristics of living organisms could have arisen by purely natural processes that did not require any supernatural designer or purpose.

Darwin did briefly address the problem of speciation (without calling it that), but he concluded that the sterility that marks the boundaries between closely related species could not have evolved by natural selection—after all, how can sterility increase by selecting for increasing degrees of sterility? By definition, sterile organisms cannot pass on the trait of sterility to their offspring.

The early Mendelians thought they had discovered a completely new mechanism for speciation: macromutations, which not only produced new species in as little as a single generation but also produced entirely new functional adaptations. The problem with this idea was that it could not easily be squared with the observation that almost all observable mutations are too small and too deleterious to qualify as either the origin of new species or as functional adaptations. Indeed, it is clear after reading some of their proposals for speciation and adaptation via macromutation that they believed in some kind of unspecified "magical" process by which just the right macromutation would come along just when a species needed to evolve into a new and different species.

Like Darwin, Fisher, Haldane, and Wright were most concerned with the process of adaptation via natural selection and how that process could cause significant changes in the average phenotypes in populations, rather than how mutations and natural selection might cause one species to diverge into two or more species whose members were incapable of interbreeding. Dobzhansky had proposed a neo-Darwinian model for the origin of new species, by means of diversifying selection. However, Dobzhansky's model did not square easily with Darwin's skepticism about the inability of natural selection to select for increasing degrees of sterility. Darwin himself had suggested that some other process, which he could not specify or explain, must somehow cause the decrease in interbreeding success that apparently accompanies the divergence of two isolated subpopulations of one species into two, non-interbreeding species.

The core concept that provided the "modern evolutionary synthesis" with a testable theory of speciation was proposed by Ernst Mayr in his magnum opus, *Systematics and the Origin of Species*, first published in 1942. In it, Mayr attempted to answer two questions: What is a species? and How does speciation occur?

The most widely used definition of "species" is Mayr's biological species concept, which defines species essentially by reproductive isolation:

> To be members of the same species, organisms must be capable of interbreeding and producing fertile offspring under natural conditions.

Therefore, organisms that can't do this (that is, organisms that are reproductively isolated from one another) are not members of the same species. This concept was originally proposed by Dobzhansky in *Genetics and the Origin of Species*, but Mayr developed it much more fully and integrated it into a synthetic theory of the origin of species from previously existing species.

According to Mayr's theory, speciation can occur whenever a small subset of a larger interbreeding population becomes reproductively isolated from the population of which it was formerly a part. Consider a simplified model of such a large population. We can picture it as a large corral, with a definite boundary drawn around it like a fence. Inside this boundary all of the members of the population are capable of interbreeding with each other and producing fertile offspring. Such a population is referred to as panmictic. Since a panmictic population is freely interbreeding (by definition), any new allele (or other genetic element) that appears within this population (that is, via mutation of an existing allele or by acquisition of a new allele from another population via gene flow) can potentially spread throughout the population.

If the new allele is a deleterious mutation (as most mutations apparently are), it will be removed from the population, rapidly and completely if the mutation is dominant, or slowly if the mutation is recessive. Once a deleterious mutation reaches a sufficiently low frequency in a population, it can be completely removed as the result of random genetic drift.

However, if the new allele is either neutral (as often happens) or beneficial (as rarely but occasionally happens), then it will tend to spread throughout the population, so long as all individuals are freely interbreeding and it doesn't get eliminated accidentally by random genetic drift. If it is dominant and beneficial (extremely unlikely, but possible), it will spread quite rapidly through the population. In any case, the end result of this process will be that any new allele will either disappear (as the result of selection or drift) or spread through the population (if it is either neutral or beneficial). This means that the whole population may change over time, but it will not become separated into two or more subpopulations that are divergent and (most importantly) genetically incompatible with each other.

However, if a small subpopulation of this original population becomes reproductively isolated from it (that is, there is reduced or negligible gene flow between the larger population and the smaller, isolated subpopulation), then any new allele that occurs in either population will not spread to the other. Therefore, the longer these two subpopulations are kept reproductively isolated from each other, the more different alleles (and other genetic elements) will accumulate in each. Eventually, the accumulation of such nonidentical genetic elements can result in partial or complete genetic incompatibility between the two subpopulations, and they will then qualify as two separate species, according to Mayr and Dobzhansky's biological species concept.

If we accept Mayr and Dobzhansky's definition of a species, then the key to speciation is anything that can cause reproductive isolation. This is easiest to understand when the cause is geographic isolation: that is, when organisms are so far apart geographically that the probability of their mating with each other is effectively zero. In technical terms, this is called "allopatry." Speciation that results from allopatry is therefore allopatric speciation.

Central to Mayr's concept of allopatric speciation is the idea that reproductive isolating mechanisms are incidental: they are not the result of natural selection. In this, Mayr is following Darwin's lead, who stated in the *Origin of Species* that natural selection cannot possibly produce increasing degrees of hybrid sterility or reproductive incompatibility. In later versions of his theory, Mayr refined his idea of allopatric speciation, proposing that it is most likely to happen when the small, isolated populations that separate from their "parent" population are geographically located in small "islands" at the periphery of the larger "continental" population. These two terms are not used arbitrarily: some of the best examples of speciation are found on small, isolated islands, such as the Galapagos archipelago, which are located far from the mainland of South America. Because the small, isolated populations are usually located at the periphery of their "parent" population, Mayr called this process peripatric speciation.

FOR GREATER UNDERSTANDING

Questions

1. Which kind of selection—directional, stabilizing, or diversifying—is most like what Darwin originally proposed in the *Origin of Species*, and why?
2. Mayr's "biological species concept" was extraordinarily useful in the development of the theory of speciation during the formulation of the "modern evolutionary synthesis." However, it cannot be applied to a wide range of living organisms and biological systems. Which ones and why not, and can some other concept be used instead?
3. The title of Darwin's most famous book—*On the Origin of Species by Means of Natural Selection*—strongly implied that natural selection was the principal mechanism driving the origin of new species from previously existing ones. Is this actually the case, and if not, what alternative mechanisms did the "modern evolutionary synthesis" include?

Suggested Reading

Mayr, Ernst. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Belknap Press of Harvard University Press, 1985.

Other Books of Interest

Dobzhansky, Theodosius. *Genetics and the Origin of Species*. New York. Columbia University Press, 1982 (1937).

Larson, Edward J. *Evolution: The Remarkable History of a Scientific Theory*. New York: Modern Library, 2006.

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Ruse, Michael. *Darwin and Design: Does Evolution Have a Purpose?* Cambridge, MA: Harvard University Press, 2004.

Websites of Interest

The Ernst Mayr Library at Harvard University features archived material and current resources in biology, including an extensive list of publications by or about Ernst Mayr. — http://library.mcz.harvard.edu

Lecture 12

Disturbing Implications

The Suggested Reading for this lecture is Richard Dawkins's *The Blind Watchmaker*.

Most people are aware that the theory of evolution has some disturbing implications. People who have thought about these implications often assume that they have to do with their implications for religion. Yes, evolutionary biology does indeed have implications that disturb some religious believers. However, there are two very disturbing implications of evolutionary theory that trouble even some atheists:

1. Evolution by natural selection seems to rule out any possibility of design, intention, or purpose in nature.
2. It also seems to rule out any possibility of human free will.

Consider the problem of purpose in nature. If you drop a rock, once it leaves your grasp it falls to the ground. One can ask at least three fundamental questions about this process:

1. What does the rock do when you drop it?

   Answer: It falls from your hand to the ground.
2. How does the rock fall to the ground?

   Answer: It falls from your hand to the ground because of the force of gravity.
3. Why does the rock fall to the ground?

   Answer: The rock falls in order to reach the ground—or does it?

