1 Evolutionary biology

What is "evolution"? If you were asking in the middle of the eighteenth century, the answer would be something to do with individual development. But from about the middle of the nineteenth century the term has meant a gradual process of law-bound development that brought about the world in which we live, especially the world of organisms, animals, and plants (Richards 1992). We usually add that we mean a natural process, that is something where supernatural forces like God play no direct role. Often we mean common ancestry, a "tree of life," although not every evolutionist has believed in such a tree. Today we think more in terms of bushes or sometimes perhaps a very odd tree like the banyan tree, where there are links all over the place.

Early years

The ancient Greeks did not believe in evolution (Sedley 2008). In a way, this seems strange, because the greatest philosophers – Plato (428–348 BCE) and Aristotle (384–322 BCE), in particular – saw this world of ours as one of change and motion. But when one person, the Sicilian pre-Socratic philosopher Empedocles (490–430 BCE), did suggest something along developmental lines, Aristotle criticized him severely. The reason is simple. The Greeks saw the world as designed, as put together for purposes, for ends (Ruse 2003). Organisms are the things in the world that more than any other exhibit what Aristotle called "final causes." If you want to understand something like the hand or the eye, then you must ask not merely what the forces making them were, but what is the reason for their existence. Hands and eyes are complex things, and could not have come about through mere chance – through the action of blind, undirected law – but

require an intelligence of some kind to make them. Hence, evolution – the epitome of blind chance – is impossible.

The coming of Christianity reinforced this mind-set. The early Christians were not at first sure that they needed to accept the Hebrew Scriptures – after all, it was the Jews who rejected Jesus. But, particularly under the influence of St. Augustine (354–430 CE), they realized that it is only through the Jewish narratives that sense can be made of Jesus and his fate. Why did he have to die on the cross? For our sins. Why are we sinful? Because of the acts of Adam and Eve, as told to us in Genesis. Augustine particularly cautioned that one should not necessarily interpret Scripture literally, especially if it conflicts with modern science. But then, and for many centuries later, no one had reason to doubt the authenticity of the Genesis creation story, which puts all down to miracle, not that long ago.

It was only at the beginning of the Enlightenment, the flowering of science and philosophy that is generally dated from the beginning of the eighteenth century, that people first started to speculate seriously in the direction of developmental origins (Ruse 1996, 2005a). It is true that increasingly there were empirical discoveries that today we would think evidence of evolution – fossils and strange transitional creatures, particularly – but then and for many years afterwards the chief attraction of evolution was ideological. The Enlightenment was the time when many people first began seriously to adopt the philosophy of Progress – the belief that through unaided human talent and effort the human condition, science, medicine, teaching, culture, and more, can be improved. The Enlightenment was the time when many people began to reject the older philosophy of Providence – the belief that we humans unaided can do nothing without God's help and to think otherwise is presumptuous and doomed to disaster. Evolution – now, without qualification, meaning the evolution of organisms – was caught up in this debate about Progress and Providence, with supporters of the former arguing that as we see Progress in the cultural world, so likewise we see progress in the biological world, going all of the way from blobs to humans, from monads to man as the saying went. (Progress with a capital "P" will refer to cultural notions of upward change; progress with a small "p" to biological notions of such change.)

Note that although evolution was taken to be something against the core beliefs of Christianity, it was not simply a matter of denying the literal words of the Bible. Augustine had prepared the way for people to do

this. It was more one of going against what was seen to be the essential relationship between God and his creatures. Not that the early evolutionists were atheists, or even agnostics. Rather, they believed in a God who works through unbroken law – a God of "deism" as opposed to the interventionist God of "theism" – and of course for such a God, the law-bound process of evolution is confirmation of his greatness rather than refutation. Note also that the P/progressionists were as convinced of the central importance of humankind as were the Providentialists. The late eighteenth-century evolutionist Erasmus Darwin (1731–1802), grandfather of Charles Darwin, shows this clearly. He was much given to expressing his ideas in verse.

