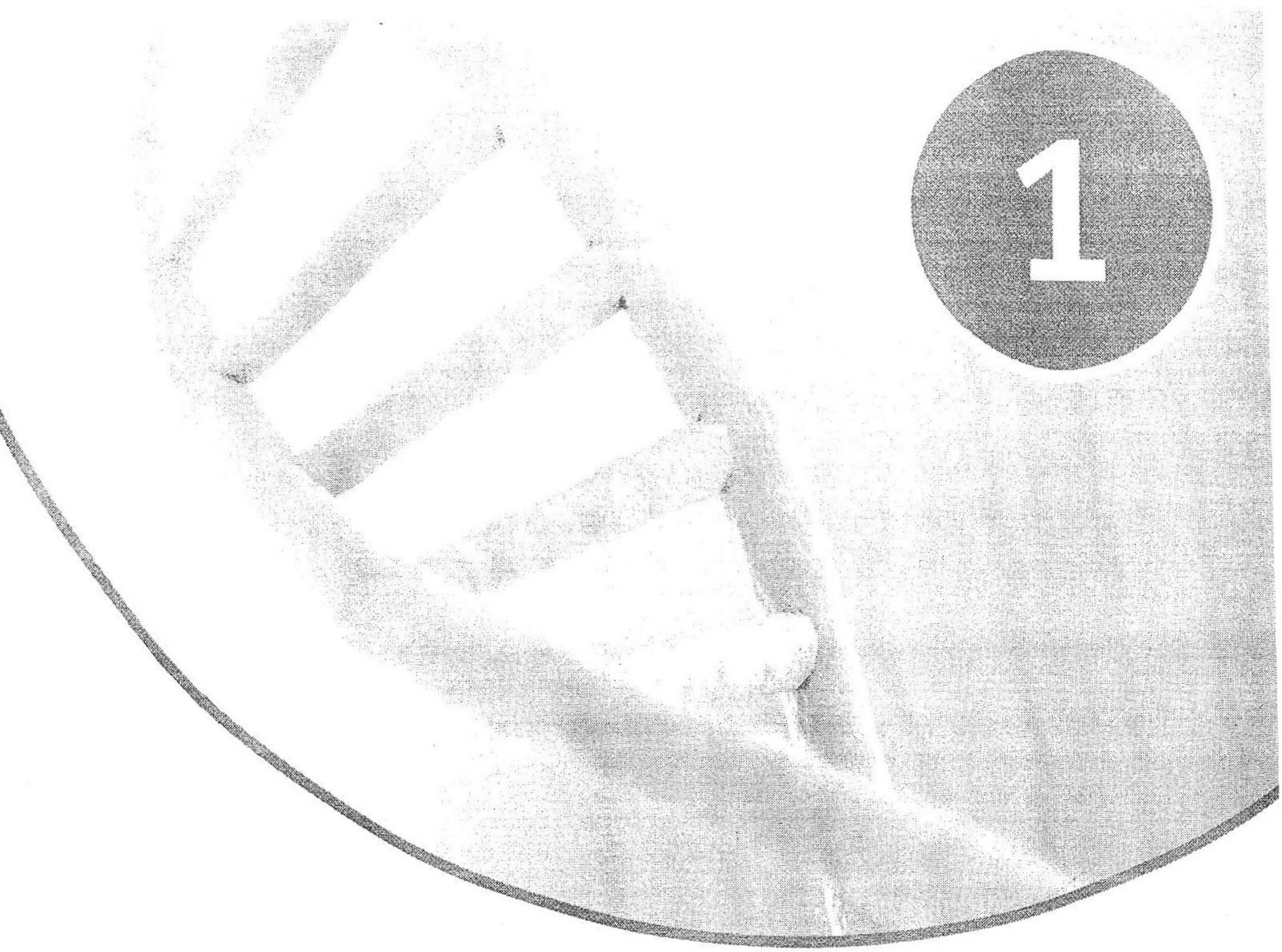
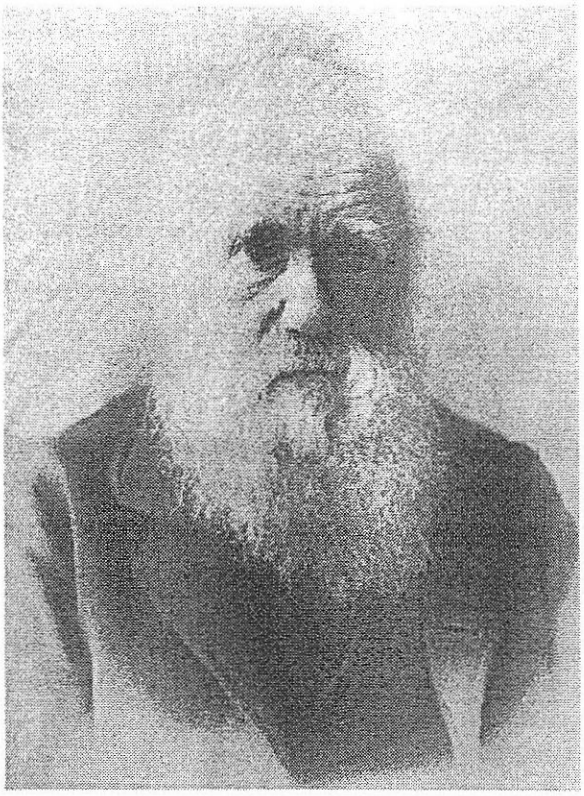


1

The significance of Darwinism

When John Simmons compiled a list of the most influential scientists of all time, he put Charles Darwin in fourth place (Simmons 1996). This is an astonishingly high ranking for a retiring Victorian gentleman naturalist who spent much of his life researching the habits of barnacles and earthworms (Figure 1.1). Darwin is well ahead of Copernicus, who established that the earth went around the sun, ahead of Galileo, father of the modern methods of physics and astronomy, and ahead of Lavoisier, father of the periodic table and modern chemistry. Darwin has a higher position than any other life scientist. The top three—Newton, Einstein, and Bohr—are all physicists who established the fundamental laws of the physical universe. Simmons ranked Darwin so highly because Darwin achieved for biology something comparable to what the top three achieved for physics: he set out, in his theory of evolution, the fundamental principles governing what happens. Interestingly, another 16 of Simmons' top 100 scientists are people

Figure 1.1 Charles Darwin, 1809–92, father of the theory of evolution. *Courtesy of The Library of Congress.*



who worked directly on developing the modern understanding of evolution. Thus, evolution gets 17 out of 100 of the top places. By comparison, the whole of psychology gets nine entries in the top 100, with anthropology contributing a couple more.

Of course, there are no completely objective criteria for compiling a list of the most important scientists and if someone other than John Simmons had attempted it, they might have produced a different ranking. However, whoever did it would be certain to include Darwin in their overall top ten, probably as the most important life scientist, and would be likely to have included several of the other key figures in evolutionary thought as well. Almost all scientists agree that evolution by natural selection is one of the most important ideas in all of science. This is because it is the central explanatory theory of biology. It, and only it, explains why living things are as they are. As the great Brazilian evolutionist Theodosius Dobzhansky (number 67 on Simmons' list) put it, 'nothing in biology makes sense except in the light of evolution' (Dobzhansky 1973). Moreover, scientists accept that the truth of the theory of evolution is as well established as the truth of any major scientific paradigm.

How striking then, that the public at large is nowhere near as convinced. Careful survey evidence shows that only 15% of Americans and a little over 30% of British people think that the theory of evolution is 'definitely true' (Miller *et al.* 2006). Another 20% of Americans and 35% of British people think it is 'probably true', but the numbers believing it to be probably or definitely false are 30% in America and 15% in Britain. The rest are not sure.

There is one thing that unites those who reject the theory of evolution with quite a few of those who accept it: they are prone to misunderstand the very theory they are taking a view on. There are numerous cultural and educational reasons why misunderstanding of evolution persists, but there is also a deeper reason, which is that evolution is actually quite hard to understand. The theory is a strange combination of extreme simplicity and deceptively subtle consequences. It took all of human history until Darwin for anyone to grasp the concept of natural selection, and even once it had been grasped, biologists struggled to understand how it could be reconciled with the mechanisms of heredity, or what kinds of competition would occur. It was not for several generations after Darwin that these problems were solved. Given that some of the greatest minds of all times have had trouble getting these processes clear, the rest of us should not be too hard on ourselves for getting muddled about them.

When we try to understand evolution, we are pushing our minds somewhere that they may not be predisposed to go. For a start, the timescale is very different from the timescales that the human mind usually has to deal with. The cats you will see in your old age will look much the same to you as the cats you saw in your youth. Thus, common experience hardly lends support to the idea that cats are transforming through time. More particularly, the cats in your old age will seem exactly as different from dogs as the cats of your youth were from the dogs of their day. This just does not really square with what we know to be evolutionary fact, that is, that cats and dogs are diverging gradually from a common ancestor and that if you were transported back a quite short distance in geological time, cats and dogs, or rather their ancestors, would be indistinguishable from each other. The timescale of human experience is but an eye-blink compared with evolutionary time. Our senses seem to tell us that animals breed according to their kind, not that their kinds change. However, our senses also tell us that the sun moves around the earth and we know that this is an illusion, an artefact of perspective. Science moves us outside our normal point of view and thus its findings often seem unnatural to us.

