# Part I

# Evolution by Natural Selection

Population biology has its roots in many different areas of natural history: the taxonomy and geographical distribution of organisms, their ecology and behaviour, and studies of heredity and hypotheses that organisms are related by descent. Charles Darwin made a synthesis of these areas in his 1859 book *On the Origin of Species by Means of Natural Selection*, and this provides us with a convenient starting point for our introduction to population biology.

The purpose of the following three chapters is to provide a historical perspective and an understanding of the philosophical content of Charles Darwin's theory of evolution through the process of natural selection. One can argue that his theory of natural selection is the most important theory in biology, and so it is important to understand this Darwinian perspective of biology, because it provides a loose framework for the remainder of this book.

The first chapter examines some of Darwin's educational experiences that probably later influenced his evolutionary thinking. His almost 5-year-long voyage on HMS *Beagle* provided him with a rich exposure to natural history on a worldwide scale and, coupled with his geological discoveries, he became a very famous scientist. His major epiphany when he questioned the fixity of species towards the end of the voyage was reinforced when he began to receive the reports on his collections about 6 months later. He immediately began to scientifically investigate the possibility of transmutation of species, but kept his newfound views a secret from his colleagues.

The second chapter examines *On the Origin of Species* in more detail to see how he structured his argument for his three theories of evolution (known as Darwinism): that all organisms are related by descent, that the main mechanism for this evolutionary change is the process of natural selection, and that this occurs at the population level and not the species level. My main sources for this historical perspective are Bowlby (1990), Desmond and Moore (1992) and Browne (1995, 2002).

Finally, the third chapter examines the theory of natural selection in more detail and presents it in the more modern framework of genetics. We also introduce the area of epigenetics and discuss some issues that arise when we consider selection at different levels. Finally, we consider some of the arguments that people use to deny evolutionary theory and discuss many of the ways that scientists counter such arguments.

# 1 Darwin Questions the Fixity of Species

Evolution was not considered to be a respectable subject at the beginning of the nineteenth century when Charles Darwin was receiving his formal education. Charles' grandfather, Erasmus Darwin, in 1794 and 1796, and Jean-Baptiste de Lamarck, in 1801 and 1809, had both proposed that different types of animals had evolved from one another, but their evolutionary ideas were firmly rejected by the British scientific establishment. The Church of England had an enormous influence on British science. At the two English Universities, Oxford and Cambridge, all professors were required to be ordained Anglican clergy, and all students were required to read theology and moral philosophy. Graduates were required to confirm that they were members of the Anglican faith and believed in all of its tenets. Consequently, most British scientists studied the world from the perspective of natural theology: the belief that the world had been created and designed by God. It was akin to heresy to question this 'fact', so what led Darwin to question this prevailing scientific and religious dogma?

## 1.1 DARWIN'S EARLY LIFE AND EDUCATION

Charles Darwin, born in 1809, was the fifth of six children of the wealthy physician Robert Darwin and his wife, Susannah. By the time he went to day school at the age of eight, he had already developed an interest in nature, identifying plants, and collecting shells, minerals and bird eggs. He took up shooting when he was 15 and revelled in hunting birds, but he was not doing well at school. His father, concerned about his lack of direction and ambition, decided that Charles should study medicine at Edinburgh University (1825–7) when he was only 16 years old.

Things did not work out as planned. Charles' interest in medicine slowly died: his medical lectures were incredibly dull, he detested the weekly dissection of human cadavers and he was horrified by surgical operations. He lacked the willpower and ambition to succeed. He stopped studying medicine at the end of his first year and spent much of his second year collecting and studying marine invertebrates.

When Darwin returned home, his father was outraged with his recalcitrant son and decided that Charles should become a clergyman in the Church of England. This was a sensible choice because vicars with interests in natural history were common. Charles dutifully agreed, and over the next 4 years (1828–31) he read for an ordinary Arts degree at Cambridge University, the first step in becoming an ordained clergyman. True to form, he soon began to neglect his

studies. He joined a craze of collecting beetles, enjoyed himself with friends, shooting birds and drinking, and playing cards with them most evenings. Not surprisingly, his tutor warned him that he would probably fail his exams. He began to study in earnest, fearing his father's reaction if he failed again. To his great relief, he passed his preliminary exam in 1830 and then his final exams in January 1831, ranking tenth out of the 178 who passed. This pleased his father; it appeared that Charles had a future career as a parson.

