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The Evolution of Life

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This book is dedicated to my incomparable students, in gratitude.

FOREWORD

This book was written after a decade's experience of teaching the Evolution course to a class of about 150 second-year students at McGill University. Students take the course because evolution is an item in their curriculum, together with courses about genetics, cell biology, ecology, and so forth. I try to explain why it is more than that. Most students are already familiar with the biology of individuals, and with the principles that govern, say, photosynthesis or DNA replication. They are often not as familiar with the biology of variable populations, and therefore with the principles that govern evolutionary change. In developing the course, I found myself emphasizing these principles, even to the extent of excluding many topics that are often taught in the context of evolution. The focus of the course sharpened as it became dedicated exclusively to the distinctive properties of evolving populations.

In particular, the course is about adaptive evolution. The intricate design of living bodies, and how exquisitely they are tailored for a myriad ways of life, has always aroused wonder. The purpose of evolutionary biology is to account for this remarkable observation. The main goal of a course on evolution must be, then, to explain how very complex and highly integrated organisms can have arisen through a natural process, with no guiding hand. This is a genuinely difficult problem that students struggle to understand, I believe, unless the mechanism of Darwinian evolution and its surprising consequences form the framework of the course and inform all its aspects.

The outcome of evolution on Earth has been the millions of species of animals and plants and other organisms that live in the sea and on the land. The underlying theme of a course on evolution is thus the radiation of living organisms during the course of Earth history. We are only one of these millions of species, but we are of course particularly interested in our own place in the world. It seems appropriate, then, to orient an evolutionary account of diversity by showing how we are related to other organisms and by tracing the human lineage deeper and deeper into the past.

The focus of the course on adaptation and radiation made it necessary to discard or downplay many familiar topics, such as the Hardy–Weinberg law, the "shifting balance", and the voyage of the *Beagle*. I regret their omission, all the more because it has been accompanied by the loss of all but the very simplest mathematical propositions, and by the restriction of theory to statements that can be supported directly by evidence. This book is not a substitute for more specialized or more extensive treatments. Its sole purpose is to provide a grounding in the main features of evolution on Earth.

A book can assist the delivery of a course in two ways. It may simply present the topics as they are taught in the course, so that the lectures follow the text quite closely and the text encapsulates the material that the students should learn. On the other hand, it may extend the material in both directions, on the one hand by reinforcing areas such as basic genetics, and on the other hand by introducing more advanced topics in areas such as population genetics, genomics or developmental biology. There is much to be said for both models, but this book belongs in the former category. I have set out to write a brief text that follows very closely the sequence of lectures in my own course. Its purpose is to provide a full course for university students who have not previously taken a course dedicated to evolution, with as little extraneous material as possible. More advanced students may benefit from a more comprehensive treatment that covers a wider range of topics in related fields. I hope, however, that this book will serve to introduce students at any level to the main features of evolution and the main principles of evolutionary biology. The Further Reading that is suggested at the end of each chapter has been chosen mainly from the secondary literature, which consists of reviews and syntheses written to provide a fairly non-technical introduction to a broad field. They are in turn based on the primary literature that reports original research findings, and on which this book is ultimately based. The reference lists of the Further Reading provide a convenient entry to the primary literature.

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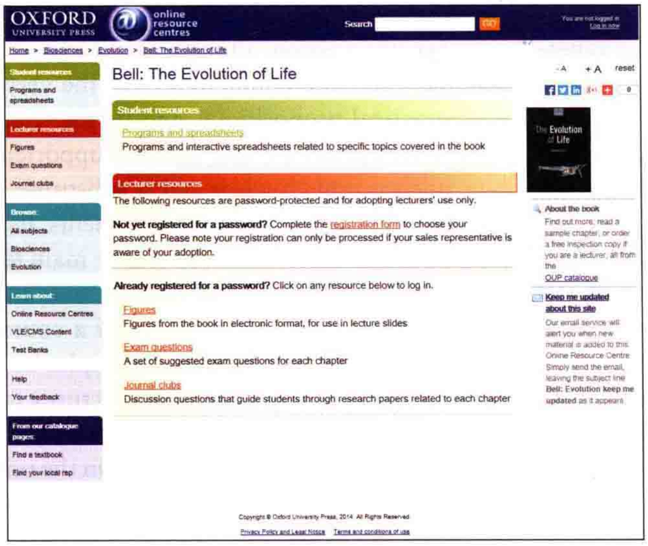