We seem to think about each species of animal or plant as having a unique and distinct 'essence'. This might be useful, since we encounter different animals and plants in our environment and we need to learn generalizations about what to do with each class (run from it, eat it, avoid eating it, etc.) from a limited number of exemplars. Creating a mental record of 'essential qualities' for each species is an efficient way of dealing with this problem. However, this is a convenient device of the human mind, not the way nature actually is. Evolution requires us to accept that different types of animal have no fixed essence and are not different in kind from each other. They change over time and are connected by extinct intermediate forms. Evolution tells us, for example, that there was an individual living a few million years ago who has many great-great-great-great- . . . grandchildren alive in the world today and some of those descendants are human beings, whilst others are chimpanzees, and there was no point in the family tree where any catastrophic or abrupt change occurred. At no point did any two siblings need to be any more different from each other than siblings normally are. The divergence between a human and a chimpanzee is only quantitatively, not qualitatively, different from the difference between two humans—just a question of how far back into the family tree you have to go before you hit a shared grandparent. That is very counter-intuitive. However, evolution seeming alien to our usual way of thinking is not any kind of argument against its truth.

The purpose of this book is to explore the basic principles of evolution and evolutionary genetics, with the hope that their explanatory power, subtle consequences, and deep beauty will become clear. I hope to steer a path between too much detail on the one side and misunderstanding on the other. My hope is that if you are sceptical about evolution, your doubts will be dispelled. Many of your objections and also fears evaporate on a very clear examination of the case. If you are already comfortable with the theory, I hope you will come to understand more deeply the nature of the processes you have signed up to, the genetics that underlies them, and the ways they can be used to explain behaviour, especially the behaviour of humans. The rest of this chapter outlines in a nutshell why the theory of evolution is so important (section 1.1) and how it works (sections 1.2 and 1.3). The remainder of the chapter examines some of the most common objections to the theory which people come up with (section 1.4). I will argue that each of these is based on a misunderstanding.

In the rest of the book, Chapters 2–5 lay out in detail the key components of evolution—variation, heredity, competition, and selection—bringing in information about genetic mechanisms as it is required. The first five chapters taken together provide the 'conceptual toolkit' of how to think about problems in evolutionary terms. The remaining chapters apply the conceptual toolkit to some of the core issues of life, namely sex (Chapter 6), the lifespan (Chapter 7), social life (Chapter 8), and learning and culture (Chapter 9). Chapter 10 looks at the recent evolutionary history of our own species, and Chapter 11 concludes by considering how evolutionary thinking is best incorporated into the study of the human mind and behaviour—is it an alternative to the existing theories of psychology, an addition to them, or a way of linking them all together?

1.1 What problems does the theory of evolution solve?

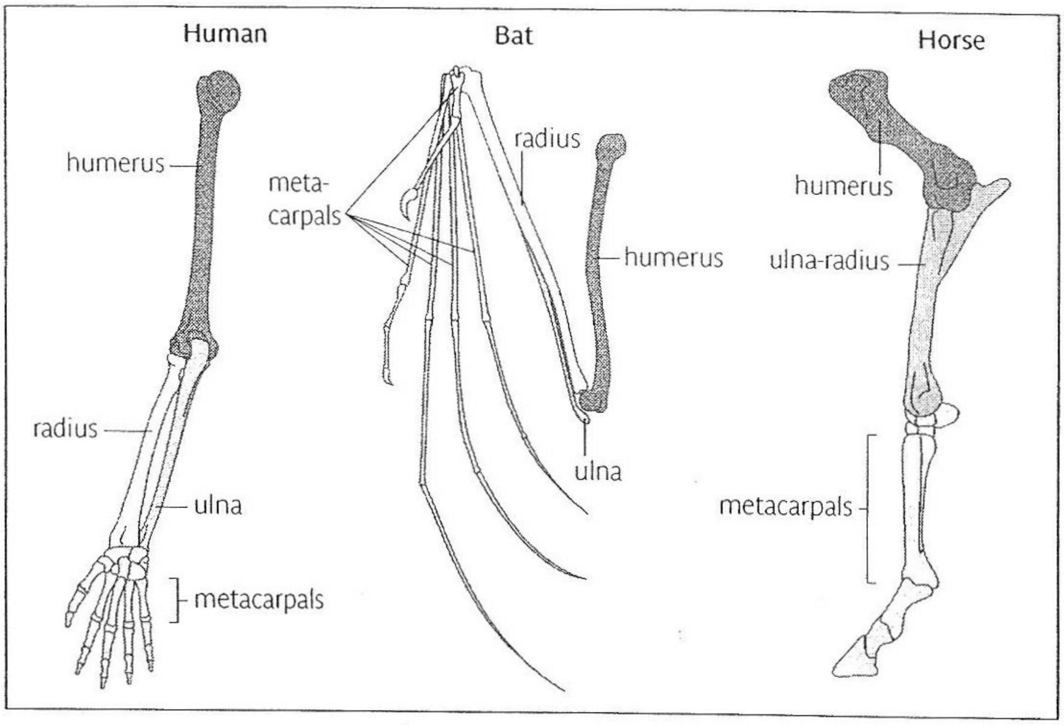
Before we turn to the theory of evolution, it is important to be clear about why it is important. Charles Darwin laid out his theory in a book published in 1859 entitled *On the Origin of Species by Means of Natural Selection* (henceforth *The Origin*). This is one of the most influential books of all time. Why? In other words, what problem does it solve? It must be a pretty important one for the book to have become so renowned. In this section, I argue that Darwin's theory of evolution simultaneously and definitively solves two major problems in understanding living things, namely the problem of history and the problem of design. No other theory can solve either one, still less both. Solving them together makes Darwinian evolution the most important idea in the study of living things.

1.1.1 The problem of history

A brief look at the natural world reveals an obvious truth. Living organisms of many different types have commonalities and divergences. The commonalities are striking. For example, the limbs of different vertebrates contain a pattern of five bones that is recognizably similar, even though the limbs are serving functions as different as fins, legs, and wings in different species (Figure 1.2). Even where the adult creature does not have all five of the phalanges (that is, fingers), as in birds or the horse, five appear in the embryo, only for some of them not to develop fully. Why should these diverse limbs all have an underlying form that is so similar?

If we go down to a more microscopic scale and examine the biochemical makeup of cells, the commonalities are even more striking. Many of the proteins involved in keeping living cells going are very similar in organisms as distinct as humans and amoebae. Consider a small protein called cytochrome c, which is found across many plants and animals. Proteins are formed of chains of smaller constituents called amino acids and there are vast numbers of different forms that proteins can take, since there are 20 different amino acids that can occur in essentially any order in the chain. The main part of cytochrome c consists of a chain of 104

Figure 1.2 The same basic pattern of bones can be identified in the limbs of many different vertebrates. This is a classic case of homology. *From Wolpert et al. (2006), p. 506.*



amino acids. If we, as it were, lay cytochrome c molecules from different species alongside each other, we find that the same amino acids appear at the same point in the chain more often than not. The number of 'matches' between amino acids in the main part of the cytochrome c molecule of some different vertebrate species is given in Table 1.1. As you can see, organisms as diverse as a fish and a monkey have exactly the same amino acid at the same position in the chain for most positions.

The same two examples discussed so far also serve as examples of how the natural world contains divergences. Although the bones are similar in all vertebrate limbs, they are not identical. The phalanges are enormously lengthened in bats, where they serve as stretchers for wings made of skin, and in the whale they make a flat flipper rather than a leg (Figure 1.2). Thus, from a common theme, many variations can be seen. We can make a similar point in respect of cytochrome c. Its exact structure varies somewhat, to a differing extent depending on which two species are being compared. There is a single difference in the chain between humans and rhesus monkeys, but over 20 discrepancies between the sequence in humans and that found in tuna. Again, we see a common theme and local variations.

Hierarchical organization in nature

Biologists realized a long time ago that the commonalities and divergences between different species had a very special property: hierarchical organization. By this, it is meant that two species that are similar in the details of system A tend also to be similar in the details of system B. For example, humans are very similar to rhesus monkeys in terms of cytochrome c (Table 1.1). When you study other proteins, such as α- and β-globins, or fibrinopeptides, the same pattern

Table 1.1 The number of amino acids in common in the 104 amino acid chain of the cytochrome c molecule in various species of vertebrates. The number of matches is high in all cases, the human molecule is especially close to the rhesus monkey, and the whale is clearly closer to the other mammals than it is to the tuna.

	Human	Rhesus monkey	Rabbit	California grey whale	Great grey kangaroo	Chicken	Tuna
Human		103	95	94	92	90	82
Rhesus monkey	103		96	95	91	91	82
Rabbit	95	96		102	98	96	86
California grey whale	94	95	102		99	94	86
Great grey kangaroo	92	91	98	99		92	87
Chicken	90	91	96	94	92		87
Tuna	82	82	86	86	87	87	