### 1.1.1 A Change of Direction

The longer Charles stayed at university, the stronger his interest in the natural sciences became. Surprisingly, he took few classes in science, but his interest developed as he read and discussed various issues with some of the great scientists of the period. The fact that they took notice of his interest indicated that he was no ordinary student. His intellectual development during university education was heavily influenced by three scientists.

During Darwin's second year at Edinburgh, he became acquainted with Dr Robert Grant because of their mutual interest in marine invertebrates. Grant collected and kept alive many curious marine invertebrates (including sponges, sea mats and sea pens) and was particularly interested in their early development. He had observed that they possessed similar free-swimming ciliated larvae and was convinced that his comparative studies showed possible evolutionary links between the various animal phyla and also between the animal and plant kingdoms. Grant was a radical freethinker and an ardent evolutionist. They discussed the evolutionary ideas of Lamarck and Erasmus Darwin, which Darwin had read during his time at Edinburgh. Although Darwin remained noncommittal about evolution, he was excited by Grant's work and scientific approach. He helped Grant with his observations and made some discoveries of his own, but his excitement was not shared by Grant, who objected to him intruding into his own area of research. Darwin became thoroughly disenchanted with him and lost interest. Nevertheless, Grant trained Darwin in a scientific approach to natural history and planted some dormant seeds about evolution in Darwin's mind.

During Darwin's second year at Cambridge, the Reverend John Stevens Henslow, Professor of Botany, became his friend and mentor and played a pivotal role in Darwin's intellectual development over the next few years. He introduced Darwin to other eminent scientists, including the Reverends Adam Sedgwick, Professor of Geology, and William Whewell, Professor of Mineralogy. They all investigated the world from the perspective of natural theology, and to Darwin there seemed to be no conflict between science and theology. He became completely indoctrinated after reading William Paley's *Natural Theology*, which argued that we live in a world designed by God and that a study of the natural world revealed the existence of God.

After Darwin's graduation, Henslow suggested that he read Alexander von Humboldt's account of his travels to South America. Darwin was entranced by his natural history observations, particularly those on Tenerife in the Canary Islands. He persuaded his father to fund an expedition to Tenerife with a few friends as a reward for completing his degree. His task was to

be the expedition's geologist, and Henslow taught him how to make field observations using technical instruments.

Henslow arranged for the Reverend Adam Sedgwick, one of the best geologists in Britain, to take Darwin on a field trip to North Wales that summer to teach him some field skills. Darwin became entranced by the subject as Sedgwick taught him how to interpret rock formations and explained why it was important to base it on theory. Crucially, Sedgwick gave Darwin confidence in his ability to make geological observations. He would soon put this newfound confidence to good use.

Upon his return home, he found a letter from Henslow who had been asked to recommend a young gentleman, interested in science and natural history, to act as a companion for Captain Robert FitzRoy of HMS *Beagle*. Henslow thought Darwin would be ideal for the unpaid job, noting that the long voyage would provide ample opportunity to conduct natural history studies. Darwin's father said no, it was time for Charles to be ordained. Fortunately, Charles' uncle, Josiah Wedgewood, persuaded Darwin's father to change his mind. FitzRoy interviewed Darwin in London and it was agreed that Darwin would join the ship.

Before dealing with Darwin's experiences on the *Beagle*, we will summarize his understanding of geology because it would have a major impact on how Darwin viewed the natural history of the world.

## 1.2 THE EARTH'S CRUST: UNIFORMITARIAN AND CATASTROPHIST THEORIES

As scientists began to examine the Earth's crust, they found that most of the rock had been laid down by sedimentary processes in a series of strata. Each rock stratum was characterized by different fossilized plants and animals, most of which were extinct. It took practice and skill to identify the various strata, but over time it was recognized that there was some regularity in their sequence, and there was speculation that the same overall sequence of rocks existed throughout the world. The complete sequence was not found in any one locality, so sequences from different localities were combined to determine the overall sequence (Figure 1.1). As the overall sequence of strata and their embedded fossils became clearer, it became possible to see whether organisms had progressively changed during the Earth's history. During the eighteenth century, two theories were developed to explain how the Earth's crust had been formed.