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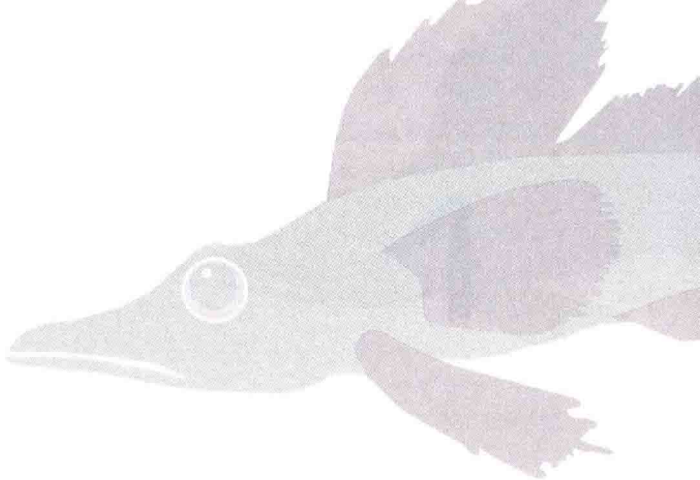
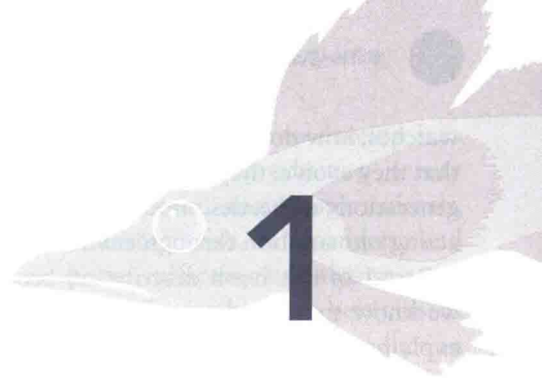


PART 1
Basics

The first part of this book describes some of the characteristics of evolving populations and the main features of the process of evolution. It is intended to introduce evolution to students who have had little or no systematic instruction in the subject, and to remind others of the outline of the field.

Part contents



1 The Evidence for Evolution

Why do you need to learn about evolution? The natural world is very complicated—think of the enormous variety of animals and plants that we take for granted. It would be very difficult to learn about every one of them separately. Science is how we understand complicated situations in terms of a few simple principles that can be very widely applied. The motion of a bird in the air, for example, is very complicated, but it is governed by a few simple laws of dynamics that also govern the flight of an arrow or an airplane. The science of evolution explains how the vast diversity of living things is likewise governed by a few simple natural principles. The object of this book is to explain these principles and to show you how all living things—including ourselves—are the products of evolution.

1.1 The uniformity of life. *Living organisms share a narrow range of materials and processes.*

Almost everything is a pebble, a watch, or a beetle. Think of an object. The chances are that it will belong to one of three categories, which I shall call pebble, watch, and beetle.

Pebbles have very simple structures. They may be a mixture of substances and they may have complicated outlines, but they do not consist of separate parts that must interact with one another in order to perform some function or activity. Snowflakes, crystals, and mountains are pebbles, in this sense. Pebbles come into being by some simple natural process that does not require conscious design.

A *watch* is a complex integrated structure whose parts must interact in a particular way in order to produce a characteristic outcome. A hammer, a building, and the computer on which I am writing this sentence are all watches, in this sense. All are prefigured in the mind of a designer and constructed by an artisan, both almost always human.