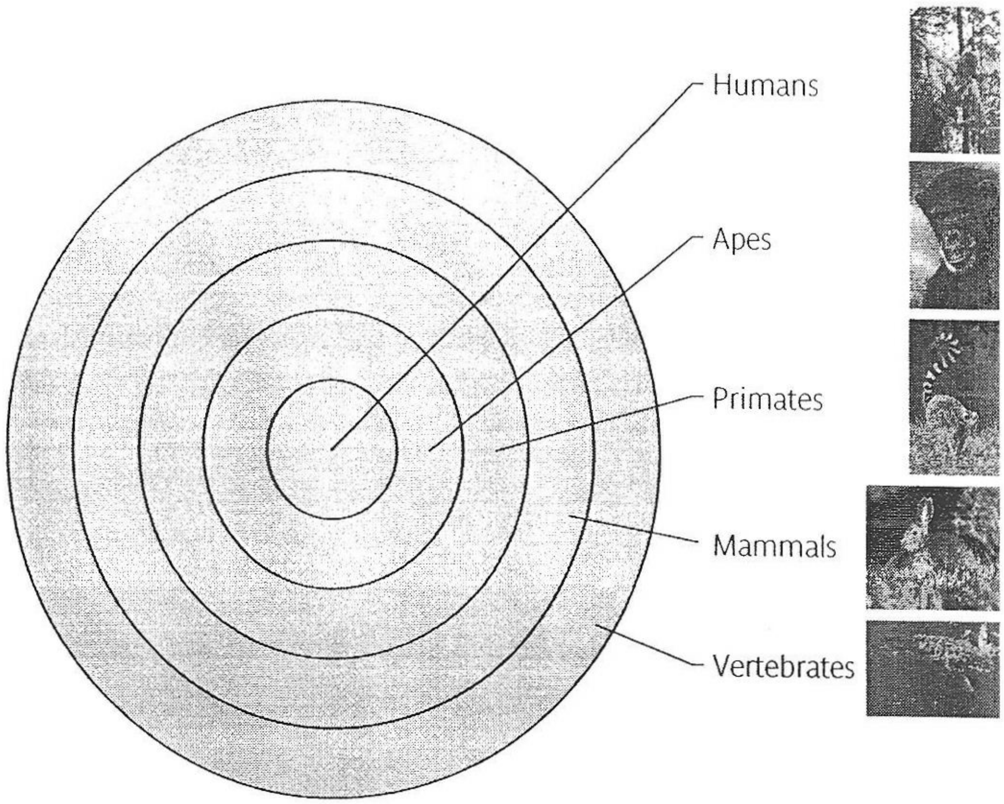
always emerges, with humans right next to monkeys and closer to all mammals than to any non-mammals (Penny *et al.* 1982). This could have been otherwise. Humans might have been most like monkeys in cytochrome c, most like kangaroos in α-globins, and most like tuna in β-globins. But this is not how it is. Humans look more like monkeys than they do rabbits in pretty much any aspect of their anatomy and physiology that you care to name, and look more like rabbits than they do kangaroos, and more like kangaroos than they do tuna.

As a consequence of this, we can group different species together on the basis of the amount of structure that they share. Humans belong in a group with monkeys, and humans and monkeys belong in a super-group with rabbits, and humans, monkeys, and rabbits belong in a super-super-group with kangaroos, and so on. At each level in the hierarchy of groupings, the amount of commonality becomes less and the amount of divergence greater (Figure 1.3). Why are we able to make hierarchical groups like this? More generally, where did all these different types of animal come from? This is what we will call the problem of history.

Solving the problem of history

One solution to the problem of history would be simply to say that the different animals have always been as they are. People have always been people, monkeys have always been monkeys, and kangaroos have always been kangaroos. However, this would not explain why structures within different animals are so strikingly similar to each other and, in particular, why structures in monkeys are consistently so much *more* similar to their counterparts in humans than structures in kangaroos are. In other words, it could not explain the hierarchical pattern of similarities and differences observed in nature. Moreover, that pattern of similarities and differences is sometimes quite surprising. For example, whales, although they live in the deep ocean, are much more similar to humans than they are to fish across numerous aspects of their anatomy and physiology. Their cytochrome c is more like that of humans than it is of tuna (Table 1.1), as is their habit of giving birth to live young and feeding them on milk. Why would this be?

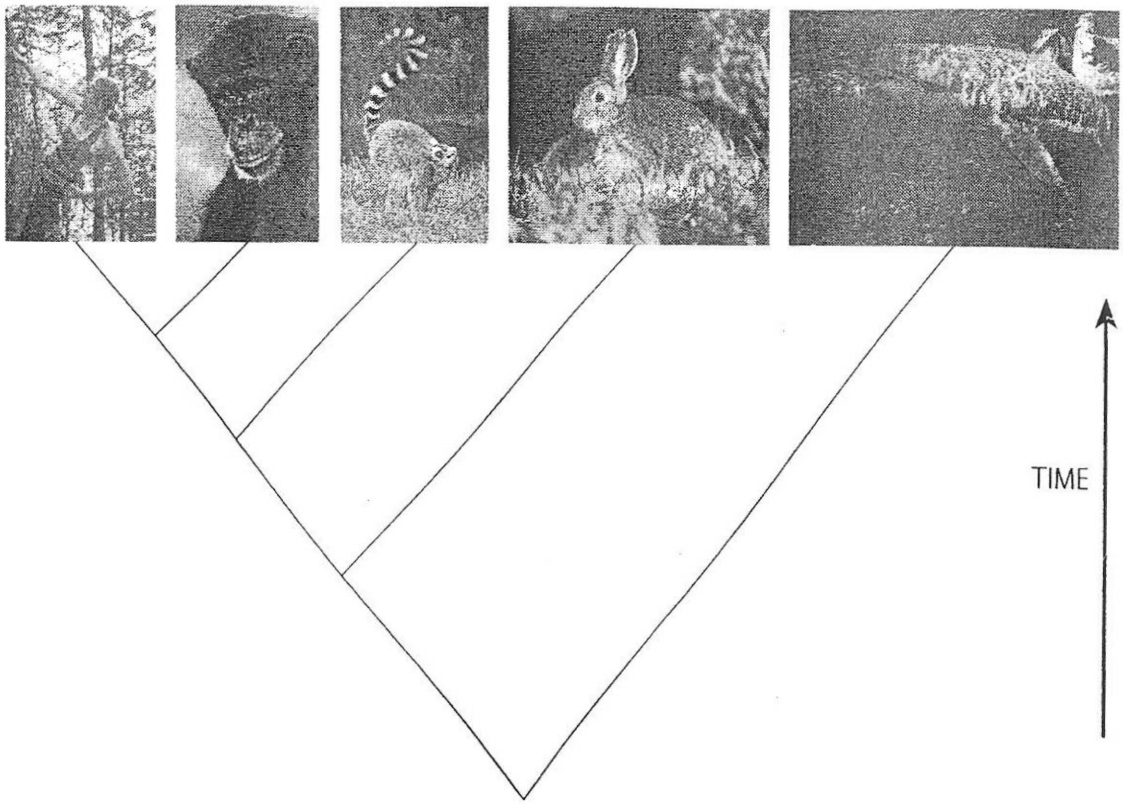
Figure 1.3 Species can be arranged hierarchically into groups, super-groups, super-super-groups, etc. on the basis of commonalities and divergences. In multiple aspects of their anatomy and physiology, humans share most with apes, a little less with other non-ape primates, a little less with other non-primate mammals, a little less with other non-mammal vertebrates, and so on. Not all the levels of grouping recognized by biologists are shown. *Photos: woman, chimp – © Digital Vision; lemur – Vladimir Wrangel/Fotolia.com; rabbit – Photodisc; shark – Corbis.*



This brings us on to Darwin's solution to the problem of history. Darwin argued that the organisms we see today are derived from a creature ancestral to them all, by a process of gradual modification. The descendants of the ancestral form, each altering slightly over the generations, have split and split again, giving rise to many distinct branches on the tree of life. Going backwards from the present, some species' ancestors diverged relatively recently, whilst the ancestors of some others diverged further back in time. This has overwhelming merit as an account of the diversity of life. It explains patterns like the vertebrate limb, with its myriad variations on the same basic structure. The shared plan is there because all vertebrates descend from the same creature, which started out with a particular configuration of bones. The bones have been stretched, fused, reduced, or twisted within different lineages over the generations, but the common ancestry is still traceable.

Descent with modification automatically assures that organisms will be classifiable into hierarchical groups. Indeed, what these groupings represent is the closeness of the common ancestor of all the species involved—the time since the split, if you will. Thus, the diagram shown in Figure 1.3 can be replaced with a representation of what it more truly represents: a family tree or, to use the biological term, a phylogeny (Figure 1.4). As the phylogeny shows, humans and monkeys share a more recent common ancestor than humans and rabbits, who in turn

Figure 1.4 The hierarchical relationships between species from Figure 1.3. are better captured by showing what they really represent—relationships on a family tree or phylogeny. Here, the distances between branching points are not to scale and many thousands of other branches are not shown. *Photos: woman, chimp – © Digital Vision; lemur – Vladimir Wrangel/Fotolia.com; rabbit – Photodisc; shark – Corbis.*



share a more recent common ancestor than humans and kangaroos, and so on. At a stroke, this explains the patterns of commonality in cytochrome c, globins, hands, blood, and many other characteristics. It also explains why whales, beneath the skin, are more like humans than they are tuna: because they have an ancestor that was a land mammal.

Several scientists before Darwin had proposed that the species we see today had not always been as they are, but had been produced by descent with modification from common ancestors. Darwin was not therefore unique in making this claim, although he did assemble a more thorough and persuasive case than anyone who went before him. More importantly, however, Darwin was the first to fully address another question. Why does modification occur? In other words, what mechanism is responsible for the development of whales from an ancestor that was a legged mammal? Darwin answered this question by proposing a novel mechanism—natural selection—and in so doing he solved another, even greater, problem in the understanding of life on earth: the problem of design.