This is an explanation of the rock's movement. However, it is not the explanation that would be given by virtually any physicist today. This is because such an answer would be based on a fundamental metaphysical assumption—that someone or something (an "intentional agent") intends the rock to fall to the ground. Largely as the result of the work of Isaac Newton, physical scientists do not include any reference to purpose when explaining natural phenomena.

In answering the "why" question posed earlier without resorting to intentions or purposes, one is adopting a metaphysical worldview. This metaphysical worldview, which forms the basis for virtually all of modern empirical science, is formally known as methodological naturalism. According to the principles of methodological naturalism, one simply investigates natural processes using empirical methods and explains those processes without speculating about why those processes happen the way they do. Answering the question of how they do it is considered sufficient. To put it succinctly, the answer to "how" questions in science is considered to be exactly the same as the answer to "why" questions.

By contrast, a "supernatural" explanation of the movement of falling objects would begin with the assumption that there are "supernatural" entities or forces that govern such movement and can therefore answer the question of why such processes happen. For example, one could answer that the reason that dropped objects fall is that such objects are made of "earth," and as such are fundamentally "contaminated" or "tainted with evil" and therefore attempt to reach the center of all evil (that is, the underworld, or Hell), and are assisted in doing so by "agents of evil" (that is, demons) that control their actions. While such an explanation would strike most people today as absurd, it is surprisingly close to many prescientific explanations of such actions.

A scientific explanation of the movement of falling objects would begin with the assumption that there are "built-in" laws of nature that govern such movement. According to most natural scientists, the universe is constructed in such a way that natural processes happen the way they happen without any guidance or choice in the matter, and the formulation of such laws has been built up over the past few centuries by the process of scientific observation and experimentation.

The overwhelming majority of scientists have not retained any belief at all in a supernatural agent that intervenes in nature, either in setting up the laws that govern natural processes or in the working out of those processes on a daily basis. In doing so, such scientists are adhering to a belief system known as ontological naturalism, which is based on six metaphysical assumptions:

1. Nature (that is, the universe) contains only energy and matter, the interactions between which cause all of the observable phenomena in the universe.
2. The interactions between energy and matter (and only these interactions) can involve the exchange of information.
3. Information separate from the interactions of energy or matter can't be shown to exist (and therefore is assumed not to exist).
4. The most useful way to understand the interactions between energy and matter is via empirical observation (and therefore the scientific method is the best way to understand nature).
5. The simplest explanation of any natural phenomenon is assumed to be the best, until proven otherwise (this principle is often called "Occam's razor" or the rule of parsimony).
6. It is not necessary to assume that intentions or purposes have anything to do with natural phenomena and, since purpose in nature is unnecessary to explain natural phenomena, it is assumed that purpose does not exist in nature.

All of these are clearly metaphysical assumptions and are not directly verifiable or falsifiable by any application of the scientific method as it is currently understood.

Most people today wouldn't say that dropped rocks fall "in order to" reach the ground. But why does it not sound just as illogical to say that we have hearts in order to pump blood through our arteries and veins? Does this mean that our hearts and blood and arteries and veins are not natural objects, and the pumping of blood by the heart is not a natural process? Are biological organisms somehow different from other natural objects and processes, and is that difference the inclusion of purpose in biology?

In 1970, Francisco Ayala, a student of Theodosius Dobzhansky and a winner of the Templeton Prize, wrote a landmark paper on this subject, entitled "Teleological Explanations in Evolutionary Biology." In it, Ayala noted that purpose as a part of evolutionary biology has been a "suspect" concept since the formulation of the "modern evolutionary synthesis." Evolutionary biologists, especially during the "modern evolutionary synthesis," tried to remove all "purposeful" language from evolutionary explanations of biological adaptations (the term "teleology" refers to the philosophical analysis of the concept of purpose). However, it does not sound absurd to say that we have hearts in order to pump blood through our arteries and veins. Ayala argued that this is because evolutionary adaptations perform a specific function for organisms. This "function" can legitimately be considered to be purposeful, although the process by which it has come to exist (that is, natural selection) is not.

In Ernst Mayr's 1974 paper, "Teleological and Teleonomic: A New Analysis," Mayr agreed:

> In spite of the long-standing misgivings of physical scientists, philosophers, and logicians, many biologists have continued to insist not only that such teleological statements are objective and free of metaphysical content, but also that they express something important which is lost when teleological language is eliminated from such statements.

Mayr went on to refine Ayala's concepts, using terminology that is completely consistent with other branches of the natural sciences. Specifically, he proposed that all phenomena (that is, "natural" events) can be classified as either teleological, teleomatic, or teleonomic.

- A *teleological* process or behavior is any goal-directed action. Teleological processes are generally considered to be dynamic rather than static; that is, they tend toward a particular end-state (that is, a goal) by changing dynamically until the goal is reached.
- A *teleomatic* process is a teleological process that simply follows the laws of nature, that is, leading to a result that is an automatic consequence of physical forces, in which the reaching of its end state is not controlled by a built-in program or an external intentional agent. The law of gravity and the second law of thermodynamics are among the laws of nature that govern teleomatic processes.

- A *teleonomic* process or behavior is a teleological process that owes its goal-directedness to the operation of a program. Like the term "teleological," the term "teleonomic" implies active goal-direction. This, in turn, implies a dynamic process rather than a static condition.

One way to distinguish a teleomatic process from a teleonomic one is that teleomatic processes generally do not respond to deviations in such a way as to return to their goal-directed path. If a dropped rock is deflected, it will continue in the deflected trajectory rather than return to its original trajectory. However, if a teleonomic entity is deflected or interfered with (such as a bird being deflected from its flight toward a perch), it will compensate for such deflection and, if possible, return to its original trajectory.

Central to Mayr's distinction between teleomatic and teleonomic processes is the existence of a guiding program in the case of teleonomic processes. According to Mayr,

> A program is coded or prearranged information that controls a process (or behavior) leading it toward a given end. According to this definition, a program is (1) something material, and (2) exists prior to the initiation of the teleonomic process. Hence, it is consistent with a causal (that is, purely natural) explanation.

Mayr distinguished between "closed" and "open" programs.

- A closed program is one in which the program itself generally cannot be changed during the lifetime of the entity whose behavior it controls. While this is easiest to apply to living organisms, in which the "closed program" is the organism's genome, it can also be applied to such things as computer programs, especially if such programs cannot be modified as the result of interactions between the entity and its environment.
- An open program is one in which the program can be modified during the lifetime of the entity whose behavior it controls as the result of interactions between the entity and its environment. In living organisms, such modification can occur as the result of learning, although it could theoretically also occur as the result of developmental plasticity or horizontal gene transfer between organisms.

Also central to Mayr's overall philosophical analysis is the distinction between teleonomic processes (and the programs that control them) and the mechanisms by which such processes evolve (that is, natural selection). Teleonomic processes (that is, processes that are controlled by a program, either closed or open), are fully "teleological," in that they are directed toward a goal that is defined within the parameters of the program. Therefore, teleological (that is, "purposeful") processes can exist and do not violate naturalistic causality, so long as the program controlling them exists prior to their execution and is encoded in some material form.

This, in turn, entails the following implication: since the processes by which the programs that control teleonomic processes arise (that is, natural selection, and so forth) are not themselves purposeful, such programs are relentlessly and inescapably driven by past experience, and past experience alone. A teleonomic program cannot possibly plan for any future that has not already participated in the modification of that program in the past. This means that the future is quite literally "open" and in a very fundamental sense unknowable. There are no guarantees, at least none that can be observed or inferred by the usual methods of natural science.

Therefore, it is neither illogical nor outside the bounds of ontological naturalism (upon which modern science is based) to say that we have hearts in order to pump blood through our arteries and veins. This is because we inherit from our ancestors genetic programs that specify the assembly of and regulate the operation of our bodies, including our circulatory systems. These programs (encoded in our genomes) literally "preexist" us, and our lives embody the working out of these programs, in combination with our developmental environment.