A *beetle* is also a complex integrated structure whose parts must interact in a particular way in order to produce a characteristic outcome, but it has been neither designed nor constructed: instead, it has evolved and developed. A dog, a daisy, and the organism who is typing this sentence are all beetles, in this sense.

A commonplace and meaningful distinction is that beetles are alive, whereas pebbles and watches are not. This is not a profound philosophical insight, just a rough guide for thinking about the world. There are some objects it would be difficult to classify in this way. A dead snail shell, or a fragment of the shell, for example, might appear to be a pebble but had once been a beetle. At the other extreme, the whole Earth (shorn of its living inhabitants) would carry out cycles of erosion, subduction, and mountain forming without either design or evolution. So is the Earth a pebble, a watch, or a beetle? You can probably think of many other debatable cases.

The distinction between living and non-living things is useful, though, because it focuses the mind on the problem of beetles. If they neither arise spontaneously through simple physical laws, like pebbles, nor are consciously designed and constructed, like watches, how do they come into being? The answer is that they evolve: they are the descendants of previous generations of beetles, modified by natural selection acting on variation through environmental change.

Part 1 of this book describes in broad terms why we know that the diversity of life has evolved, and explains how the mechanism of evolution works. Subsequent parts discuss the main themes of evolution in more detail. This book will show you how all the physiology, biochemistry, and genetics that you have learned in other biology courses are the consequences of a few natural mechanisms. If you have not learned about these mechanisms before, this will be the most interesting course you will ever take.

1.1.1 All living organisms share the same basic features.

The outward diversity of animals and plants is based on a very restricted range of materials, body plans, power sources, and instructions, relative to those we use in everyday life. Figure 1.1 lists the features that distinguish beetles from watches. This is not because animals and plants are better designed than our own tools; on the contrary, they are in many ways inferior. It is because they have been neither designed nor constructed, but have instead evolved.

Suppose that you visit the hardware store, then the pet store. The hardware store has a wide range of "watches" (tools) and the pet store has a wide range of "beetles" (animals). At the hardware store you could buy a screwdriver, a barbecue, or a light bulb. At the pet store, you could buy a goldfish, a parrot, or a puppy. The variety available at these stores might seem to be comparable, but this is misleading: in many ways, tools are more diverse than animals.

- Tools are made of a great variety of different materials: metals, ceramics, plastics, concrete, silicon, and glass, besides organic materials like wood or rubber. Animals and plants are made of only a few basic kinds of substance—amino acids, nucleotides, and sugars—all based on carbon.

Watch		Beetle
Very diverse: metals, ceramics, plastics, concrete, silicon and glass, besides organic materials like wood or rubber	Material	A few basic kinds of substance — amino acids, nucleotides, and sugars — all based on carbon
Many: lever, wedge, crank, pulley, screw, wheel, etc.	Mechanism	Few, e.g. lever; screw and wheel unknown
Many: clockwork, gravity, electricity, internal or external combustion engines, nuclear power, etc.	Energy source	Weaker and more complex processes such as fermentation, respiration, and photosynthesis
Wide: temperature of liquid nitrogen to the melting point of iron or beyond	Working range	Narrow: freezing to boiling point of water
Many kinds: an oral description, a drawing, a recipe, a computer file, or a model	Instructions	One kind: sequence of nucleotides in a nucleic acid

Figure 1.1 Features that distinguish beetles from watches.

Watch courtesy of Pierre EmD. Beetle courtesy of AlbertHerring.