1.1.2 The problem of design

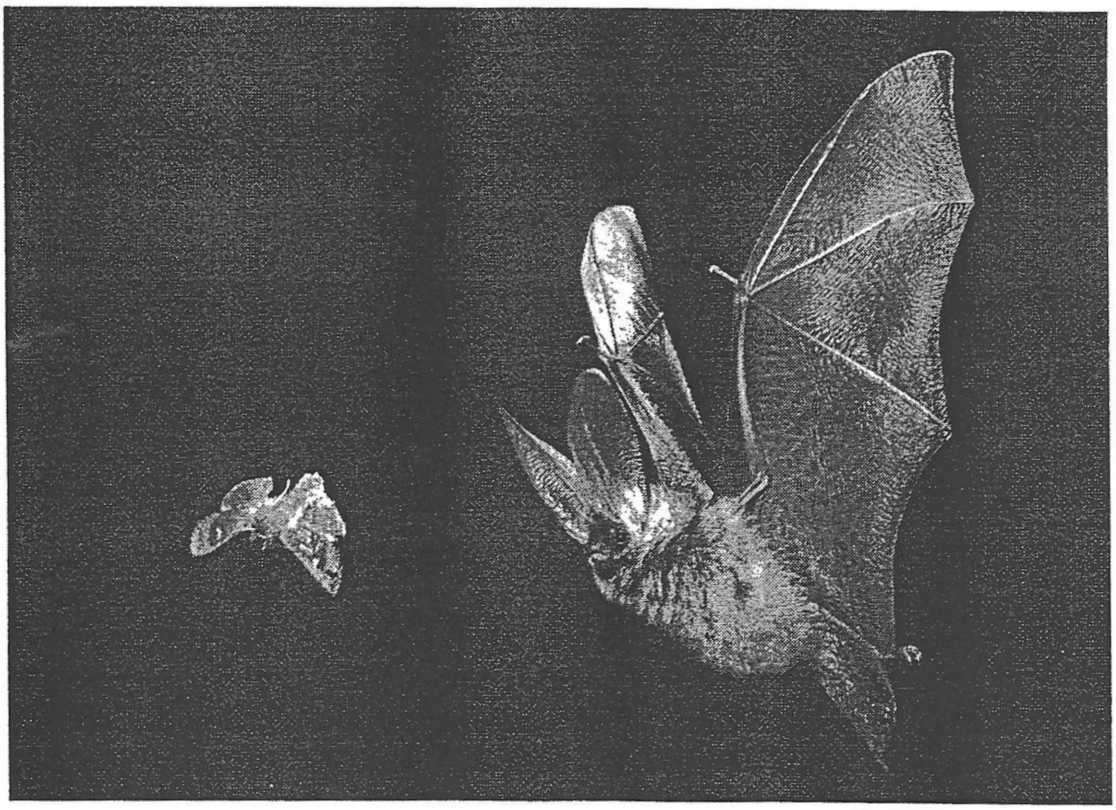
A second striking aspect of the natural world is that the various creatures that we see seem quite well designed for the tasks that they have to perform. Bodies consist of a large number of distinct subsystems, each of which is efficient at solving a particular problem—the heart for pumping, lungs for transferring oxygen to blood, the gut for digestion, and the liver for detoxifying blood. All of these contribute to the continued functioning of the individual and, perhaps even more impressively, all the systems communicate and cooperate in an integrated way. Some of these systems are impressive feats of engineering. Let us take just one example —the echolocation of bats (Dawkins 1986; Jones & Holdereid 2007).

Design in nature: bat echolocation

Bats, of which there are a large number of different species, have to solve the problem of navigating and hunting insects at night (Figure 1.5). The system they use to do this is a breath-taking masterpiece of good design. They use what human engineers—who did not make use of the principle until well into the 20th century—would call sonar, but it is referred to by biologists as echolocation. The bats emit high-frequency sounds and then use the echoes returning to their ears to calculate the position of obstacles and prey.

The first piece of good design is that echolocation only appears where it is needed. Echolocation of some form has evolved several times in nature and only where the organism is active in the dark or in murky waters. Where light is available, creatures prefer the less energy-intensive solution of vision. Old World fruit bats can rely on good night vision for finding their less evasive dinner and they have no echolocation. Amongst bats that do echolocate, there are a number of different call types that can be used. Some are better suited than others to, for example, open versus cluttered spaces and bats use the form of signal most suited to their habitats.

Figure 1.5 **Many bats have sophisticated echolocation abilities that appear well designed for solving the problem of manoeuvring and hunting at night.** *© Dietmar Nill/Photolibrary Group.*



Using echolocation causes many design problems. The pulse of sound needs to be short, with plenty of gaps for listening for echoes, and thus bat signals are a tiny fraction of a second long. To get a good fix on a rapidly moving target, you need a rapid succession of echoes and bats are able to produce up to 200 sound pulses per second. However, this is energetically very costly. Bats have hit on the sensible solution of a much lower 'cruising' rate of pulse emission—about 10 per second—which rises only when a potential target has been detected and needs to be pursued. For the echoes to be strong enough to detect at any kind of distance, the original signal has to be extremely loud. Bats have evolved two kinds of sound production, tongue clicking and calling using the larynx, both of which are capable of producing incredibly intense bursts of sound (in many species, these are outside the range of human hearing, so they have to be recorded with special equipment). However, this immediately causes other problems. The bursts of sound are so loud as to be much louder than the echoes (obviously), but also so loud as to deafen the bat when they are emitted. This is a real quandary. Make the ears any less sensitive and they would not be able to detect the echoes; keep them sensitive and they will be deafened.

Human radar and sonar engineers encountered exactly the same problem and solved it with a design that switches off the signal receiver as the pulse is emitted. It turns out that some bats had hit upon this exact principle millions of years earlier. A set of muscles damps the transmission of vibrations to the eardrum exactly as the outgoing pulse is produced, thus reducing the impact of the outgoing signal on the auditory mechanisms. These damping muscles can be contracted and relaxed up to 50 times per second, in exact synchrony with the production of sounds.

The marvels of bat echolocation do not stop there. Some bats use a fixed pitch of signal at the frequency at which they hear best (others have an even more complex system of frequency modulation over time). However, if the bat itself is moving, the apparent pitch of the returning signal will be distorted by the Doppler effect. (The Doppler effect is the reason a police siren appears to change pitch if you are in a car moving towards or away from it. The reason it occurs is that your own motion affects the rate of arrival of sound waves at your ear.) These bats therefore lower the pitch of the signal in proportion to the speed at which they are flying, so that echoes always return to them at the frequency they would if the bat was at rest, thus close to their auditory optimum.

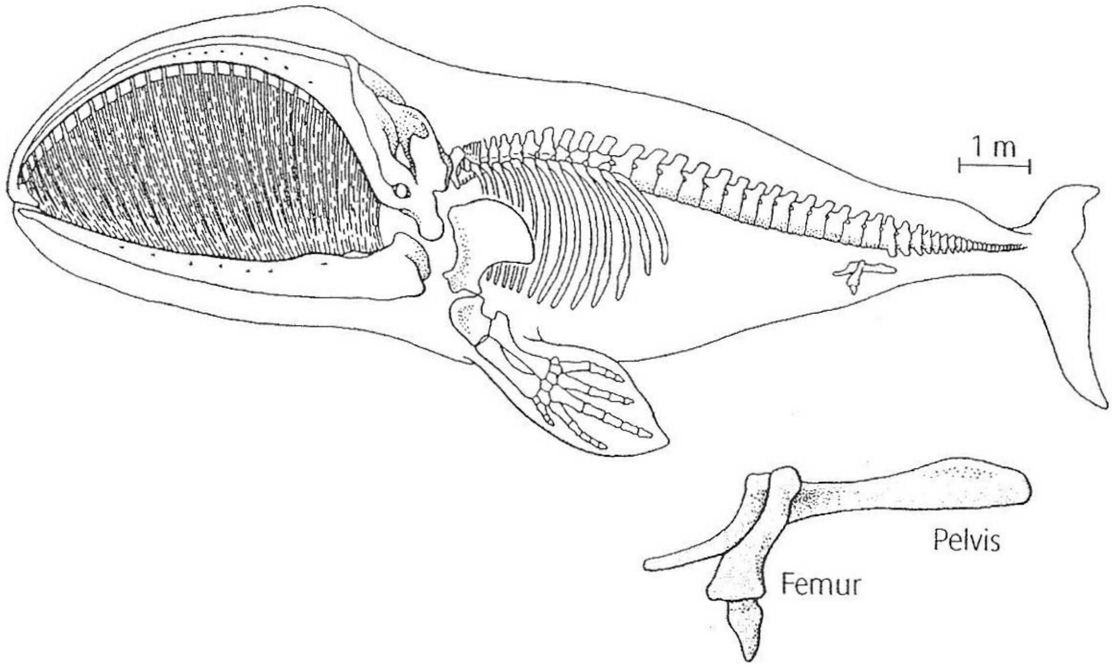
Design oddities in nature

You cannot examine bat echolocation systems without being impressed at what appears to be good design. Several different systems, the larynx or tongue, the ears, the muscles connecting them, the brain, the mouth, and the wings, all have to interact to make the whole thing work and it does work astonishingly well. Again and again, the bat system turns out to embody solutions which human engineers have painstakingly worked out are really good ways of solving the problems of locating targets where there is no light. However, design in nature also has some puzzling limitations. Certain types of whale, it turns out, have a pelvis (Figure 1.6). The pelvis is a bony structure whose function in other animals is to attach the hind legs. As whales have no hind legs, this makes no design sense at all. Tuna and sharks make their livings in similar ways to whales and they do not need a pelvis. If nature can produce such brilliant designs, what is this useless structure doing there?

Solving the problem of design

We thus need to explain (a) how nature comes to be so full of generally good design solutions and (b) why those design solutions sometimes have curious non-functional features. The first point to make is that the designs we see in nature are far too complex and sophisticated to be

Figure 1.6 Some whales have a pelvic girdle. This is a classic example of a vestigial structure. Vestigial structures are strong evidence for evolution. *From Freeman & Herron (2004), p. 46.*



due to chance. You could shuffle all the proteins that make up a bat together at random billions and billions of times and never come with anything that functioned at all, let alone had the remarkable design features of an actual bat. So some process has structured the material that makes up a bat in a non-random way.

The traditional pre-Darwinian solution to the problem of design is that there must be a designing agent. In particular, the English theologian William Paley had argued in 1802 that, were one to come across a watch upon a heath, the intricacy and functional organization of its parts would immediately make one assume that, somewhere, there must be a watchmaker who had made it. So it was, argued Paley, with the design of living things. Their intricacy and functional organization is so great that we must accept that there is a designer (in Paley's case, God).

The problems with this hypothesis are several. First, it is what scientists call unparsimonious. Scientists always prefer the explanation that invokes fewest unknown forces and objects, a principle known as parsimony. The designer hypothesis invokes a being whom we have never been able to observe or measure, presumably outside the physical universe, who must have powers of some unknown kind to work on matter. Thus, it requires a lot of extra processes for which there is no independent evidence and which are currently mysterious. If we can find another candidate explanation that invokes only things that we already know to exist, that other explanation will be more parsimonious and should therefore be preferred.