The theory of uniformitarianism was originally proposed by James Hutton in 1785 and published in 1788 and 1795. He believed that the Earth was extremely old and that its crust had been and was still being formed by an endless cycle of subsidence and sedimentation followed by uplifting and erosion. The fossil record showed that organisms became extinct and were replaced, but it was not clear how. He believed that there was no progression in the fossil record. His publications were extremely long and confusing to read, and so his views were not very popular. However, the theory was persuasively reargued by Charles Lyell in his three-volume book, *Principles of Geology* (1830–3). Lyell argued that the Earth must be very old

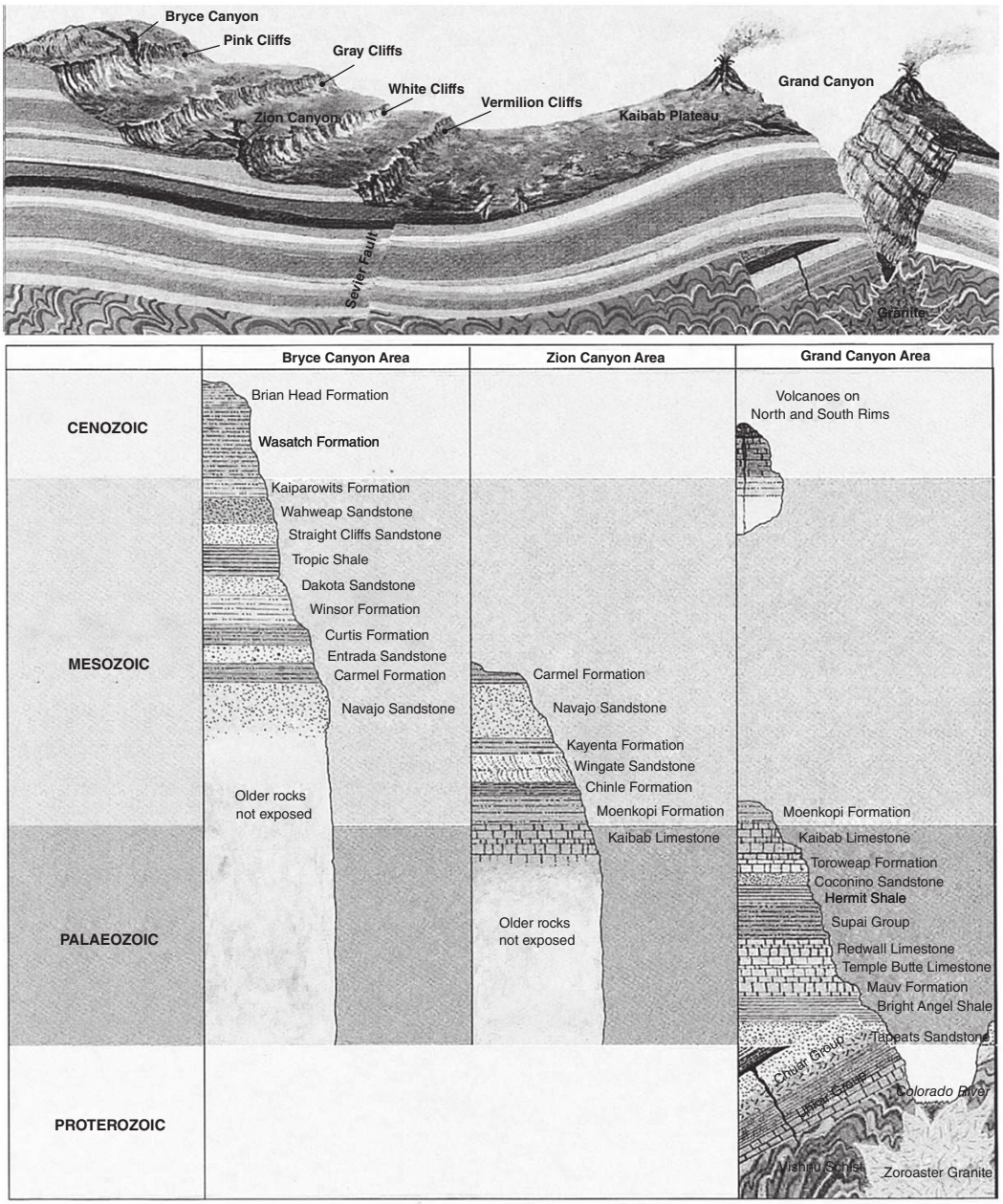


**Figure 1.1** Geology of Bryce Canyon, Zion Canyon and Grand Canyon, USA, showing the sequence of rock strata and their relationship to the major geological eras. The exposed sequence is approximately 2.1 km in depth: 1500 m at the grand Canyon and 300 m at each of the other two localities. (Modified from Wise 1998. Copyright © 1998. Reprinted by permission of American Scientist and the artist, D. W. Miller.)