- Tools vary because the material used for each is the best suited for its purpose: metal is best for edge tools, ceramic for tableware, glass for windows, and so on. Organisms use a much more restricted set of materials that are neither as strong nor as stiff as those we can make: calcium carbonate, cellulose, chitin, and bone.
- Tools use a variety of mechanisms: lever, wedge, crank, pulley, screw, wheel, and so on. Organisms use only a few of these: levers are used by animals with jointed limbs, for example, but screws and wheels are almost unknown.
- Again, machine tools make use of many sources of energy: clockwork, gravity, electricity, internal or external combustion engines, and so forth. None of these are used by organisms as prime movers; the living cell is instead powered by weaker and more complex processes such as fermentation, respiration and photosynthesis.
- Tools can be devised to operate over a very wide range of conditions, from the temperature of liquid nitrogen to the melting point of iron or beyond; organisms operate only between the freezing and boiling points of water.
- The instructions for making a tool can be presented in many ways: an oral description, a drawing, a recipe, a computer file, or a model. The instructions for making an organism of whatever kind are encoded in only a single way, as a sequence of nucleotides in a nucleic acid.

Evolution is modification through descent. All organisms are similar, not because they have been perfectly engineered, but rather because they all descend from the same common ancestor. The mechanism that produces modification is described in the next chapter. This chapter is concerned mainly with descent—how we know that the diversity of living forms springs from a single root.

1.1.2 Similarity implies common descent.

Children resemble their parents. Everyone knows that children tend to look like their parents. In some organisms, in fact, they look exactly like their parents. Dandelions, duckweed, water fleas, and many other animals and plants reproduce in a very simple manner by using cells from a single parent to develop into new individuals. This asexual reproduction is very common among microbes and microscopic animals, but it also occurs in some fish, salamanders, and lizards. In these species, offspring are almost exact copies of their parents and resemble them very closely. In most animals and plants, of course, reproduction is more complicated because it involves two parents, and the cell from which a new individual develops bears material from both of them. Offspring that are produced sexually therefore resemble both parents, although the resemblance is incomplete.

Children of the same parents resemble one another. Because children in the same family resemble their parents, they necessarily also resemble one another. In sexual organisms they differ because they receive different combinations of material from their mother and father. Nevertheless, they will often share attributes such as stature and facial features, and on average they will be much more similar than two randomly chosen individuals from the same population. In exceptional cases they may be very similar indeed. If the fertilized egg divides in two, and each daughter cell then develops into a new individual, the result is identical twins, children who have received the same genetic material from their parents. Identical twins may be so similar in appearance and behavior that strangers cannot tell them apart.

Relatives are similar because they share ancestral genes. The physical basis of inheritance is the gene, which is a short length of DNA that can be translated into a protein by the biosynthesis machinery of the cell. Genes do two things. In the first place, they encode the proteins that are responsible for the underlying physical make-up of an individual. Individuals that have the same genes are therefore likely to be very similar in most ways, although they will always differ to a greater or lesser extent because development is influenced by the environment as well as by the genes. Secondly, genes are copied in the process of forming the reproductive cells, so that offspring bear copies of the genes borne by their parents. Consequently, offspring will tend to resemble their parents because they bear copies of the same genes. The same principle applies to all kinds of relatives: great-grandchildren or second cousins, for example, are more similar than randomly chosen individuals because they share some fraction of their genes through descent from a common ancestor.

Sister species are very similar because they are closely related. At a broader scale, all individuals belonging to a given species are more closely related to one another than they are to members of any other species. This is because the most recent common ancestor of any two individuals belonging to the same species will normally itself have been a member of that species.

Species that have recently evolved from the same common ancestor (sister species) will also be closely related. The whitefish of northern lakes provide a good example of species that are currently emerging. Many lakes contain two types, a large type that feeds on worms and shrimps in the mud and weeds, and a small type that feeds on plankton in mid-water, as illustrated in Figure 1.2. Although they are different in appearance and behavior they separated very recently (since the retreat of the glaciers about 10,000 years ago), are still capable of interbreeding, and share most of their genes. At this very early stage, in fact, they are somewhere between two ecotypes of the same species and two completely separate species. In situations like this, we can actually witness the emergence of new species—Figure 1.2 also shows some of the many kinds of whitefish that have recently evolved in Swiss lakes.