The second problem with the designer hypothesis is that it is non-explanatory. Explanation in science is the business of showing how complex things that we do not understand arise from simpler things that we do understand. Logically, any agent with the capacity to design something as complex as an animal must be more complex than an animal. Thus, the question arises, where does the complexity of the designer come from? Do we need to then, following the very same argument that got us the designer, come up with a super-designer who created the designer, and a super-super-designer who created him or her? The problem with Paley's argument is that you end up having to postulate an infinite series of increasingly powerful designers. Since each of these is more complex than the previous one, and the properties of each are even less well understood than the last, then the promise of explanation is unfulfilled. In fact, you have gone from something we understand moderately well (the form of organisms), to something that we understand not at all (the properties of the infinite über-designer). This is not explanation in the scientific sense.

Finally, if these two problems with the designer hypothesis were not enough, there is the whale's pelvis. If some benign and omnipotent agent were brilliant enough to come up with the designs of all the creatures in nature from scratch, why would he or she put a pelvis in the whale?

Darwin's solution to the problem of design

Despite these problems, the idea of a designer persisted as the most widely accepted solution to the problem of design for a long time. This was because putting the design of living organisms down to chance was so obviously wrong and there just did not seem to be any alternative other than divine agency. What Darwin did in *The Origin* was to show that there is in fact a third possibility. He argued that organisms have the design-like features they do as a result of the cumulative effects of natural selection over the course of their evolution.

Natural selection is the process of non-random survival of useful innovations that, cumulatively, can lead to what seem to be well-designed structures without the involvement of a designer. We will be discussing how it works in detail later in the book, but the idea of natural selection is parsimonious, in that it does not invoke anything that we do not already know to occur, and explanatory, in that it shows how something complex (apparently well-designed organisms) arises from forces that are actually very simple. Crucially, it also predicts that designs will not always make current functional sense, as in the case of the whale's pelvis. This is because natural selection takes a long time and always works by modifying existing forms, not creating new ones from scratch. Thus, if a land mammal returned to living in the sea, it would not lose its hind legs instantaneously. Instead, they might gradually reduce in size over many generations, until they disappeared completely, but there would be many thousands of years when some parts of the now functionless leg structures—the pelvis, for example—would be visible. We call these 'vestigial structures' and they are an anatomical testament to the creature's evolutionary history.

The next section will examine what natural selection is in a nutshell, but the important point to note here is that Darwin's theory of evolution does not just solve the problems of history and design: it solves them in terms of each other. That is, the reason organisms have (mostly) good design is because of the historical modifications they have undergone, and the reason they have undergone historical modification is (mostly) because of differences in design functionality.

1.2 Evolution by natural selection in a nutshell

It is time to look briefly at what Darwin's theory of evolution by natural selection involves. It consists of four elements: variation, heredity, competition, and natural selection, and taken together these produce descent with modification and also build up what appears to be good design. The four elements work as follows:

1. *Variation*. Individual organisms may be similar but are not identical to each other. They have minor variations in their characteristics.
2. *Heredity*. Many of the characteristics that vary from individual to individual are passed on from parents to offspring.
3. *Competition*. Not all individuals leave the same number of offspring. Some die early in life, or do not manage to reproduce, or reproduce but have fewer offspring than others. As a consequence, not all individuals have the same representation in the next generation.
4. *Natural selection*. As long as individuals' success in survival and reproduction depends at least partly on the characteristics that they have and which they pass on to their offspring, then characteristics which confer an advantage will become more common and persist, whilst those conferring a disadvantage will disappear.

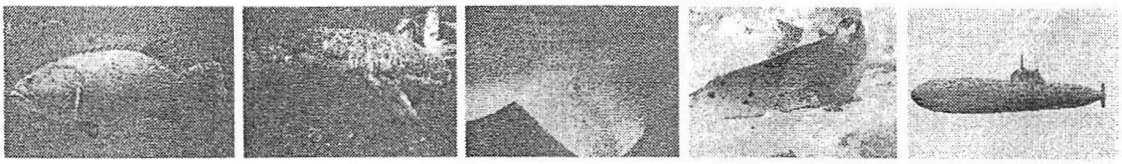
Darwin saw that the cumulative effect of these principles would be powerful. If in a certain generation there are some individuals who have a characteristic that is useful, then those individuals would do better in the competition to reproduce than the individuals who lacked the characteristic because they are more likely to stay alive, they are better at getting a mate, or they have more energy to produce and protect healthy offspring. Since their offspring would also have the characteristic (because of heredity) and would also then in turn be advantaged in their own competition for reproduction, it follows that the proportion of the population bearing the useful characteristic would increase from generation to generation, until the point where all individuals have it. Imagine this process repeated for thousands and thousands of generations. Any new variation in form that happened to arise and which conferred some advantage in survival or reproduction—was a better design, if you will—would be increasingly represented in the generations that followed. This solves the problem of design since, gradually, by the retention of advantageous characteristics, functional systems well designed for that particular environment could be built up in simple steps. The systems built up in this way are called adaptations.

Homologies and analogies

Natural selection solves the problem of history, since it suggests that lineages of organisms will gradually modify over the generations. In particular, cousins who go off and populate different habitats will experience different design problems, develop different adaptations, and thus become more dissimilar over time. However, distantly related species living in similar ways and thus experiencing the same design problems may come up with similar adaptations and thus become in some respects more similar over time. Darwin's theory thus predicts that we will be able to identify two types of similarity in nature. The first type are called homologies. These are similarities stemming from common origin. Thus, the phalanges of the bat, which it uses to stretch out its wings, may be said to be homologous to the fingers of the human, and the functionless pelvis of the whale may be said to be homologous to the altogether more useful version found in land mammals. Homologies, because they reflect history, are useful for constructing the phylogenies of different organisms.

Similarities of the second type are called analogies and the process that produces them is called convergent evolution. Whales and tuna have very similar, streamlined shapes. This cannot be explained by homology since, as we have seen, whales are more closely related to

Figure 1.7 Similar streamlined shapes have been hit upon by sharks, fish, whales, and seals, none of which are particularly close phylogenetic relatives of each other. Human designers of submarines have also exploited the same principle. *Left to right: © Klaas Lingbeek-van Kranen/istock.com; Corbis; Ingram; Corel; Megaport/Fotolia.com.*



humans than they are to fish. This shape is efficient for moving through water, as fish and whales seem to have independently discovered. In fact, it is not just fish and whales. The streamlined hydrodynamic shape has arisen multiple times in organisms which are not closely phylogenetically related, but which have to move through water, and the designers of submarines have hit upon the very same principle (Figure 1.7). You can generally identify analogies because the analogical characteristic does not pattern with the other characteristics of the organism. We have already seen this with whales and tuna, and, to take another example, a bat has wings like a bird, but the rest of its anatomy and physiology has a closer resemblance to those of mammals. The natural world contains exactly the mix of homology and analogy in the form of organisms that Darwin's theory—and only Darwin's theory—predicts.

The conceptual power of Darwin's theory

The next four chapters will examine in detail how the process of natural selection actually works, but for now it is important to note that what Darwin is doing here is coming up with a new *kind* of process that is neither chance (as it is often wrongly characterized), nor has any goal, or intention, or conscious designer involved. A new kind of process means that we have a new kind of explanation available to us. We can explain a structure in a way which is neither 'X is as it is because it just worked out that way', nor 'X is as it is because of what its creator was trying to achieve', but 'X is as it is because ancestral versions which were slightly more X-like had an advantage relative to competitors that were slightly less X-like'. This opens the door to a whole new way of looking at things.

1.3 Incorporating genetics: the modern synthesis

At the time Darwin was writing, the mechanisms of heredity and variation were not really understood. Although common experience shows that individuals vary from each other in ways that are transmissible from parent to offspring, we did not really know why this was the case. More specifically, we did not know how, in sexual species, the characteristics of one parent combined with those of the other. Biologists assumed that the characteristics of the two were

Figure 1.8 Gregor Mendel, 1822–84, the father of modern genetics. *With kind permission of The U.S. National Library of Medicine.*

simply blended, in much the way that cream and coffee are blended in a cup, and this looked like a problem for evolution by natural selection (see Chapter 3).

Almost simultaneously with Darwin, a brilliant Moravian monk called Gregor Mendel (Figure 1.8) was establishing that inheritance in sexual species does not work by blending in this way. Instead, each parent provides the offspring with a set of 'heredity particles', which we now call genes. The particles from each parent do not blend together, but are carried separately within the offspring and may in turn be passed on intact to subsequent generations. This is why a characteristic from a grandparent can turn up intact in some of the grandchildren, having not been at all visible in the intervening parental generation.

Mendel's ideas were not integrated with Darwin's until well after both figures had died. Indeed, for some decades, Darwinism, which emphasized gradual modification, and Mendelism, which emphasized that discrete particles are passed from generation to generation, were considered opposing schools of thought. Fortunately, in the 1930s, some of the great thinkers of modern evolution established, mainly through mathematics, that Darwinism and Mendelism were not just compatible, but that Mendelism provided the basis for natural selection to work in the way Darwin had envisaged it would. This step forward is known as the **modern synthesis**, after the title of a book published by Julian Huxley in 1942. (You may also see it referred to as **neo-Darwinism**.) The modern synthesis made possible the great growth of evolutionary knowledge that we benefit from today.

The modern synthesis clarified how natural selection actually worked. Natural selection amounts to changes in the relative frequencies of different forms of genes in the population over the generations. You therefore cannot understand natural selection without appreciating what it is doing at the genetic level. It is in the spirit of the modern synthesis that genetics and evolution are not presented separately in this book, but introduced in an intertwined way.