because the accumulated strata of sedimentary rocks had a depth of a few kilometres and sedimentation rates were low. He also showed how one could observe the processes of subsidence and uplifting. He did not explain how extinct species were replaced with new species in the fossil record. However, he firmly rejected that it involved transmutation (evolution) of species by maintaining that there was no progression in the fossil record.

In contrast, the catastrophist theory of Georges Cuvier, published in the first two decades of the nineteenth century, proposed that sedimentary rocks had been laid down intermittently as a result of cataclysmic forces, rather than continuously. Consequently, he thought that the world was relatively young, perhaps just a few million years old. There was a progression in the fossil record in the sense that the fossils in the more recent deposits were more similar to present-day biota than the fossils in deeper deposits. However, he vehemently opposed the evolutionary ideas of Lamarck because he saw no gradual changes between species, and scrupulously avoided mixing science with his religious views. Consequently, it was rather unfortunate that Robert Jameson translated his work into English, putting a biblical slant on the theory: fossils were the result of a series of catastrophes (floods) sent by God, who then replaced the extinct organisms with new species, and the world was only a few thousand years old. This revised form of Cuvier's theory was particularly popular in England when Darwin received his education. Some of the general beliefs of the two camps at the time of Darwin are outlined in Table 1.1.

### 1.2.1 Darwin's Geological Education

Darwin was taught the catastrophist theory by Robert Jameson at Edinburgh, and then by Professor Sedgwick during their week-long field trip to North Wales. Sedgwick was scathing about Lyell's uniformitarian theory, in particular Lyell's assertion that there was no progression in the fossil record. Darwin was given the first volume of Lyell's *Principles of Geology* by Captain FitzRoy just prior to the *Beagle* 's voyage (the other two volumes were sent to him during the voyage). Consequently, he learned the principles of uniformitarianism by reading. Over the course of the voyage, he adopted most of the uniformitarian theory to interpret the Earth's crust, but agreed with Sedgwick that there was progression in the fossil record.

Darwin's geological interest influenced his thinking in two important ways. First, it made him consider the history of life on Earth on a worldwide scale. Secondly, he developed the skills to explain how a landform or rock formation had formed over time, and later these skills helped him to theorize how organisms changed over time.

## 1.3 THE VOYAGE OF THE *BEAGLE* (1831–1836)

Darwin had the interest and training to become a good naturalist, having been mentored by some gifted scientists in the areas of marine invertebrates, botany and geology. However, he

Table 1.1 **Some components of uniformitarian and catastrophist views at the time of Darwin. Darwin would eventually adopt the uniformitarian views 1 and 2, and the naturalistic aspects of 4, but would adopt the catastrophist view of 3**

| Phenomenon or process | Uniformitarian view | Catastrophist view |
|---|---|---|
| 1. Age of Earth | Extremely old; measured in many millions of years | Not very old; measured in thousands of years |
| 2. Geological processes of rock formation | The causes of volcanic action, uplifting, erosion, sedimentation and subsidence operate at all times with the same intensity as the present | Different causes operated in the early history of the Earth when irregular cataclysmic events laid down rocks; now little change is occurring |
| 3. Directional change in fossil records? | Rejected; the world is in a steady state, but there may be cyclical changes over time | Yes; progressive change with recent fossils more like living forms than older fossils |
| 4. Theological aspects | (a) Naturalistic; life may have been created by God but now changes are always the result of secondary causes<br>(b) Mainly naturalistic, but there may be occasional divine intervention | Always allows for direct divine intervention |

After Mayr (1982).

developed very conventional views at Cambridge and was a convinced creationist, and he interpreted the world's natural history from the perspective of natural theology.