However (and this is crucial), the programs themselves need not have come into existence by a process that can in any way be considered as purposeful.

- If you do not make the jump from "need not" to "have not," you are a methodological naturalist.
- If you do make the jump from "need not" to "have not" (a jump that is not entailed by any empirical observation or inference), then you are an ontological naturalist.

Free Will

According to Professor William Provine of Cornell University, a noted historian of science and recent winner of the David Hull Prize, evolutionary biology has several philosophical and religious implications:

- The argument from design is dead, along with all gods worth having.
- Gods that work entirely through the laws of nature or that simply create the universe and then let it run without further interference are unharmed by the demise of the argument from design.
- Such gods are also utterly worthless.

Professor Provine has become notorious for asserting that "evolutionary theory is the greatest engine of atheism ever devised." According to this viewpoint, if one accepts the underlying premises of the theory, several implications immediately follow:

- There are no "ultimate" foundations for any theory of ethics. From where in human evolution could such ultimate foundations possibly have arisen?
- There is also no "ultimate" meaning in life, either individually or collectively.

- Human "free will," as traditionally defined, does not exist.

Of these, the demise of free will is by far the most difficult to accept. Even most atheists, including such prominent philosophers of evolutionary theory as Daniel Dennett, cannot accept the idea that human free will does not exist. However, Professor Provine asserts that the concept of "free will" is not only unintelligible, it is one of the very worst ideas ever invented, as it justifies and provides additional fuel for the basic human desires for blame and revenge.

Like Professor Provine, Charles Darwin believed in all of these implications of the theory of evolution. And, like Professor Provine, Darwin believed that the loss of ultimate foundations for ethics, ultimate meaning in life, and the idea of human free will carried little "sting." Let's consider these implications one at a time:

- *There Are No Gods Worth Having, Nor Any Life After Death*: Professor Provine has pointed out that the theory of evolution implies that when you're dead, "you're dead, dead, dead!" Professor Provine himself has a potentially fatal brain tumor and has accepted his own mortality and that of those closest to him. He believes that "the loss of gods is better for our rational minds and our emotional health."
- *There Are No Ultimate Foundations for Ethics*: Professor Provine has also asserted that if any ultimate foundation for human ethics did exist, its implications for ethics would be terrible. The environment that we live in changes so rapidly and in such fundamental ways, that any "ultimate" (that is, unchanging and unchangeable) theory of ethics would be an evolutionary "dead end" for any being who was bound by it.
- *There Is No Ultimate Meaning in Life*: Professor Provine has pointed out that, although ultimate meaning in life may be nonexistent, the proximate meanings that we find in life—our families, our friends, the rewards of life in our communities, our work, and all of the things that make day-to-day life liveable—are more than enough to fill our lives with meaning. Indeed, believing fervently in some "ultimate" meaning in life is often to ignore such sources of immediate happiness and enjoyment, and to live a life set apart from (and essentially denying the importance of) such proximate values.
- *Human Free Will Is an Illusion*: Finally, Professor Provine has asserted that the concept of "free will" is logically unintelligible. It cannot be defined in a way that avoids logical circularity or which does not contradict what we understand about nature and evolution.

The concept of universal determinism (that is, that everything everywhere is determined by some omniscient, omnipotent, omnipresent entity or force) is both unproveable and irrelevant, especially to the concept of "free will."

According to the theory of evolution, human actions and motivations are entirely locally determined by a combination of heredity and environment and the interactions between them. However, and contrary to the beliefs of some scientists, one cannot reduce all human actions to chemistry and physics.

However, it is possible to reduce the cause of human actions to a combination of genetic information and environmental influences, without inferring any other causes (such as supernatural influences or forces). Therefore, according to Professor Provine, to assert that such supernatural influences or forces exist is pointless and irrelevant.

Philosophers escape from the problem of the indefinability of the concept of "free will" by erecting logically circular definitions of free will. They do this primarily to preserve some justification for revenge. For example, philosopher Ted Honderich defines "free will" in such a way as to preserve our "retributive desires" (that is, our desire for revenge). This is just arguing for something on the basis of its effects (which one desires), rather than its logical coherence.

According to Professor Provine, we do not live on a planet on which organic beings have free will. He believes that this is good—he believes that the recognition of the absence of free will can be the greatest boon for the increase in kindness and understanding in society. He has emphasized that he is not saying that we should not stop people from doing things of which we do not approve. However, we can stop people from performing actions of which we do not approve without resorting to revenge. By not making monsters out of people who do "bad things" we make it possible to understand them and their motivations and to work to end the cycle of revenge.

At some level, all human behaviors (both bad and good) have the same "involuntary" quality—they are determined by our genetics and our personal histories. Hence, the concepts of both blame and praise are nonsensical, except insofar as they alter our behavior in the future . . . and when they do so, they are determining that behavior. Rather than expecting people to use their free will to act morally, we must recognize that children (and other members of society) can and must be programmed to act morally. Acting morally is not innate in humans—anyone who has raised a two-year-old knows this. The idea that human behavior can be "programmed" also has implications for science and scientists. Scientists can be "programmed" (that is, taught) to accept their hypotheses based on empirical evidence, rather than on their beliefs or desires.

Finally, Professor Provine has pointed out that if you accept the foregoing, it is also possible to see that atheistic science and religion can agree:

- Both counsel (for different reasons) that we should forgive sins.
- Both state that revenge is not a justifiable human response, regardless of our desire that it be so.

FOR GREATER UNDERSTANDING

Questions

1. Computers can be programmed, just like living organisms are programmed. Is there any fundamental difference between a computer and a living organism?
2. Are religious beliefs necessary for people to behave morally?
3. Would we treat people differently if we believed that they had no "free will"?

Suggested Readings

Dawkins, Richard. *The Blind Watchmaker*. New York: Penguin, 2006.

Other Books of Interest

Dennett, Daniel C. *Freedom Evolves*. New York: Penguin, 2004.

Miller, Kenneth R. *Finding Darwin's God: A Scientist's Search for Common Ground Between God and Evolution*. New York: Harper Perennial, 2007.

Ruse, Michael. *Darwin and Design: Does Evolution Have a Purpose?* Cambridge, MA: Harvard University Press, 2004.

Websites of Interest

1. Cornell University provides a reprint of an article entitled "Teleological and Teleonomic: A New Analysis" by Ernst Mayr that first appeared in the *Boston Studies in the Philosophy of Science,* XIV, (1974) pp. 91–117. — http://evolution.freehostia.com/wp-content/uploads/2007/07/mayr_1974_teleological_and_teleonomic.rtf
2. The *Faith + Evolution* website provides links to five articles that debate the concept of "free will." — http://www.faithandevolution.org/debates/is-darwinian-evolution-compatible-with-free-will.php
3. The John Templeton Foundation's *The Humble Approach Initiative* website features the article "Purpose in Evolution: Is Convergence Sufficiently Ubiquitous to Give a Directional Sign?" by Mary Ann Myers, Ph.D., based on a foundation-sponsored symposium from 2004. — http://humbleapproach.templeton.org/Purpose_in_Evolution

Lecture 13

Disastrous Digressions

The Suggested Reading for this lecture is Daniel J. Kevles's *In the Name of Eugenics: Genetics and the Uses of Human Heredity.*

Evolutionary biology is a natural science, like physics and chemistry. One of the most fundamental principles of the natural sciences is that describing or explaining something is *not* the same as advocating it. Physicists can describe nuclear fission, and even point out how it could be used in a weapon, without necessarily advocating that it be used for this purpose.