1.4 Common objections and misunderstandings

Despite the abundance of scientific evidence for the validity of Darwin's theory, resistance persists and misunderstanding abounds. This section discusses a few of the more common objections raised by doubters. I shall endeavour to show how they can be dislodged once the logic of evolution and the evidence for it are set out carefully.

1.4.1 Evolution is just a theory

From time to time, religious anti-evolutionists make efforts to have Darwinism taught 'alongside other theories' of the origin of life. Underlying this demand is the idea is that 'evolution is just a theory' and therefore might not be true. Partly, this rests on a confusion about the word 'theory'. In everyday usage, the word means an idea we have that we suspect may be true but is not yet supported by evidence, as in, 'My theory is that there will be a last-minute rush before the shop closes.' In everyday usage, there is an implied contrast between 'theory' and 'fact'. Evolution is *not* a theory in the everyday sense, since it is supported by a mass of factual evidence.

Scientists use 'theory' in a technical sense, to mean a body of principles that explain phenomena and can be used to make predictions about them. Evolution is a theory in this sense. Thus, in science, we have the theory of gravity, the theory of relativity, and so on. No one says, Gravity is just a theory; it ought to be taught alongside other alternatives.' The existence of gravity is supported by a mass of facts, but the laws of gravity can also be described as a theory in the scientific sense. So it is with evolution.

Related to the 'evolution is just a theory' objection is the assertion that we have never actually seen evolution happen. The evidence is only indirect, the doubters say, and the case for evolution relies on inference and conjecture. It is untrue that we have never seen evolution happen. Evolution can be directly observed. Most of the best examples come from organisms with fairly short lifespans, since these are easier to study in a reasonable time.

We will examine just one example here. This comes from the finches of the Galapágos Islands—Darwin's finches, as they are known, since Darwin spent time observing them during his voyage on *HMS Beagle*. There are several different species of finch across the different islands and they show a striking pattern of homology and local divergence. The biologists Peter and Rosemary Grant studied the finches, in particular the medium ground finch, *Geospiza fortis*, on the island of Daphne Major, for many years (Boag & Grant 1981; Grant 1986). This is an excellent population to study, not least since the island is small and few finches migrate on and off the island. Thus, the researchers are able to capture, measure, mark, and release essentially the whole population.

The Grants and their colleagues were able to show that the population of finches contained variation in beak size (element 1 of Darwin's theory). This variation is important, since birds with larger beaks can handle larger and harder seeds (seeds are what the finches feed on). Moreover, the Grants showed that beak size was heritable, or transmitted from parents to offspring (element 2). In 1977, there was a drought and, as a consequence, fewer seeds were available for the finches to eat and those that were available were larger and harder than usual. A large proportion of the finches died during the drought (element 3), but the larger an individual's beak, the more likely it was to survive. Because of this increased survival, when we compare the distribution of beak sizes of all living finches before and after the drought, we can see that the average has been moved to the right, or towards larger beaks. Since the large-beaked survivors tended to produce large-beaked offspring, the next generation of finches too had larger beaks (Figure 1.9). Over just a couple of years, the species had been shifted in its characteristics towards a form better adapted to the new environmental challenge (element 4). This is natural selection in action. We now have a substantial number of examples of natural selection going on in wild populations and biologists agree that selection in the wild is often strong and easily strong enough to account for all the changes we see over the history of life (Endler 1986).

People sometimes respond to examples like the finches by accepting that natural selection brings about change *within* a species, but disputing that it could account for evolution *between* species. That is, larger-beaked medium ground finches are still medium ground finches. The example has not shown how a new species could be produced by descent with modification. As it happens, there is another species of finch in the Galapágos, the large ground finch, which differs mainly from the medium ground finch in body and beak size. Peter Grant calculated that,

Figure 1.9 **Natural selection occurring in the Galapágos Islands. (a) In 1977, drought conditions mean the seeds available to eat are larger and harder; (b) as a result, survivors of the drought have a larger average beak size than the population before it; (c) as a result the birds born in 1978 have larger beaks on average than those born in 1976. The species has changed.** *(a) From Boag & Grant (1981); (b) From Grant (1986); (c) From Grant & Grant (2003).*

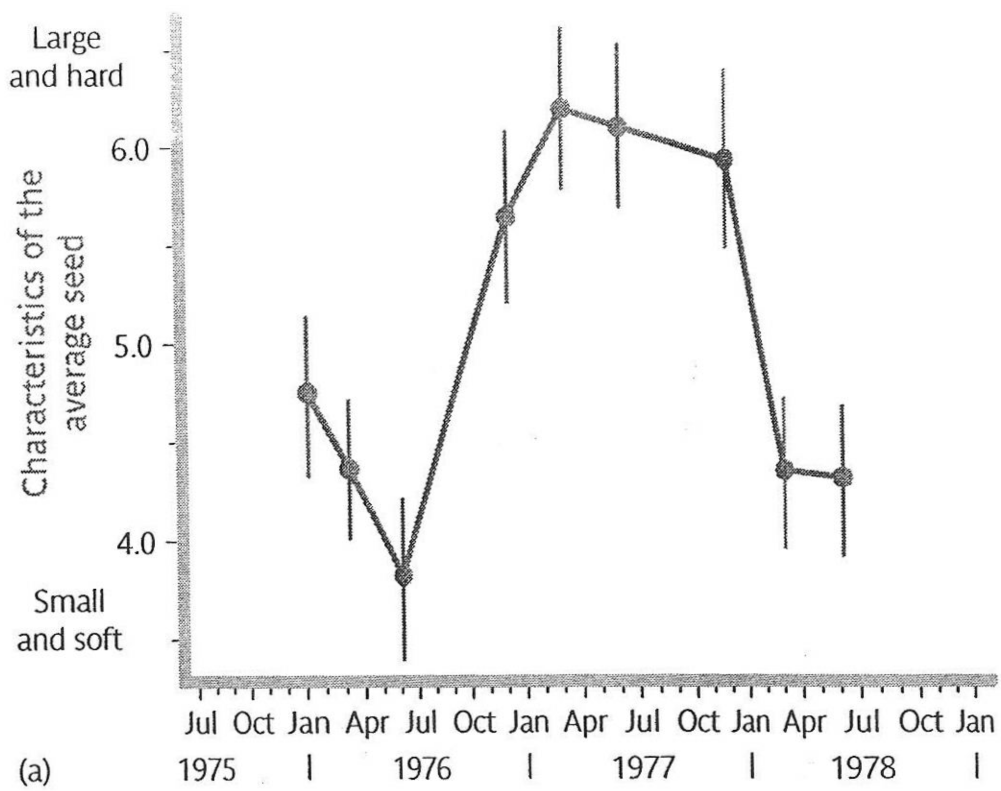
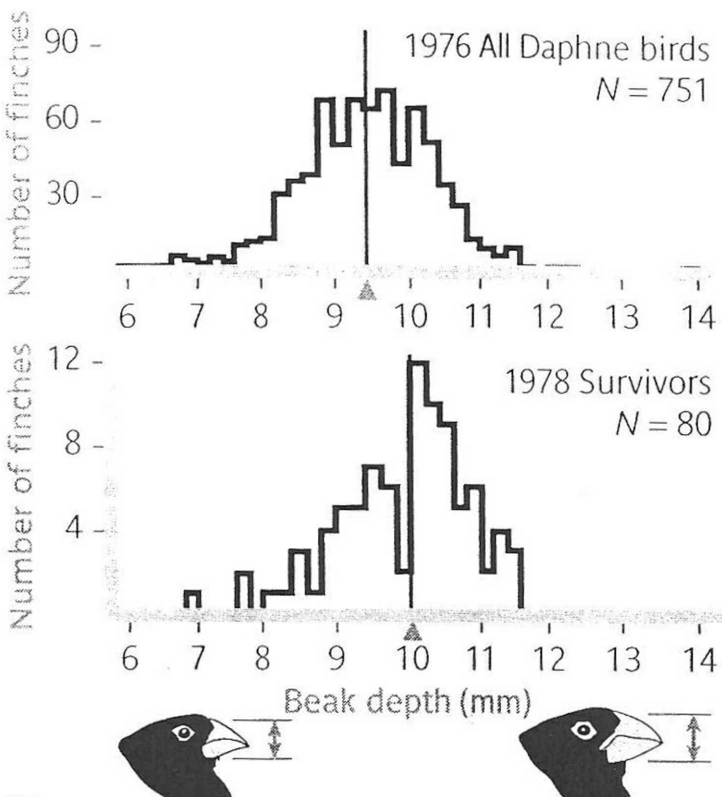
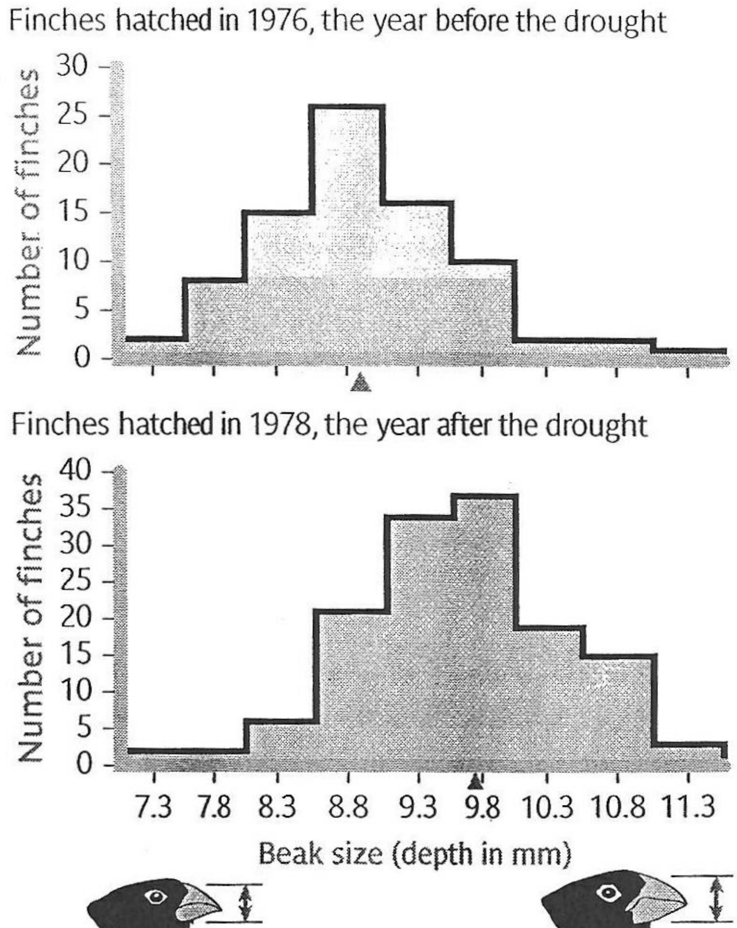


Figure 1.9 Continued



(b)



(c)

if the selective pressures of the 1977 drought continued, it would take no more than 46 years to produce the large ground finch from the medium ground finch. A different species of finch would have been produced in what is a mere eye-blink of time. (In fact, the drought conditions of 1977 did not persist and so the selective advantage of larger beaks was not maintained.)