After two false starts, the *Beagle* left Plymouth on 27 December 1831 on a voyage that would last almost 5 years. They sailed to the Cape Verde Islands, located approximately 720 km off North Africa, landing on the volcanic outcrop of St Jago (Santiago). Darwin had a good eye for detail, noticing a white band of compressed seashells and coral embedded in the volcanic lava about 14 m above sea level for miles along the coast. He reasoned that lava had flowed over the sea bed and then been raised above the sea. The band was not distorted and so it seemed to conform to Lyell's uniformitarian theory of gradual uplifting rather than representing a violent, cataclysmic upheaval. He was so excited by this observation that he made geology the main focus of his studies throughout the *Beagle* 's voyage; his biological observations were secondary. He wrote 1384 pages on geology and just 368 pages on zoology during the voyage (Grant and Estes 2009).

Sailing on to South America, he settled into the ship's routine and became disciplined in his work. He read widely, collected and carefully labelled all his specimens, and made copious notes on all he observed. He wrote to friends and relatives, particularly his sister, Caroline, and Professor Henslow. He got on well with FitzRoy and the rest of the ship's crew. Being the


**Figure 1.2** Map of South America showing some of the places that Darwin visited between 28 February 1832 and 6 September 1835 and some of the topics of his observations (see text).

captain's companion meant that any of Darwin's wishes were attended to by the rest of the crew, which was a great help as he carried out his scientific work.

They reached Bahia (Salvador) in north-eastern Brazil on 28 February 1832. FitzRoy and his crew would spend the next 42 months charting the coastline of the southern half of the continent. This allowed Darwin time to collect specimens at various landings along the coast and make more extensive inland journeys into Uruguay, Argentina and Chile (Figure 1.2). In fact, Darwin was to spend more time ashore than on the ship during the voyage, spending 39 months on land and only 18 months at sea (Browne 1995). While ashore, he worked like a

man possessed, making his observations and collections quickly because he was seldom sure when the *Beagle* would move on. The intensive fieldwork on land was complemented by periods on the ship where he could review his work and carefully annotate and pack his collections of plants, animals, fossils and rocks, before planning his next adventure ashore.

Darwin made a number of significant observations during his time in South America. He noted that closely related organisms replaced one another from north to south over the continent and also on either side of the Andes, but often assumed they were different varieties of the same species. When the *Beagle* visited the Falkland Islands, he learned that the endemic Falkland Island fox (*Dusicyon australis*) differed in size and colour between the two main islands, and confirmed this by collecting one specimen from the West Island and three from the East Island. He also collected a number of fossils in Argentina of giant extinct Pleistocene mammals, which appeared to be related to some of the present-day forms living in South America.

He continued to interpret the geology of the various areas from the uniformitarian viewpoint. Sailing along the Chilean coast in January 1835, he witnessed the violent eruption of the Orsono volcano. A month later, he experienced a severe earthquake in the town of Valdivia. He connected the two events, suggesting that volcanic activity caused the earthquake. The inhabitants told him it was as severe as the one of 1822, and it was clear that earthquakes were common in the area. They sailed 200 miles north to the city of Concepción, which had been virtually destroyed. In that area, he noticed that beaches had been raised between 1 and 4 m above the previous sea level. During his transit of the Andes, from Santiago in Chile to Mendoza in Argentina, Darwin observed deposits of sea shells as high as 3700 m and the remains of a silicified coastal forest on the Argentinean side at 2000 m. To Darwin, the reason was obvious: a series of earthquakes over an immense period of time had combined to elevate the land, increment by increment, on a continental scale. He was observing that the Earth was not static and that a series of small changes could combine to produce a major change.

### 1.3.1 On to the Galápagos Islands

The *Beagle* finally left South America on 6 September 1835, bound for the Galápagos, a group of 14 islands and numerous islets of volcanic origin, straddling the equator, approximately 1000 km off the west coast of South America. Darwin knew from the journals of previous visitors that the islands were populated by a rich variety of species found nowhere else, which was consistent with Lyell's theory that islands isolated from the mainland would have unique species created by God. However, being a creationist, he never imagined that species would vary significantly between the islands and so generally collected few specimens and in most cases did not record their island localities except for plants.

They reached the islands (Figure 1.3) on 15 September and Darwin visited and made collections on four of them over the next 5 weeks, noting that the volcanic islands were geologically young (Grant and Estes 2009). Many of the nondescript plants were in flower, and Darwin made large collections of them, separating them by island. He was astonished at the tameness of the animals; they were totally unafraid of humans and could easily be collected.