However, one of the common reactions many people have to the theory of evolution and its implications for humans is that they assume that evolutionary biologists are somehow *advocating* for evolution, or at least arguing that it's "natural" and therefore necessarily "good" or "right." This is essentially a confusion between the principles of "science" and the principles of "morals" or "ethics." As shown, *science* is the empirical study of nature—what it is and how it works. By contrast, *ethics* is the philosophical study of what we believe to be "good" and "bad," "right" and "wrong," and why we believe such things.

The confusion between science and ethics is often framed as a confusion between "is" and "ought"—the way the world *is*, as opposed to the way we think it *ought* to be. Although it seems that people should see the fundamental difference between "is" statements and "ought" statements, many people, including both opponents and supporters of evolutionary theory, believe that "is" and "ought" not only can be reconciled, but may be the very same thing.

Two episodes in the history of evolutionary thought illustrate this basic confusion between "is" and "ought" statements: the rise and fall of social Darwinism in the latter half of the nineteenth century and the rise and fall of eugenics in the first half of the twentieth century. These two social movements used evolutionary ideas and language to justify what were clearly moral and political positions, rather than scientific principles, and as such they constitute the two most disastrous digressions in the history of the science of evolutionary biology.

Before addressing these two social movements, we should also clearly draw a distinction between "science" and "technology." We have already considered what science is: the empirical study and explanation of what nature is and how it works. Science is supposed to be dispassionate, objective, and unbiased.

But the same is not the case for technology, which is the application of scientific knowledge for the "good" of humans and human society. The inclusion of the word "good" in that definition indicates that technology, unlike science, necessarily includes an ethical dimension. Strictly speaking, science has no ethical dimension. There is nothing "good" or "bad" about the molecular biology of the human immunodeficiency virus (HIV) that causes AIDS. However, the development and use of antiviral drugs to control HIV infections, while based on a thorough scientific understanding of the molecular biology of HIV, is an application of that knowledge that is intended to benefit people infected with the virus. The application of scientific knowledge, unlike the acquisition of such knowledge, always includes an ethical dimension.

Social Darwinism and eugenics weren't sciences; they were technological applications of evolutionary ideas. They involved the application of scientific ideas and information to what was intended by their advocates as the betterment of humankind. Notice the word "intended." As learned, scientific descriptions of reality do *not* include intentions in explanations of how nature works. This is particularly the case with evolutionary biology, which began with Darwin's theory of natural selection, which he developed specifically because it did *not* require any design, intention, or purpose in nature to bring about either adaptation or descent with modification. Both social Darwinism and eugenics explicitly included both an ethical dimension and intentions; they were intended to bring about a "better" society. What they did instead was to lead to perhaps the most horrific perversion of both science and morals in the history of Western civilization.

Social Darwinism and eugenics cannot be considered separately, nor can they be completely separated from the science of evolutionary biology. The social prescriptions worked out by the social Darwinists included concepts taken directly from evolutionary biology and were in turn used by eugenicists to further what they erroneously called the "science" of eugenics. Both began in England in the latter half of the nineteenth century, but they reached their highest pitch elsewhere: social Darwinism in America and eugenics in America and Germany. And both collapsed and were finally repudiated at about the same time: in the aftermath of World War II and the social movements that arose out of it.

Social Darwinism is essentially an economic and political theory based on the idea that natural selection tends to produce the "greatest good for the greatest number" of the members of a society. If you are acquainted with some of the language of ethical theory, you will recognize the phrase "greatest good for the greatest number" as the foundational principle of *utilitarianism*, one of the two or three dominant forms of ethics in Western society. According to its proponents, utilitarianism is justified by its *effects*: an action is "good" or "right" if it tends to bring about the greatest good for the greatest number of the members of a society; it is "bad" or "wrong" if it does otherwise.

According to this viewpoint, social Darwinism is based upon the premise that allowing natural selection to run its course is the most ethically justified position. Social Darwinists believed (there aren't many of them now, hence the past tense) that successful people *deserve* to be successful, while unsuccessful people *deserve* to fail. Successful people represented the highest, most noble members of society, while unsuccessful people represented the lowest, least deserving members of society.

Credit (or blame) for the invention and promotion of social Darwinism is usually assigned to Herbert Spencer, an English economist, ethicist, philosopher, and sociologist. Largely unremembered today, Spencer was unquestionably the most popular, influential, and widely read philosopher and social theorist of the nineteenth century.

Spencer wrote one of the first book-length works on biology—*Principles of Biology*, published in 1864—in which he coined the phrase "survival of the fittest" to describe Darwin's theory of evolution by natural selection. Politically, Spencer was a radical nonconformist, opposed to the class system in England and dedicated to the advancement of the middle and lower classes. He believed that natural selection—"survival of the fittest," in his terminology—caused the most talented, hard-working, and therefore deserving members of society to rise to positions of social prominence, regardless of their social class. In particular, he forcefully argued that "laissez-faire" economics—that is, economics with little or no governmental regulation—was the best system in which to promote the "survival of the fittest" and therefore promote the best and brightest in society.

Spencer's radical social theories met with considerable resistance in England, where the social class system was firmly entrenched and which many English believed to be hereditarily based. In America his ideas met with considerably more success, not the least because his economic theories reinforced the nineteenth-century American political and economic system of unfettered laissez-faire capitalism. Captains of industry like Andrew Carnegie and Henry Ford promoted economic and social policies similar to those advocated by Spencer, including the idea that those who had "risen to the top" of society had a responsibility to help those less fortunate than themselves . . . as long as those less fortunate were also hard-working and didn't demand special treatment (and, as we will see, were members of the "right" race).

Historian Richard Hofstadter has argued that from the end of the Civil War to the Great Depression, social Darwinism was the dominant social theory in American economics and politics. It was opposed by the "progressives," many of them from the farm states of the Midwest, who believed that social Darwinism was a regressive social system that held down the American farmer and working man, who were the true foundation of America's greatness. Perhaps their greatest champion was William Jennings Bryan, three times Democratic candidate for president of the United States and secretary of state under Woodrow Wilson. Known as “the Great Commoner,” Bryan fought the Republicans and their wealthy supporters, the big corporations and the big banks, and advocated tirelessly for small farmers, small businessmen, and industrial workers.

Bryan is also famous for being on the “wrong” side in the “Scopes monkey trial” in 1925. John T. Scopes, a high school biology and health teacher, was arrested and put on trial in Dayton, Tennessee, for violating the Butler Act, a law that made it “unlawful for any teacher in [Tennessee] . . . to teach any theory that denies the Story of the Divine Creation of man as taught in the Bible, and to teach instead that man has descended from a lower order of animals.” Bryan volunteered to help the prosecution, while famous atheist and defense attorney Clarence Darrow led Scopes’s defense. Unable to call scientists as witnesses for the defense, Darrow called Bryan to the stand and proceeded to humiliate him in the eyes of the public, through the courtroom reporting of newspaper correspondent, H.L. Mencken.

Bryan is rightly accused of being a “creationist” at the Scopes trial, but he was far from a “rube” or a proponent of ignorant and reactionary “fundamentalism.” On the contrary, Bryan was extremely well-read and educated, and he took the political positions he did because of his commitment to his progressive ideals. He believed that evolutionary theory (in the form of social Darwinism) was a pernicious political doctrine intended to hold down the farmer and working man, and hold up the captains of industry and the big banks and “eastern trusts.” He used fundamentalist religion as a weapon in a political battle against what he perceived to be the opponents of “the laboring interests and the toilers everywhere.” It is one of the greatest ironies of American history that “the Great Commoner” was a Democrat and opposed the Republicans, who today by and large reject the theory of evolution and progressive politics, while at the same time supporting big business and laissez faire capitalism.

