1 Biological Evolution

The Beginnings of the Story

This book is about scientific ideas and the evidence needed to exemplify and support the theory of evolution. It explores current biological diversity and asks the question how all the various life forms on our planet came about. Why do we have so many different species, and what processes cause biological change over geological time?

The Development of Evolution as a Science

An evolutionary narrative is often thought to begin with Charles Darwin, but historically evolutionary ideas have been with us for at least two millennia. Classical Greek philosophers such as Theophrastus (371 BC–287 BC) and Aristotle (384 BC–322 BC) were keen naturalists providing some of the first direct observations and empirical accounts of the natural world. And just as Theophrastus was studying plants (he was the first to systematically group plants) in lagoons nearby, Aristotle was contemplating the essential differences between plants and animals. Aristotle was interested in boundaries between species; not that he was presupposing speciation – for Aristotle believed in the 'Ladder of Life', a fixity of animal forms, moving from worms and simple creatures, through stages, to fish etcetera with Man at the top superseded only by the Gods. But Aristotle was prescient in that he saw nature as 'changeable' (in the manner rivers change the landscape over time) and 'graded' (as animals vary both from one another and from other animals), but species he believed were immutable and unchanging. Regarding the origins of life, he disagreed with both Empedocles (490 BC–430 BC) who had earlier suggested that life arose through chance assemblages in some early primordial soup and Anaximander (610 BC–546 BC) who speculated that all life arose in water. Charles Darwin himself thought Aristotle to be a proto evolutionist (not surprising as he was an acute observer of nature and keen to remove mysticism from the debate). But he was mistaken on this count due to an error made by a local town clerk who had mistranslated Aristotle's 'physics'. Aristotle was not supporting any species change but rebutting the argument put forward earlier by Empedocles. Darwin was not a classicist!

Later, as the classical texts of the Middle Ages gave way to the European Renaissance (fourteenth to seventeenth centuries) and then to the 'Age of Enlightenment' (eighteenth century), a profound shift in thinking was taking place. Encouraged by voyages of discovery around the world, wealthy individuals began to collect attractive and interesting specimens and display these within their 'cabinets of curiosities'. Notably, the collection of Sir Hans Sloane became the basis of the collections now contained within the British Museum. Similarly, improvements in the technology of observation (telescopes and microscopes) together with developments in mass communication printing provided a further impetus for human *intellectual* voyages of discovery and with it the popularisation of science.

The process of collecting, cataloguing and displaying specimens eventually developed into a much more systematic endeavour. Collections of minerals and biological specimens were described and organised to uncover underlying organising principles. Explanations were also sought for the observations now being made. In truth, a *scientific revolution* was taking place where myth was to be replaced by theory, conjecture with evidence and simple curiosity with systematic investigation. Francis Bacon's empirical approach led ultimately to 'new ways of knowing'. Classical thinkers of the Middle Ages had been overtaken by what is referred to as the natural philosophers of the seventeenth and eighteenth centuries. Natural philosophy was a thoughtful and systematic study of the natural world. Subsequently the 'scientist' (a new term coined by Thomas Whewell in the mid-nineteenth century) would be associated with a practice involving hypothesis formation and rigorous testing of ideas. Charles Darwin (1809–1882) of course was an inspired scientist.

Darwin's observations on biological complexity were systematic and his explanation of how this complexity arose took the form of a carefully reasoned argument. He used *evidence* to support his claims; evidence that could be checked and replicated by the wider scientific community. The earlier world views of Newton, Leibniz and Hobbes provided a rigid, almost clockwork view of the world, whereas in the mid-nineteenth century a more historical thinking prevailed. Examples of this new mind set include political thinkers such as Marx and Hegel who employed a dynamic and historical view of world events. Their thinking relates to a view of the world changing not the fixed view of their predecessors. Darwin's half-cousin Francis Galton (1822–1911) had already explored increases in human population and its potential consequences while his grandfather, Erasmus Darwin (1731–1802), a prominent poet and biologist, alluded to a process of evolution and biological change in two of his long poems.

Contemporary with Charles Darwin, nineteenth century geologists such as Charles Lyell (1797–1875) and Adam Sedgewick (1785–1873) emphasised that the planet too was not a fixed entity but had undergone profound change 'throughout the long expanse of history'. Limestone rock strata scattered throughout the British Isles demonstrated that these locations were once shallow seas with teeming marine life and not the Southern uplands and Yorkshire dales scenery that we see now.

The seventeenth-century image of an unmoving, static world was slowly being replaced by a more dynamic perspective. In the early nineteenth century, following the French revolution, there was a break with the more 'classical' approach. And proponents such as Lamarck and Saint-Hilaire challenged the (by now becoming outdated notion) of the 'fixity of species'. This mind set affected Charles Darwin in his attempts to understand biological complexity. In 1859 Darwin published his *On the Origin of*

Species by Means of Natural Selection together with his own description of biological change – 'descent with modification'. Darwin also included a means by which these events could be explained, 'natural selection'.

Charles Darwin was both a product of and contributor to this new way of thinking (or paradigm shift as Thomas Kuhn [1996] later called it).