Objectors might wish to say that a large ground finch may be a different species, but it is still a finch. They might continue to be sceptical that natural selection could produce an organism different *in kind*, like a mouse from an ancestor that is not a mammal. This objection implies that there are natural kinds in the history of life and it is difficult to cross from one kind to another. However, the theory of evolution says that there are no natural kinds. There is only one tree of life and all organisms differ only by degree from each other. The big difference between, say, a bird and a mammal, is just a long chain of little differences. To get to a large ground finch from a medium ground finch you go via a chain of intermediate forms, each one of which is just a little different from the last. To get to a mammal from some ancestor that is not a mammal is exactly the same, but the chain of steps is very much longer. If you were a very long-lived researcher who could observe the gradual evolution of mammals from a non-mammalian ancestor, you would observe a sequence of small, gradual changes in form. Sometimes they might go faster, and sometimes slower, but there would be no point at which there was a sudden leap or change of kind. It is only after the event, when the intermediates have died out, that you find yourself in a position to say, 'now we have a different kind of thing: a mammal'.

1.4.2 There are gaps in the record

A second area of objection to evolution by doubters concerns the fossil record. The doubters assert, correctly, that Darwinism requires that there have existed over time a continuous sequence of intermediates connecting any two living species. There must, for example, have been ancestral forms intermediate between humans and chimpanzees. Where is the fossil evidence that this is the case?

As it happens, there are fossils, designated with the generic name *Sahelanthropus*, dating from around the correct period of 6–7 million years ago, which are in many ways intermediate between humans and apes (Chapter 6). However, the doubter can then point out that *Sahelanthropus* is very different from modern humans and evolution requires that there was an intermediate form between *Sahelanthropus* and modern humans. We could then produce the remains of *Australopithecus*, living 2 or 3 million years ago and more human-like than *Sahelanthropus*. Aha, says the doubter, but where is the intermediate between *Australopithecus* and modern humans? We might produce a specimen from the genus *Homo* dating to around 1.5 million years. But again, the doubter asks for another intermediate between this latest candidate and modern humans.

You can see what is happening here. The doubter can keep on asking for more and more intermediates between the intermediate we just produced and the modern creature. Although the fossil record concerning human and chimpanzee ancestors is actually very abundant, eventually the doubters will find a gap that they feel pleased with. Indeed, logically, the doubter could only be satisfied if we had the fossilized remains of *every single* generation that had lived for the past 7 million years. Fossilization is incredibly rare. Most skeletons decay or are destroyed and probably only one in many millions survives to be discovered by palaeontologists. Thus, the determined doubter will always find a gap in the record.

The problem is that the doubter has misunderstood the evidence for evolution. An overwhelming case could be made for the truth of evolution even if there were not a single fossil in existence. The case would rest on the patterns of homology and adaptation we see in the organisms currently alive. The existence of fossils is merely a bonus.

Fossils do exist and, although the record is patchy, they often provide satisfying support for evolutionary relationships. The fossils in continents like Australia, which today have marsupials rather than placental mammals, are fossil marsupials, not fossil placental mammals. Extinct intermediate forms can often be found more or less when and where we predict they will be found. For example, there is a fossil form given the generic name *Ambulocetus*, dating from around 50 million years ago, that is rather whale-like in some ways but has hind legs, which are a little reduced compared with those of land mammals. Then there is *Basilosaurus*, dating from around 38 million years ago, which has a tiny pair of hind legs that could not possibly have supported the creature's body, but may perhaps have been used for grasping. Finally, in today's whales there are no hind legs at all, although there is, as we have seen, a vestigial pelvis. These three form a satisfying evolutionary progression (Figure 1.10), but even without the fossils, the evidence that whales had descended from a land mammal would still be overwhelming.

1.4.3 The theory of evolution says living things arose by chance

Richard Dawkins recounts numerous examples of doubters about evolution pointing to some of the complex structures like the eye and saying, 'Look at the intricacy of this. How could something so complex arise by chance?' (Dawkins 2006a). Well, they are quite right. It could not. But this is not an argument *against* evolution; it is an argument *for* it. The doubters seem to believe that evolutionists believe the form of organisms is due to chance, but nothing could be further from the truth. Evolution is a theory of the *non-random* persistence of particular characteristics, so the very complexity the doubters point to is amongst the best evidence for evolution.

1.4.4 It all happened so long ago, who knows, and who cares?

This objection tends to arise when researchers propose to take an evolutionary perspective on some aspect of behaviour, especially human behaviour. Critics respond by saying, 'Who cares what might have happened thousands of years ago? We weren't there and so we can never know. What I care about is explaining the behaviour in the present.'

This objection is misguided. Evolutionary explanations for behaviour are not explanations of what happened in the past. They are explanations of *why* things are as they are in the present. However, because Darwin solves the problem of design in terms of history, the explanation of the present must invoke selective pressures that have acted over evolutionary time.

To take an example, let us consider how an evolutionary perspective helps us to understand nausea and vomiting of pregnancy (also known as morning sickness and henceforth referred to as NVP). The majority of women, all over the world, experience NVP when they are pregnant. They often feel sick and develop strong aversions to some foods whilst craving others. Until recently, no one understood why this happened. Several evolutionary researchers have proposed that NVP evolved to protect the mother and embryo from dangerous substances contained in foodstuffs (see Fessler 2002; Sherman & Flaxman 2002).

What the evolutionary hypothesis entails is that, at some point in human history, women with a capacity for NVP (and their children) survived better than women with no such capacity and this is, of course, difficult to verify. However, it also makes predictions about the features and consequences of NVP *as it is experienced right here in the present* and these are amenable to empirical test.

Figure 1.10 **Fossils document the descent of whales from a legged ancestor.** *(a) From Freeman & Herron (2004), p. 46. (b) From Gingerich, Smith & Simons (1990), pp. 154–7. (c) From Thewissen, Hussain & Arif (1994), pp. 210–12.*