Social Darwinism fell rapidly from prominence in American social theory during the Great Depression and the “New Deal” era. The Republican Party, which had presided over the boom years of the 1920s, was blamed with bringing on the Great Depression and was driven from political power for a generation. Following the Great Depression and taking hold during the administration of Richard Nixon, both the Democratic and Republican parties underwent a paradoxical transformation. The Democratic Party, which had been the party of rural America, the “solid (and racist) South,” and religious fundamentalism and anti-evolutionism became the party of urban America, the east- and west-coast educated “elites” and pro-evolutionism, while the Republican Party became the party of the rural south, the Midwest, the intermontane west, and anti-evolutionism.

According to the organizers of the Second International Eugenics Conference, *eugenics* is “the self-direction of human evolution.” The roots of eugenics go back to the ancient Greeks. Plato, in his *Republic*, advocated for a system of eugenic mating, in which people with desirable characteristics (such as philosophers) would be given preference in mating over those with less desirable characteristics. The Spartans of ancient Greece had a tradition of "exposing" deformed, unwanted, or weak infants to the elements (thereby killing them) as a way of improving the strength and toughness of the survivors. In Roman society, Roman law required that "deformed" infants be destroyed and that patriarchs could "dispose" of unwanted children by giving them away, selling them into slavery, or killing them.

Eugenics as a so-called science began with Francis Galton, a polymath and the cousin of Charles Darwin. He coined the term "eugenics" in 1883, defining it as "the study of all agencies under human control which can improve or impair the racial quality of future generations."

Galton was deeply influenced by his cousin's *Origin of Species*. He was particularly influenced by the first chapter, in which Darwin discussed selective breeding in domesticated animals and plants. Galton became convinced that humans had been bred, unconsciously but nonetheless systematically, as the result of economic and social policies that governed who could marry and have children.

According to Galton, the social classes of England were primarily the result of hereditary traits, especially intelligence, with the lower classes being less intelligent and the upper classes more intelligent. He developed a number of statistical methods for analyzing intelligence, some of which became the precursors of modern intelligence ("IQ") tests. He believed that the various human races, genders, and social classes were genetically distinct, with white, Anglo-Saxon males at the pinnacle of the species and black African females at the bottom. Asians, he believed, were somewhere in the middle, and he advocated their emigration to Africa, where they could rebuild their ancient civilizations and reclaim the riches of the African continent from the black Africans, who had no use for such riches and were despoiling their environment and wasting its resources.

Galton mostly advocated what has been called "positive eugenics," a social system in which those people judged to be "superior" would be encouraged (through financial, political, and social incentives) to have more children. He based this policy on his observation that the less desirable members of English society—the lower classes, and especially Catholics—were reproducing at a much higher rate than the more desirable members of society—the upper classes, especially Protestants. His most famous book on this subject—*Hereditary Genius*, published in 1869—presented his criteria and methods for measuring and comparing human intelligence, and laid the groundwork for his proposals for encouraging the "intellectual elite" to increase their reproductive rate.

Like social Darwinism, Galton's ideas of "positive eugenics" were less influential in England than in America. Perhaps some of this difference can be explained by the legacy of slavery in the United States. The English abolished slavery earlier than the United States and did not seem as inclined as Americans to justify it on the basis of racial inferiority. That this is the case is illustrated by the fact that the first "eugenic" laws to be enacted were laws prohibiting miscegenation—that is, marriage between people of different races—mostly, but not exclusively, in the states of the former Confederacy. The South was not alone in this, however. Many states, including northern and eastern states, passed laws during this same period regulating who could marry and under what conditions. The now widespread idea that the government could regulate marriage through the issuance of marriage licenses has its roots in the eugenics movement of the late nineteenth and early twentieth centuries. Such regulations were intended to limit the reproduction of genetically unfit people, by prohibiting marriages between close relatives and between people with "social diseases" and "genetic defects."

The eugenics movement in America had many supporters, including some who are still remembered and revered in American history for other reasons. For example, L. Frank Baum, author of *The Wizard of Oz* and other children's books, was a racist and eugenicist who advocated the extermination of the plains Indians. Supreme Court justice Oliver Wendell Holmes Jr. wrote the majority opinion in the 1927 case of *Buck* v. *Bell*, in which the court upheld the state-enforced sterilization of a Virginia woman who was claimed to be of below average intelligence:

> It is better for all the world, if instead of waiting to execute degenerate offspring for crime, or to let them starve for their imbecility, society can prevent those who are manifestly unfit from continuing their kind . . . Three generations of imbeciles are enough.

John Harvey Kellogg, founder of the Kellogg's cereal company of Battle Creek, Michigan, was also a dedicated eugenicist, founding the *Race Betterment Foundation* with Irving Fisher and Charles Davenport in 1906 (more on Davenport in a minute). Kellogg was strongly in favor of racial segregation and believed that immigrants and especially non-whites would damage the American gene pool. Finally, Margaret Sanger, founder of Planned Parenthood and icon of the feminist movement, was a dedicated eugenicist who believed that the "positive eugenics" of the English was mostly ineffective.

Whereas most English eugenicists advocated "positive eugenics," some of the most influential American eugenicists advocated "negative eugenics"—that is, the prevention of marriage and interbreeding of people deemed genetically inferior, up to and including forced sterilization of people deemed sufficiently degenerate as to present a "drain" on society.

Chief among the American advocates of negative eugenics was Charles Benedict Davenport. An early convert to Mendel's theory of genetics, Davenport was made director of the Cold Spring Harbor laboratory of experimental genetics on Long Island in 1898. While there, in 1910, he founded the Eugenics Record Office, which became a center for the study of human genetics and heredity, and one of the organizing centers of the American eugenics movement.

That movement was extraordinarily successful during the first four decades of the twentieth century. Eugenics was a regular topic of popular books and articles in the public press. Speakers promoted eugenics in public meetings and private organizations, and local eugenics societies sprang up around the country. Undergraduate and graduate courses in eugenics were offered at many American colleges and universities. By 1928, there were 376 college and university courses in eugenics in the United States.

The American eugenics movement, spearheaded by Davenport, had perhaps its greatest impact on the eugenics movement in Germany. In 1916, Madison Grant, an American lawyer, eugenicist, and historian, wrote *The Passing of the Great Race, or the Racial Basis of European History*, in which he asserted that the Nordic race was the most advanced among human racial groups, and that immigration, "race-crossing," and social policies that allowed blacks, Jews, and other "inferior" races to replace Nordics at the pinnacles of society were destroying the "great Nordic race." Grant advocated anti-miscegenation laws, such as Virginia's Racial Integrity Act of 1924, where the "one drop rule" (which classified anyone with any African ancestors at all, no matter how few or how distant, as "Negro") was made the basis for discriminatory laws.

Grant's book never became a best-seller in the United States, but in Germany the situation was very different. Under Adolf Hitler, the Nazi party made "racial purity" part of the foundation of the National Socialist political platform. *The Passing of the Great Race* was reinterpreted by Alfred Rosenberg, the principal Nazi race propagandist, as referring to the Aryan race, whose greatest enemy and perennial opponent was the culturally and genetically degenerate Jewish race. After the Nazi takeover of power in Germany in 1933, the so-called "Nuremburg Laws" were promulgated, outlawing intermarriage between Jews and other Germans and stripping Jews of their German citizenship. The Nuremburg Laws also made extramarital sex between Jews and non-Jews illegal, and even went so far as to prohibit Jews from hiring German women as housekeepers for Jewish households.

Beginning in 1934, a series of laws requiring forced sterilization were put into effect in Germany. These laws were modeled after similar laws passed in several American states, especially California and Virginia. In the United States more than 64,000 people (predominantly women) were sterilized against their will between 1907 and 1963. In Germany under similar legislation, more than 400,000 people were forcibly sterilized between 1933 and 1945 under the *Law for the Prevention of Hereditarily Diseased*

Offspring. Put in force in July 1933, this law required physicians to report to the government every case of hereditary illness they encountered (except in post-menopausal women), or pay a fine.