> Organic Life beneath the shoreless waves
> Was born and nurs'd in Ocean's pearly caves;
> First forms minute, unseen by spheric glass,
> Move on the mud, or pierce the watery mass;
> These, as successive generations bloom,
> New powers acquire, and larger limbs assume;
> Whence countless groups of vegetation spring,
> And breathing realms of fin, and feet, and wing.
>
> Thus the tall Oak, the giant of the wood,
> Which bears Britannia's thunders on the flood;
> The Whale, unmeasured monster of the main,
> The lordly Lion, monarch of the plain,
> The Eagle soaring in the realms of air,
> Whose eye undazzled drinks the solar glare,
> Imperious man, who rules the bestial crowd,
> Of language, reason, and reflection proud,
> With brow erect who scorns this earthy sod,
> And styles himself the image of his God;
> Arose from rudiments of form and sense,
> An embryon point, or microscopic ens!
>
> (E. Darwin 1803, I, lines 295–314)

He was also unambiguous about the way in which he tied his biology into his philosophy. This idea of organic progressive evolution "is analogous to the improving excellence observable in every part of the creation … such as the progressive increase of the wisdom and happiness of its inhabitants" (E. Darwin 1794–96, 509).

The opening of the nineteenth century saw many other people embracing evolutionary ideas. ("Transmutation" was a popular term for the idea.) Probably the most famous was the French biologist Jean Baptiste de Lamarck (1744–1829), who gave his name to the process of change that supposes that acquired characteristics (like the blacksmith's strong arm) can be inherited directly. But enthusiasm generally outran evidence, and virtually no one even tried to speak to the problem of final causes. No one really grappled with the Greeks' problem, how can blind law bring on complex functioning? It was not until 1859 that this all changed, when the British naturalist Charles Robert Darwin (1809–82) published his great work *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. Now finally the world was presented with a full-bodied attempt to explain origins, of organisms living and dead, in purely natural terms, at the same time speaking to the Aristotelian worries about the functioning of organisms. More precisely, Darwin tried to make reasonable or commonsensical the very fact of evolution – all organisms have a common descent by natural processes from one or just a few original simple forms – and at the same time provide a mechanism of change that speaks to final cause, this mechanism being something Darwin called "natural selection."

Charles Robert Darwin

In some respects Darwin does not seem a very likely candidate for the role of the "father of evolution," as he is often called (Browne 1995, 2002). Born into a rich, upper-middle-class English family – his maternal grandfather was Josiah Wedgwood, responsible for the modernization of the British pottery trade – he had conventional schooling, aiming first to be a physician (like his father) and then when that failed to be a clergyman in the state-established Church of England. Things changed when, after university (Cambridge), Darwin spent five years on board the British warship HMS *Beagle*, as she mapped the coast of South America. As ship's naturalist, he made massive collections of specimens, and developed rapidly into a full-time scientist, primarily in the early years as a full-time geologist, but then more and more as a biologist. We know that he became an evolutionist and discovered the mechanism for which he is famous, natural selection, in the late 1830s; but for reasons that are still not entirely

clear he did not publish for another twenty years. Instead, he married his first cousin Emma Wedgwood, moved to the country outside London, raised a large family, and spent much of his time battling unknown, but very draining, bodily ailments. Evolution was put to one side as Darwin engaged in a massive study of barnacle taxonomy, and it was only when that was finished (in the 1850s) that Darwin turned again to evolution. Famously, he was finally spurred into print when a young naturalist in the Malay Archipelago, Alfred Russel Wallace (1823–1913), sent to Darwin of all people a short essay which showed that quite independently he had hit upon the same mechanisms as the older man. In fifteen months, Darwin wrote the *Origin of Species*, which was published late in the year 1859.

In his *Autobiography*, written late in life, Darwin spoke of the *Origin* as containing "one long argument" (C. Darwin 1958, 140). But what was this argument? Actually it came in several (at least three) parts. In a letter written a year or two after the *Origin* was first published, Darwin made explicit mention of his strategy.

> In fact the belief in natural selection must at present be grounded entirely on general considerations. (1) on its being a vera causa, from the struggle for existence; & the certain geological fact that species do somehow change (2) from the analogy of change under domestication by man's selection. (3) & chiefly from this view connecting under an intelligible point of view a host of facts. (Letter to George Bentham, May 22, 1863; C. Darwin 1985–, XI, 433)

Let's start there. The *Origin* went through six, increasingly revised, editions, although most scholars today prefer the first (1859), untouched version. As you open the *Origin* you find that in fact it is the analogy with the domestic world that comes first. Probably reflecting his personal route to discovery, Darwin pointed out at length that breeders have taken organisms like pigeons and dogs, like cattle and sheep, not to mention vegetables and other plants, and simply transformed them, creating many different forms and varieties. And that this has all been done by means of taking those with features one desires – shaggier coats, prettier feathers, fiercer fighting natures – and breeding from and only from these specimens.

> The great power of this principle of selection is not hypothetical. It is certain that several of our eminent breeders have, even within a single lifetime, modified to a large extent some breeds of cattle and sheep.