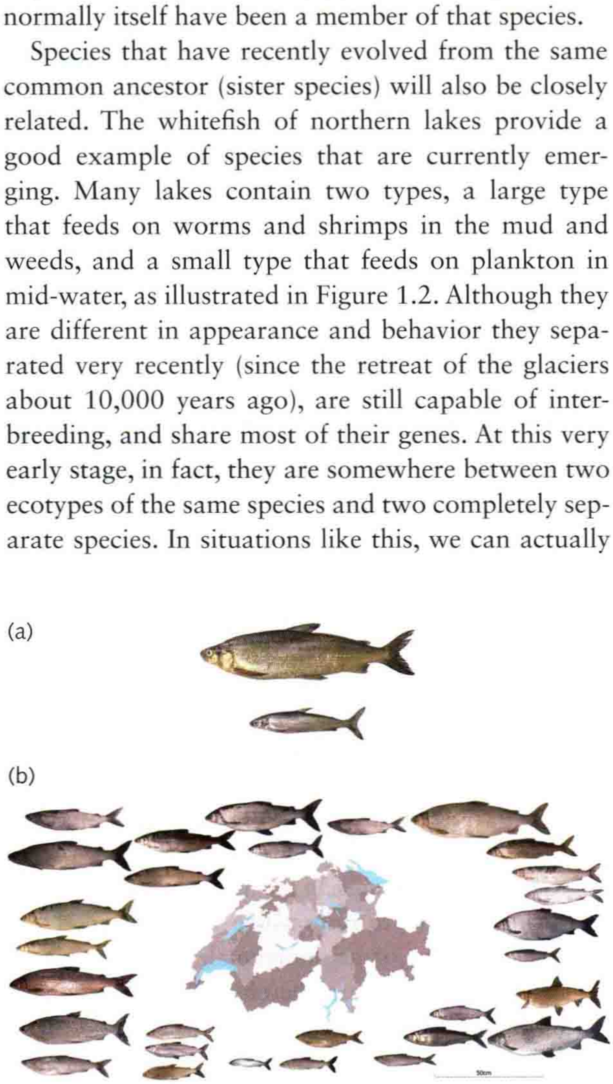


Figure 1.2 Sister species of whitefish, *Coregonus*. (a) Normal (benthic) and dwarf (limnetic) forms from a Quebec lake. (b) A cloud of recently evolved species of whitefish from lakes in Switzerland.

(a) Reproduced with permission from Jeukens, J. and Bernatchez, L. 2012. Regulatory versus coding signatures of natural selection in a candidate gene involved in the adaptive divergence of whitefish species pairs (Coregonus spp.) *Ecology and Evolution* 2 (1): 258–271 doi: 10.1002/ece3.52. (b) From Pascal Vonlanthen, Eawag, and kindly provided by Bänz Lundsgaard-Hansen.

Species share attributes of their common ancestor. As time goes on, newly formed species will become steadily more different because they have separate and independent histories, each with a unique pattern of adaptation to environmental change and variation. The physical basis of adaptation to some new environment is altered versions of genes. Hence, two species will tend to become less closely related over time as they become adapted to different ways of life. At first (about 100,000 years after diverging from their common ancestor), they are as closely related as the two kinds of lake whitefish; later (more than 1 million years after) only as closely related as different kinds of whitefish such as lake whitefish and mountain whitefish; then (more than 10 million years after) as different kinds of salmonid fishes, such as whitefish, grayling and trout; then (more than 100 million years after) as salmonid and centrarchid fishes, such as bass and pumpkinseed; and so forth. We will explain how these events are dated in Chapter 5.