Forced sterilizations were only the beginning. In May 1939, the *Committee for the Scientific Treatment of Severe, Genetically Determined Illness* was established at the express order of Adolf Hitler. Its function was to develop criteria for use in a systematic program of infanticide, designed to kill infants identified as having genetic or developmental disabilities. Jewish infants were automatically included, as simply being Jewish was defined as a degenerative genetic disease. In September, simultaneous with the outbreak of the war, this program was expanded into what was known as the T-4 program (an abbreviation for "Tiergartenstraße 4," the address in Berlin where the headquarters of the program were located. The name of this program was "The *Charitable Foundation for Cure and Institutional Care."* Its mission, as stated in Hitler's explicit order, was so "that patients considered incurable according to the best available human judgment of their state of health, can be granted a merciful death." Between 1939 and 1945, at least 200,000 physically or mentally handicapped people were killed by medication, starvation, or gas chamber.

But forced euthanasia was only the beginning. On January 20, 1942, members of the upper echelon of the Nazi government met to inform the various government officials responsible for government policies and regulations pertaining to Jews that Reinhard Heydrich had been named as the chief executor of the "final solution to the Jewish question." Heydrich presented a plan for the forcible deportation of the Jewish population of Europe and north Africa to German-occupied areas in eastern Europe. There they would be sorted, and those among them who were able-bodied would be assigned to hard labor on road-building projects, in the course of which they would eventually die from overwork, disease, or starvation. Any surviving Jews (and those deemed unfit for such labor) would be exterminated.

That was the plan; however, as the war progressed and German troops were pushed back toward the pre-war borders of Germany, the plans to use the deported Jews (and others, including gypsies, homosexuals, and the able-bodied mentally ill) for road-building and other labor projects were abandoned, and the captive populations were simply killed. The extermination programs were accelerated as the Allies pushed closer to Germany, with the intention that all evidence of the camps be destroyed before they were discovered by the Allies. However, as German military strength collapsed following the failed invasion of Russia, the Allies moved more quickly than the Nazi bureaucracy could react, so many of the camps were liberated before all of their inmates could be killed and their bodies cremated.

The horrors of World War II and the Nazi holocaust put an end to the eugenics movement. Its association with the atrocities committed by the

Nazis made it so unpopular that virtually all colleges and universities stopped teaching courses in eugenics, publishers stopped printing (and the public stopped reading) books on the subject, and anyone who wrote or spoke about eugenics with anything except horror and revulsion was lumped together with the Nazis. At the Nuremburg trials in 1945–46, at which the Nazi leadership was tried for war crimes and "crimes against humanity," the "negative eugenics" programs were included among such crimes. The surviving Nazi leaders who promoted such programs were executed, and those who supported them were imprisoned. In 1950, the United Nations Economic, Social, and Cultural Organization (UNESCO) issued a statement on race in which the concepts that formed the basis of eugenics were explicitly repudiated. This statement was revised three times, in 1951, 1967, and 1978, with input from geneticists and evolutionary biologists, including Theodosius Dobzhansky.

Was the eugenics movement a product of the science of evolutionary biology? Although eugenicists used much of the vocabulary of evolutionary biology and genetics, the answer to this question is clearly *no*. Like the relationship between nuclear physics and nuclear weapons, the relationship between evolutionary biology and eugenics was essentially the relationship between a science and a technology that used some of the principles of that science for political and social purposes.

However, if one asks a slightly different question—do scientists, including evolutionary biologists, bear any responsibility for the horrors of war and the Holocaust—the answer is yes if they did not speak out against such things once their evil aspects had become known. Anyone who does not resist evil, scientist and nonscientist, evolutionary biologist and creationist, male and female, of any and all races, religions, ethnic backgrounds, and sexual orientations, who perceives that evil is being done and does nothing to stop it is responsible for that evil. As Edmund Burke once wrote, "All that is necessary for the triumph of evil is that good men do nothing."

FOR GREATER UNDERSTANDING

Questions

1. What is the relationship, if any, between ethics, morals, and science?
2. Does unrestricted laissez-faire competition necessarily promote the "greatest good of the greatest number" in human society?
3. Is eugenics currently "dead," or has something very similar (but with a different name) taken its place?

Suggested Readings

Kevles, Daniel J. *In the Name of Eugenics: Genetics and the Uses of Human Heredity*. Cambridge, MA: Harvard University Press, 1998.

Other Books of Interest

Black, Edwin. *War Against the Weak: Eugenics and America's Campaign to Create a Master Race*. New York: Dialog Press, 2008.

Gould, Stephen J. *The Mismeasure of Man*. New York: W.W. Norton & Co., 1996.

Hofstadter, R. *Social Darwinism in American Thought*. Boston: Beacon Press, 1992 (1944).

Websites of Interest

1. This site from Allen MacNeill features a pdf of Brian Kaviar's 2003 Tallman Prize-winning essay "A History of the Eugenics Movement at Cornell." —
   http://macneill.allen.googlepages.com/2003_Tallman_Prize_Kaviar.pdf
2. Fordham University's *Modern History Sourcebook* website provides an article by Paul Halsall entitled "Herbert Spencer: Social Darwinism, 1857" from a paper by Spencer entitled "Progress: Its Law and Cause," which specifically discusses race and class. —
   http://www.fordham.edu/halsall/mod/spencer-darwin.html

Lecture 14

A Temporary Unity

The Suggested Reading for this lecture is George Gaylord Simpson's *Tempo and Mode in Evolution.*

Jacob Bronowski, author of *The Ascent of Man*, famously described the theories of quantum mechanics and relativity in physics as the "greatest collective work of art of the twentieth century." Essentially the same could be said of the "modern evolutionary synthesis." It involved the collective work of hundreds of field ecologists, laboratory biologists, mathematicians, and theoreticians from around the world. Historian William Provine has stated that the "modern evolutionary synthesis" was essentially complete by 1959, when it was celebrated at the centennial of the publication of the *Origin of Species* at Chicago University. At that celebration, many of the participants in the "modern synthesis" got together to compare notes, to reminisce about their work together, and to present papers that consolidated the broad outlines of the synthesis for posterity.

The "modern evolutionary synthesis," like Darwin's *Origin of Species*, was a true synthesis, spanning nearly all of the major disciplines of the biological sciences and including scientists from many different nations. So far, all of the contributors to the "modern evolutionary synthesis" have been geneticists or population geneticists. However, scientists from other disciplines also contributed to the synthetic theory.

Principal among these was George Gaylord Simpson, curator of the departments of geology and paleontology at the American Museum of Natural History in New York, and later curator of the Museum of Comparative Zoology at Harvard University in Cambridge, Massachusetts. Simpson was a paleontologist; that is, a scientist who studies ancient (and usually extinct) organisms, usually by studying their fossils and other remains. He was an expert in comparative anatomy, particularly of mammals, and most especially of horses and their evolutionary ancestors. In his most important book, *Tempo and Mode in Evolution* (first published in 1944), Simpson presented two major concepts that were essential to the modern evolutionary synthesis:

- That the fossil record generally supports the theories presented by population geneticists, especially Fisher, Haldane, Wright, and Dobzhansky.
- That the pace at which evolution has occurred has varied over geologic time, based primarily on observations of the fossil record.

The first idea was probably less important in the long run than the second. The reason was that Simpson's suggestion that the rate of evolutionary change could speed up or slow down seemed to some evolutionary biologists to depart somewhat from Darwin's theory, which most evolutionary biologists interpreted as implying that evolution was both continuous and gradual. As we will see, this idea was challenged in 1972 by Niles Eldredge and Stephen J. Gould in their landmark paper on punctuated equilibrium. This development was particularly ironic, as Simpson is usually credited with bringing paleontology into the "modern evolutionary synthesis," whereas Eldredge and Gould are perhaps the most famous challengers to that same synthesis.