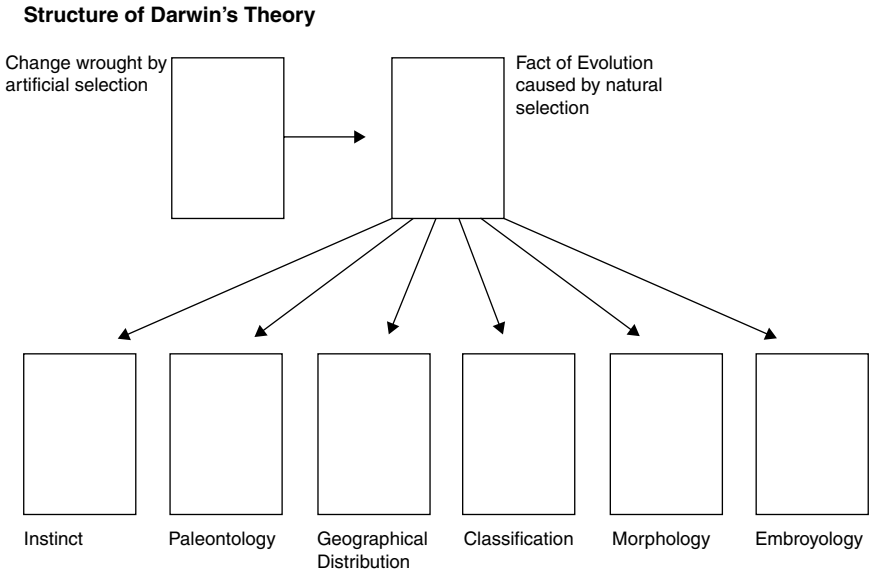

Figure 1.1 The structure of the *Origin*. Note first the analogy between the world of the breeder and the world of nature, and how Darwin then uses the central mechanism of evolution through natural selection to explain in different areas of biology and conversely uses these explanations as support for his central mechanism.

> In order fully to realize what they have done, it is almost necessary to read several of the many treatises devoted to this subject, and to inspect the animals. Breeders habitually speak of an animal's organisation as something quite plastic, which they can model almost as they please. If I had space I could quote numerous passages to this effect from highly competent authorities. (C. Darwin 1859, 31)

Next, picking up on the first point he mentioned in the letter to Bentham (a nephew, incidentally, of the philosopher Jeremy Bentham), Darwin introduced his main mechanism of natural selection. He did this in two parts. First, arguing from the tendency of organisms to multiply in number, he agreed with the political philosopher Thomas Robert Malthus that because space and food will always be limited, there are going to be inevitable "struggles for existence."

> A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during

> some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them. (C. Darwin 1859, 63–64)

Darwin then drew on the fact that whenever you have a population of organisms, that is a group all in the same species, you find nevertheless that there are differences between them and that every now and then something new seems to pop up into being. This led Darwin to speculate that in the struggle some types or forms are likely to prove more successful than others, simply because these types or forms will help their possessors against others. Given enough time, these types will spread through the group and eventually there will be full-blooded change.

> Can the principle of selection, which we have seen is so potent in the hands of man, apply in nature? I think we shall see that it can act most effectually. Let it be borne in mind in what an endless number of strange peculiarities our domestic productions, and, in a lesser degree, those under nature, vary; and how strong the hereditary tendency is. Under domestication, it may be truly said that the whole organisation becomes in some degree plastic. Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life. Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable

> variations and the rejection of injurious variations, I call Natural Selection. (80–81)

Note a point made above but sufficiently important to be worth making a second time. Darwin's natural selection does not just bring about change; it brings about change of a particular kind. Organisms are adapted – they have adaptations, features that aid them in the struggle to survive and reproduce. Hands, eyes, teeth, penises, vaginas, leaves, flowers, seeds, and more – these are things that are "as if" designed, that is to say that they are put together in order to help their possessors. And it is Darwin's claim that this all comes about naturally. There is no need to invoke God or any other force making for the design-like nature of the organic world. Darwin does not deny final causes, not at all. He simply wants to give them a natural beginning.