Clearly, species become steadily more different and less closely related as time goes on. Nevertheless, they continue to resemble one another in many ways. Whitefish and bass both have fins and jaws, for example. This is not because fins and jaws have evolved independently in each new species of fish, but rather because the most recent common ancestor of whitefish and bass (a member of a group called the Pholidophoroformes living in the upper Triassic period, about 220 million years ago) possessed both characteristics and transmitted the genes responsible to its modern descendants. Whitefish and rabbits are still more different, but both possess a backbone and a thyroid gland, for example, which they have inherited from a still more distant common ancestor.

Universal characters are inherited from a distant common ancestor. The characters involved in the formation of new species are usually adaptive responses to some ecological challenge or opportunity, such as avoiding a predator or being able to grow in salty soil. They may be caused by alterations in only a few genes, or even a single gene. More fundamental changes, such as the ability to form bone and to use it to develop a skeleton, happen less often because they require alterations in many genes.

The most fundamental features of the biochemical machinery of the cell have scarcely changed at all since life began, since they are common to all known organisms. The simple explanation is that they have been inherited, with minimal alteration, from a very remote common ancestor. The uniformity of basic processes and the molecules responsible for them shows how all living organisms have evolved in a single unbroken line of descent from a universal common ancestor that lived between three and four billion years ago.

1.2 Extinction. *Fossils of extinct organisms are the physical remains of past evolution.*

Living organisms provide very strong circumstantial evidence of evolution. It would be even more convincing to see the ancestors themselves. This is seldom possible, because most individuals decay and disappear soon after they die. In exceptional circumstances, however, their remains may be preserved in sediments that have hardened into rocks under heat and pressure. These are fossils. They are the direct evidence of how ancient organisms have evolved into modern animals and plants.

1.2.1 The majority of species are extinct.

Fossils are extremely abundant and diverse. Wherever you live, there are likely to be outcrops of fossil-bearing rocks not far away. The local natural history museum will know where they are and may have a representative collection of fossils on display. Many fossils are immediately recognizable because they clearly resemble some familiar living organism such as a clam or a fish. Others are more difficult to identify because they are only part of an organism, or may be difficult to see because they are very small.

Even if you searched a site very carefully and found every fossil, however, you would still not have found every species that once lived there, because whether a particular species is likely ever to be fossilized depends on how it is built and where it lives. Small soft-bodied animals such as worms and jellyfish quickly decompose leaving no remains, so they are preserved as fossils only in exceptional circumstances. The remains of animals and plants that live in forests or grassland are likely to be consumed or simply weather away. The remains of animals that have hard parts such as shells and skeletons and that live in the sea or freshwater, on the other hand, are likely to sink into sediments that later turn into rock, where they are preserved as fossils. Marine invertebrates, for example, are very abundant as fossils and have been very thoroughly described. About 300,000 living species of sponges, corals, crabs and shrimps, barnacles, starfish, and similar animals have been catalogued, grouped into about 60,000 genera. Only about one-third of these species and genera, however, have hard parts that would fossilize easily. Another 30,000 genera are known only from fossils, and almost all of these can be confidently assumed to be completely extinct. If only one-third of extinct forms were fossilized, then about 90,000 genera have previously existed, but are now extinct. This is about 50% more genera, and hence about 50% more species, than are currently alive. This is an underestimate of the true number of extinct species, because fossils are much more difficult to find than living organisms, and because the fossils of many species are likely to have been destroyed by geological processes in the past. Hence, more species have become extinct than are currently living.

A species has a limited lifespan. The frequency of extinction emphasizes the limited lifespan of a species. This can be estimated from the first and last occurrences of a species in the fossil record. For marine invertebrates the average lifespan of a species is about 4 My ("My" stands for "million years," and "Mya" stands for "million years ago"), and other groups give rather similar values. Horses provide a very well-studied example with abundant fossils. At present there is only a single species of horse, which is native to Asia but has been domesticated and spread around the world by humans. In the past there were many species of horse, living in different parts of the world, including North America. Their relationships are shown in Figure 1.3; each species lived for about 3 My on average. There are some species in other