Another central figure in the "modern evolutionary synthesis" was German ornithologist Bernhard Rensch. His name is often left out of accounts of the development of the "modern synthesis," mostly because his books and scientific publications were almost all published in German. The one major exception was his 1947 book, *Evolution Above the Species Level*. In it, Rensch presented a theory of speciation very similar to the theory proposed by Ernst Mayr, along with much supporting evidence from his own work. More importantly, Rensch argued forcefully that the same mechanisms that cause the origin of new species from existing ones could also explain the origin of all of the higher taxa (genera, families, orders, classes, phyla, and even kingdoms). Rensch's argument was essentially that all of the higher taxa originated by the same mechanisms as species—principally natural selection, but also (possibly) genetic drift—and that the main difference between the origin of new species and higher taxa was the much longer spans of time involved in the latter. According to Rensch, there is fundamentally no difference between microevolution—natural selection and genetic drift acting over relatively short periods of time within populations—and macroevolution—those same mechanisms extended over millions or billions of years.

Finally, in 1950, botanist G. Ledyard Stebbins published *Variation and Evolution in Plants*, which extended the "modern synthesis" to plants. Stebbins showed how natural selection and genetic drift could be used to explain virtually all of the evolution of plants, and he thereby put an end to the remnants of Lamarckian thinking, which still persisted among some botanists at that time. Stebbins's contribution to the "modern evolutionary synthesis" was twofold: it extended the theoretical population genetic models of Fisher, Haldane, and Wright to plants (something that only Haldane originally attempted), and it put the final nail in the coffin of non-Darwinian evolutionary mechanisms, such as Lamarckian inheritance of acquired characteristics.

By 1959, most biologists (following Ernst Mayr's lead) agreed that evolutionary theory had been "unified" and that it had reached its final form. Among the tenets of the "unified" theory of evolutionary biology at that time were the following:

- That evolution is best defined as "changes in allele frequencies in populations over time."
- That there is an essentially direct one-to-one correspondence between genes and the traits for which they code.

- That the genomes and resulting phenotypes of most organisms are essentially "homeostatic" over time—they react to perturbations by returning to a balance of adaptive characters or change smoothly over time via directional selection.
- That genetic recombination is more important than mutation as a source of variation.
- That natural selection is the primary mechanism of evolution at all levels.
- That competition, especially between members of the same species, is the principal driving force in natural selection.
- That genetic drift is also an important mechanism in evolution, explaining changes (such as the "founder effect") that happen in small populations.
- That the inheritance of acquired characters (that is, Lamarckian inheritance) is either impossible or irrelevant to biological evolution.
- That the evolution of gross phenotypic characteristics (such as eyes, wings, and so forth) is a good model of evolution at the molecular level.
- That the "biological species concept" provides an unambiguous and widely applicable definition of nearly all species.
- That speciation is almost completely understood, at least in principle.
- That speciation is virtually always the result of geographic isolation (allopatry).
- That macroevolution (the origin and evolution of higher taxa) proceeds via essentially the same mechanisms as microevolution (that is, natural selection, sexual selection, and genetic drift).
- That neither design nor purpose played any part in biological evolution, nor in biology in general.

This grand unified theory of evolutionary biology was an extraordinary achievement, as significant as the collective formulation and elaboration of the theories of quantum mechanics and relativity in physics, although less well known. The celebrants at the Chicago centennial could be justly proud of having produced a synthetic theory at least as fully realized as Darwin's, and supported by much more field and laboratory research.

However, it should also be said that the collective achievement of the makers of the "modern synthesis" simply amplify Darwin's extraordinary achievement. His theory, like theirs, was a truly synthetic theory, drawing together animal and plant breeding, theoretical population ecology, natural history, animal behavior, paleontology, biogeography, embryology, and systematics. And both theories—in 1859 and 1959—were truly revolutionary. They both upended the theories of the origin of species and adaptation that preceded them, and both generated controversies among the general public and among scientists.

There is one significant difference between Darwin's synthesis and its "modern" counterpart: Darwin did not believe that his theory was the final comprehensive answer to the questions of the origin of species and adaptations. In the *Origin of Species*, Darwin was very candid at pointing out the weak points in his theory, and especially those parts of the theory for which there was little or no evidence, and even those parts which were almost entirely speculative. The same cannot be said for the "modern evolutionary synthesis." It was almost immediately incorporated into biology textbooks, where it remains almost unchanged to this day. When creationists challenge the theory of evolution, the version of the theory that they challenge is almost always the version at the heart of the "modern synthesis" as it was conceived of in 1959. And when evolutionary biologists come to the defense of evolutionary theory, the theory they usually defend is the one still known as the "modern evolutionary synthesis." That theory, in other words, has done something that evolutionary biologists have asserted can't happen: it has *not* evolved.

This amounts to evolutionary biology's "best kept secret." Considered from the perspective of the half century that has passed since 1959, most historians of evolutionary biology now know that almost all of the major tenets of the "modern synthesis" listed earlier were either grossly inaccurate or just plain wrong. Research and additional theoretical work since 1959 has shown:

- That "changes in allele frequencies in populations over time" is a wholly inadequate definition for much of the evolution revealed by the fossil and genomic records.
- That genes and traits are only weakly associated (that is, the "one gene–one enzyme" theory does not apply to most of the genome, and when it does it does so in peculiar and unpredictable ways).
- That the genomes of most organisms are chaotic, with bits and pieces of gene sequences being added, removed, and rearranged in nearly random patterns, often by "parasitic DNA."
- That there are at least fifty different mechanisms that produce genetic and phenotypic variation, of which recombination is only one (and perhaps not the most important one).
- That mutation is immensely important, not only as a source of evolutionary novelty but also as a source of overall genetic change, especially in short-lived organisms such as bacteria.
- That much of evolution is selectively neutral, especially at the level of nucleotide sequences in DNA.
- That natural selection is only one mechanism of microevolutionary change, and possibly not the most important one.

- That cooperation, especially between members of different species, has been a crucial process in evolution, especially macroevolution.
- That much of the genome of most organisms, especially eukaryotes such as ourselves, is stuffed with redundant sequences, modular gene segments, and regulatory regions do not code for polypeptides at all, but some of which are nevertheless essential to phenotypic expression.
- That random genetic drift is not an important mechanism in evolution (and may not even exist, at least in the way described by Sewall Wright).
- That the inheritance of acquired characteristics is a real and potentially very important mechanism of biological evolution (important enough to be given its own name, "epigenetics," a rapidly developing subdiscipline of evolutionary genetics).
- That phenotypic and protein evolution is largely decoupled from the evolution of much of the DNA sequence in most organisms, especially eukaryotes.
- That the biological species concept is largely inadequate to characterize species at many levels (especially the most abundant and diverse organisms on Earth, the bacteria), and that uncritical adherence to it has inhibited research into the mechanisms of speciation.
- That the mechanisms of speciation, like those of macroevolution, are still largely unknown.
- That speciation not only *can* happen without geographic isolation (a process called sympatric speciation), but may happen that way much of the time.
- That macroevolution proceeds by fundamentally different mechanisms than microevolution, and that these macroevolutionary mechanisms are still largely unknown.
- That microevolution and macroevolution can both be saltatory—indeed, macroevolution almost always is.
- That the use of teleological language—that is, "design" and "purpose"—is legitimate when describing the development of organisms via the expression of their genetic programs, but that neither design nor purpose play any part in the evolution of those programs.