At this point, Darwin introduced a secondary form of selection, sexual selection. Just as natural selection is modeled on the features in the world of the breeder that might be expected to have analogous roles in survival and reproduction against competitors and elements in the natural world – thicker coats, better egg-laying abilities – so sexual selection is modeled on features in the world of the breeder that obviously help in reproduction against fellow species members. Darwin spoke of male combat, as when two stags fight for the harem and as a result the antlers are under strong selection pressure to increase in size – modeling this on dog and cock breeders selecting for fiercer fighters – and female choice, as when the peahen chooses the male with the biggest display of tail feathers – modeling this on breeders selecting for more beautiful birds and other like organisms. Later in this book, we shall take up sexual selection in some detail. For now it is enough to note that it was always an integral part of Darwin's thinking.

There were other things that Darwin talked about, including something he called the "principle of divergence," where he argued that organisms split into different groups because of the pressure to exploit different ecological niches – in-between kinds are literally neither fish nor fowl, and cannot do as well as specialists. This splitting led Darwin to his metaphor of the history of life as being like a massive tree, with the past in the roots and the present at the tops of the boughs.

> The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth.

> The green and budding twigs may represent existing species; and those produced during each former year may represent the long succession of extinct species. At each period of growth all the growing twigs have tried to branch out on all sides, and to overtop and kill the surrounding twigs and branches, in the same manner as species and groups of species have tried to overmaster other species in the great battle for life … As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications. (129–30)

Darwin next moved over some problems he was not able to solve very satisfactorily, including the nature of heredity, what we today would call "genetics." We can skip this now because it will come up again shortly. He was now ready, for the rest of the *Origin*, to turn to the third part of his argument – "& chiefly from this view connecting under an intelligible point of view a host of facts." Basically what Darwin now did was to go through the whole range of the life sciences, looking at the problems facing researchers, and then offering solutions based on his central hypothesis of evolution through natural selection. Conversely, in a kind of feedback argument, he was using these solutions as evidence for the truth of his hypothesis. Just as a detective facing a murder will hypothesize that some unlikely person is the culprit and then turn to the clues – the bloodstains, the broken alibi, the motive, the method of attack – to convict, so Darwin turned to the clues of biology to establish the truth of his bold conjecture. I should say that he was not flying blind at this point, as it were, but that he was following the methodological prescription of the British historian and philosopher of science William Whewell (1840), who argued that such a type of explanation, what he called a "consilience of inductions," was just what is needed when you are trying to explain using a cause that no one sees and that may indeed be unobservable. Whewell was thinking in the context of the wave theory of light, where even though no one sees the actual waves it is accepted on circumstantial evidence such as the interference patterns in Young's Double Slit experiment. Darwin never thought we would ever see natural selection in action, but undeterred he set out to convince on the bloodstains, the broken alibis, the motives, of biology.

One of the first areas to which Darwin turned was that of instinct and social behavior. Like many of his contemporaries as well as those before him, Darwin was fascinated by the world of insects, particularly those that live in nests or hives, and he showed the power of his theory through selection of a beautiful example of what Richard Dawkins (1982) has called the "extended phenotype." Why is it that honeybees build hexagonal spaces for their young? Why not squares or circles or whatever? Through a number of rather ingenious experiments (involving the use of colored wax to see exactly how and when the bees use their building materials), Darwin was able to show that this is the most efficient use of the wax and makes for a structure as strong as you are ever going to get. He also spent some time comparing different groups of living insects, showing that there is a line of bees from those that make the crudest honeycombs to those that make the most complex and perfect, and from this he argued that we can as it were in one place and time see the chain through time that would have produced the hexagonal spaces that distinguish the most sophisticated insects today. Also, given that it is the social insects that yield some of the most wonderful examples of instinct, it is perhaps not surprising – although certainly a mark of his genius – that Darwin found himself wrestling with what is today known as the "levels of selection problem" (Brandon and Burian 1984). As is well known, honeybee workers (always female) are generally sterile and lay no eggs of their own. How can a process like selection, produced by the struggle for existence and reproduction, bring on something like this? Who benefits from the adaptations produced by natural selection? Is it always the individual or can it sometimes be the group? Later we shall look in more detail at this question, one that has been of much interest in recent years, including in the context of humankind. Suffice it to say here that Darwin had things of importance to say, although without a full theory of heredity he could not hope for a fully satisfactory answer.

Moving on to the fossil record, much of the time Darwin was on the defensive, trying to show why it is that there are so many gaps in the record. But then he started to make the positive points, particularly about the extent to which one finds earlier fossils in the record, fossils that look like the combination of very different extant organisms. Lying behind a discussion such as this was the kind of Germanic thinking that led the anatomist Richard Owen (1848, 1849) to his archetypal theory, where organisms within a group (like vertebrates) are seen as modifications of a basic