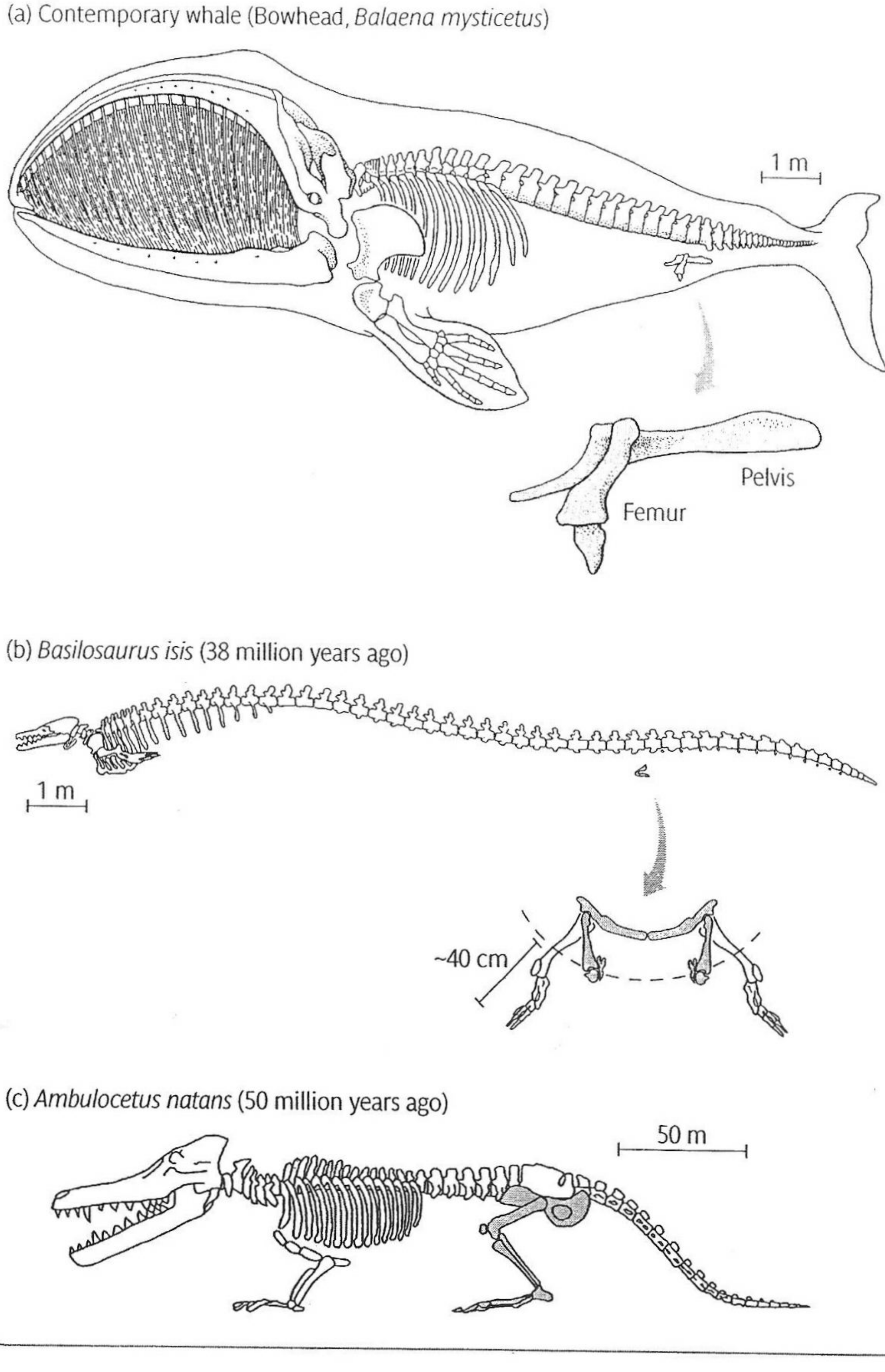
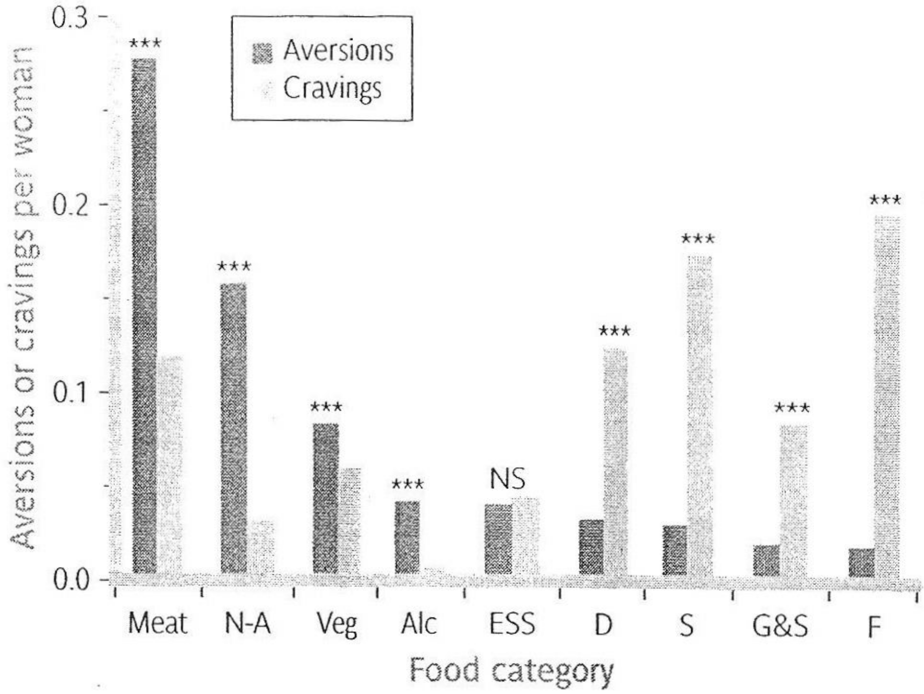


Figure 1.11 Frequency of aversions and cravings to different food types during pregnancy, based on interviews with 5,432 and 6,239 women. The triple asterisk indicates that the difference in frequency between aversions and cravings for that food type is highly significant. *Meat*, includes fish and eggs; *N-A*, non-alcoholic beverages, including coffee and tea; *Alc*, alcohol; *ESS*, ethnic and spicy foods; *D*, dairy and ice cream; *S*, sweets and desserts, *G&S* grains and starches, *F*, fruits and fruit juices; *NS*, not significant. *From Sherman & Flaxman (2002).*

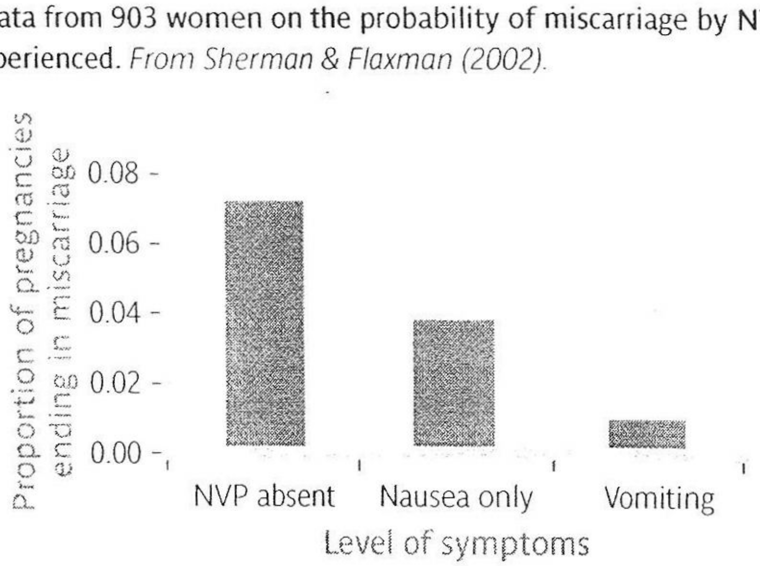


If the evolved function of NVP is to protect women and embryos, then it should appear when they are most vulnerable. The embryo is most at risk from damage in the first trimester of pregnancy, when the major organ systems are differentiating, whilst the mother is also particularly vulnerable in this period, as her own immune system is down-regulated to stop her attacking the partly foreign tissue that is the embryo. And indeed, it is in the first trimester that NVP appears, largely disappearing after week 20 of pregnancy.

Furthermore, NVP should be particularly directed to foods likely to contain substances that are dangerous, particularly whilst the mother is immunosuppressed. The most obvious of these are meats, which can contain dangerous micro-organisms. NVP should thus switch food preferences away from meat and towards fruits and sugars as alternative, safer forms of energy. This is exactly the pattern that NVP shows—nausea is directed most strongly towards meat and animal products, whilst cravings are towards fruits and related sweet things, and to a lesser extent grains (Figure 1.11). Moreover, in cultures where the diet contains little meat and has as a staple a bland grain-like maize, women experience less NVP than in other cultures.

Another prediction of the evolutionary theory is that the presence of NVP should actually benefit the embryo, protecting it from the kinds of developmental abnormalities that could lead to it being miscarried. Here, too, the evidence is compelling. Pooling across nine studies involving 22,305 pregnancies, the presence of NVP reduces the miscarriage rate sharply (Figure 1.12 shows data from one such study; the more severe the NVP, the better).

Figure 1.12 Data from 903 women on the probability of miscarriage by NVP symptoms experienced. *From Sherman & Flaxman (2002).*



Thus, the evolutionary theory explains why contemporary women experience NVP when they do, why it affects the foods that it does, and what the consequences of not having it will be. It reassures women that their experiences are neither abnormal nor bad for their babies, suggests reasons why physicians should not try to suppress NVP with drugs, and also reveals what diet will best minimize the symptoms, namely fruit and bland cereals. All of this understanding concerns the present, not the past, and none of it would have been derived without some idea, based on evolutionary thinking, of what NVP is for.

Summary

1. The theory of evolution is firmly accepted by scientists as one of the most important bodies of scientific knowledge that we have.
2. Despite this, large numbers of people do not accept that evolution occurs.
3. Darwin's theory of evolution was set out in a book called *On the Origin of Species by Means of Natural Selection*, published in 1859. In it, he simultaneously solved two major problems in the understanding of living things: the problem of history and the problem of design.
4. The problem of history is the question of where all the different types of organisms come from. Darwin argued convincingly that the pattern of homology and divergence we see in the natural world is best explained by the idea that all the current forms have descended with gradual modification from a single ancestral form.
5. The problem of design is the question of why organisms have characteristics that are well designed for the requirements of living that they have. Darwin argued that the cumulative effect of non-random survival of beneficial characteristics would be to produce well-designed structures. He called this mechanism natural selection.

6. Natural selection solves both of the major problems in terms of each other. Organisms have the design they have because of their history, and the history they have primarily because of changes in their design, and natural selection is the causal mechanism.
7. The full power of Darwin's theory only became clear once it had been integrated with genetics in what is known as the modern synthesis.
8. Many of the objections to evolution evaporate once misunderstandings of the theory and the evidence for it are clarified.

? Questions to consider

Write a paragraph in answer to the following questions:

1. In *The Origin*, Darwin spent a lot of time considering issues such as the following: In several different parts of the world, insect species that live in deep caves and that lack eyesight are found. These blind forms are more similar to the sighted forms living immediately outside their caves than they are to the blind forms living in cave systems on other continents. What would a non-evolutionary approach to biology have predicted here? How might Darwin explain the pattern we actually do see and why is this such good evidence for Darwin's theory? Finally, what are the analogies and homologies in this case?
2. In the chapter, it was suggested that natural selection could explain how the whale, descended from a land mammal, has come to have a streamlined shape with no hind limbs, more like that of a fish. Explain exactly how this might come about through a long series of small changes, using the terms variation, heredity, competition, and selection in your answer.
3. Darwin argued that whenever there was variation, reproduction with heredity, and competition, a process of natural selection producing adaptation would ensue. This raises the possibility that there might be things in the world other than living organisms that evolve in a Darwinian manner. Can you think of any examples? What would be the similarities and differences between these systems and living organisms?

Taking it further

One of the best modern writers on evolution is Richard Dawkins. Dawkins gives a readable introduction to the phylogenetic history of life (going backwards through time from modern humans) in *The Ancestor's Tale* (Dawkins 2004). On the modern doubters about evolution and the case against them, Kitcher (2007) is excellent. For a readable and short treatment of how natural selection works, and how it can change the way we think about many different aspects of our lives, try Wilson (2007). Dennett (1995) examines the revolutionary conceptual power of Darwinian theory at greater length.