As recent investigations of the whole genomes of several species have shown, the vast majority of the underlying genetic code of living organisms does nothing like what the originators of the "modern synthesis" thought the genome was doing. It is essentially a "boiling chaos" of noncoding genetic information, which mutates at an astonishingly high rate, with effects that we have only begun to understand.

This does not undermine the importance of natural selection in evolution, at least not insofar as it is believed to be the basis for adaptations. However, following John Endler's lead (in his landmark book, *Natural Selection in the Wild*, published in 1986), some evolutionary biologists now no longer consider natural selection itself to be a "cause" of anything. It is, rather, an *effect*—that is, an *outcome* caused by other processes, including:

1. *Variation*, both genetic and phenotypic, resulting from mutation, genetic recombination, and epigenetic transformation.
2. *Inheritance*, both genetic and epigenetic, resulting from the expression of the genetic code and its interactions with the environment of its carrier.
3. *Population expansion and contraction*, resulting from the general tendency of organisms to produce more offspring than is necessary to replace themselves, but also from such catastrophic processes as mass extinction and adaptive radiation.
4. *Differential survival and reproduction*, including both directional change and purely random changes in both genotypes and phenotypes.

These four underlying conditions, working together, produce the changes in genotype and phenotype that we call "natural selection."

Overall, the evolution of the theory of evolution has swung back and forth like a huge pendulum, in approximately fifty-year cycles:

- 1759 to 1809: formulation of the species concept and the system of biological classification, based on the *Systema Naturae* of Linnaeus, which assumed the origin of species by means of special creation by God.
- 1809 to 1859: Lamarckian evolution by inheritance of acquired characteristics, with evolution conceived of as a progressive, purposeful process tending toward ever-increasing perfection.
- 1859 to 1909: Darwinian evolution by natural selection, eventually replaced by evolution by Mendelian macromutation.
- 1909 to 1959: evolution by macromutation, eventually replaced by neo-Darwinian gene-level microevolution.
- 1959 to 2009: neo-darwinian gene-level microevolution, replaced by multilevel selection and macroevolution via evolutionary developmental mechanisms.

In almost every case, the underlying focus has been on the "engines of variation" and how they affect what George Gaylord Simpson called the "tempo and mode of evolution." Ever since Darwin first presented his theory of descent with modification, the real mystery has been where the variations that provide the raw material for evolution come from. An investigation of the multifarious sources of variation and the discovery of multiple mechanisms of descent with modification will be the topic of the next series of lectures in this conceptual history of the Darwinian revolutions.

FOR GREATER UNDERSTANDING

Questions

1. Does evolution proceed at different rates and via different mechanisms?
2. What were the main tenets of the "modern evolutionary synthesis"?
3. What has happened to the "modern evolutionary synthesis" over the past half century?

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1. Allen MacNeill provides an entry on the *Evolutionary Psychology* blog entitled "The Modern Evolutionary Synthesis." — http://evolpsychology.blogspot.com/2009/03/modern-evolutionary-synthesis.html
2. A *Facebook* "Interest" page on modern evolutionary synthesis. — https://www.facebook.com/pages/Modern-evolutionary-synthesis/108410322522628/
3. The BioMed Central website provides a pdf of a paper by Michael R. Rose and Todd H. Oakley entitled "The New Biology: Beyond the Modern Synthesis." — http://www.biology-direct.com/content/pdf/1745-6150-2-30.pdf

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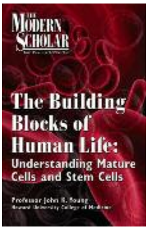

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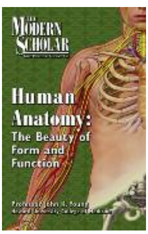

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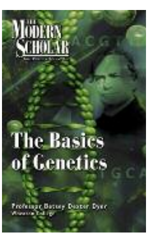

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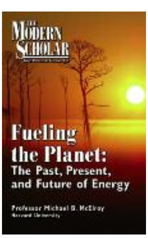

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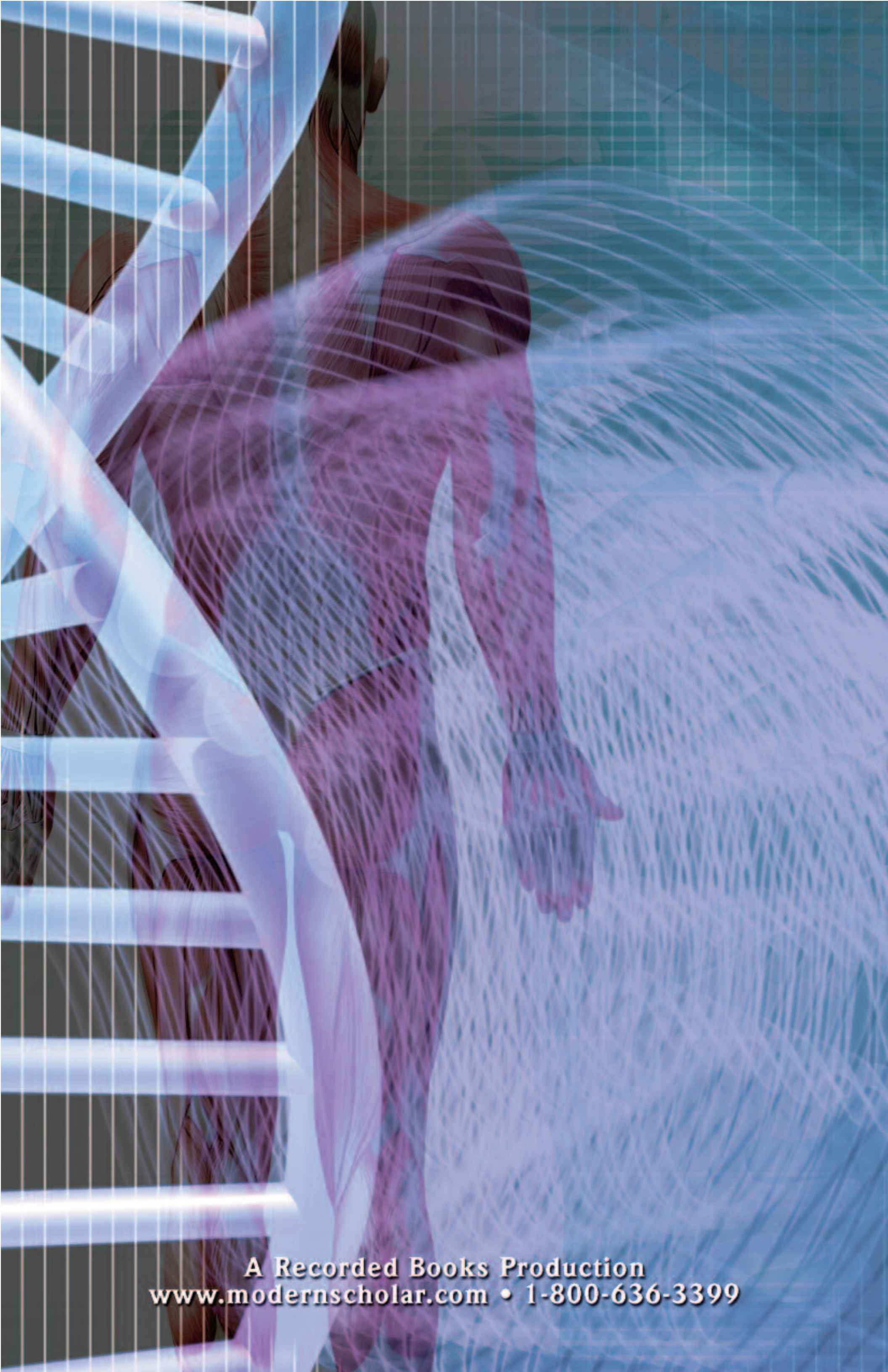

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