As 'natural philosophy' gave way to 'natural science', a more rigorous, experimental approach or *scientific method* began to define scientific endeavour. Individuals such as Francis Bacon, 1561–1626 (philosopher, parliamentarian and scientist), Michael Faraday, 1791–1867 (the most eminent experimental chemist of his day) and William Whewell, 1794–1866 (President of the Geological Society) exemplified this approach. Whewell was a source of inspiration for Charles Darwin. Later that century biological science (the term 'biology' was coined in 1800 in an obscure German footnote) developed concepts such as the cell theory, principles of homeostatic control and impressive advances in animal and plant physiology through rigorous observation and experimentation. Biological evolution was slightly different, however. It did not at that time employ experimentation, but rather a systematic collection of evidence to answer questions together with an acutely reasoned argument. Following its synthesis with twentieth-century genetics, biological evolution rapidly became the cornerstone of biology; as Theodosius Dobzhansky famously says in his 1973 essay, 'Nothing in biology makes sense except in the light of evolution'.

The history of evolution as an idea has had a long gestation, at times controversial, continuing in the twentieth century with development of evolutionary genetics. Genomics, a subject that did not exist before the twenty-first century, heralds a new chapter in our understanding.

The Years before Publication of *Origin of Species*

The year 1830, like many of those in the previous four decades, had been a turbulent one in French history. There had been revolution in Paris and the King was forced to abdicate. So when a friend called on the German poet Johann Wolfgang von Goethe in Weimar, he was prepared to agree that a great explosion had taken place in European affairs. But he was flabbergasted to discover that Goethe was referring not to French political upsets but to an acrimonious debate between two of the most noted comparative anatomists of the day, Georges Cuvier and Étienne Geoffroy Saint-Hilaire. For Goethe too was a considerable anatomist and appreciated the significance of the event.

The debate between the two former friends and current colleagues was not about evolution. The question, debated before a noisy audience in the premises of the Académie de Sciences in Paris, was about the correct way to interpret anatomical resemblances between different species of animals. To Cuvier, identity of structure meant identity of function; an animal, any animal, remained alive because it functioned like a well-coordinated machine. Every characteristic, internal and external, was created to serve its current way of life – no further explanation was required.

Geoffroy Saint-Hilaire agreed that functional anatomy was a worthy study, that anatomical features subserved a vital function. But to him functional anatomy was not a complete explanation. Quite apart from their function, the anatomical features suggested variation on an underlying plan. The proper task of 'philosophical anatomy' was to elucidate that plan – what, apart from their various ways of life, did all vertebrate animals have in common: could one reconstruct a basic vertebrate animal?

Over the years, Geoffroy Saint-Hilaire had attempted to implement this programme to the increasing irritation of Cuvier, but when Geoffroy Saint-Hilaire suggested that invertebrate animals, such as insects, lobsters and molluscs, also shared the same plans as vertebrates, open disagreement broke out.

Cuvier was a student of **adaptation** (that is the machine-like coordination of animal parts and the 'fit' of the whole animal to its environment), while Geoffroy was a student of **homology** (resemblances between species reflecting a common plan). Homology does not necessarily imply common ancestry, but it was due to the genius of Charles Darwin, through his *Origin of Species*, published in 1859, that both aspects of comparative biology were combined into a successful theory of evolution (Darwin, 1859).

So, What Is Evolution?

What do we mean by the term 'evolution'? There are several different interpretations. Originally evolution implied some sort of unfolding, like the opening of a flower (Latin = *evolutio*: an unrolling), but latterly it has acquired a wider meaning, implying a general process of change. Darwin's phrase 'descent with modification' accurately describes the process of biological change. This book is about biological (or organic) evolution – a system of theories put forward to explain both diversity and the relationships between different types of living thing.

If we wish to understand the theory of evolution, we need to consider the answer through a series of subordinate questions.

A theory is an established idea or organising principle used to explain a body of information. It covers a wide range of facts and forms and is said to possess both explanatory and predictive power. A theory is more than just mere speculation; a theory is a precise conceptual framework that supports the data. The theory of evolution by natural selection is a powerful explanatory tool. It makes predictions such as the existence of genetic variation (otherwise evolution could not happen) and patterns of speciation found in fossils (as seen in rock strata). It is supported by evidence from a range of sources, palaeontological, genetic, anatomical, behavioural and biogeographical; it even supports what Coyne (2009, in his book *Why Evolution Is True*) refers to as retrodictions, facts and data that 'make sense only in the light of the theory of evolution'.

In the construction of any theory there are two component parts:

1. the data to be explained (in philosophical terms we call this the **explanandum**) *and*
2. the theory or the explanation itself (the **explanans**).

So, what does evolution attempt to explain, what is its explanandum? Several answers have been offered to this question but there is a difference of emphasis among experts. Here are some possibilities.

The explanandum – evolution attempts to explain:

1. Why there are a staggering number of different types of living things alive on Earth today (some 30 million possible species)?
2. How it is possible to classify organisms in a hierarchical grouping, in Darwin's phrase 'in groups within groups'. Is there something real about biological classification? Does it suggest genuine relationships?
3. How the fossil record chronicles the biota – a sum of all life forms over time.
4. Why organisms appear to be particularly well adapted to their environment.

From these four questions above stem different schools of evolutionary research. And in order to answer the four questions above we can suggest,

The explanans

(In the same order as the questions were posed these are):

1. Those wishing to explain biodiversity and the 'staggering number of different types of living things' are likely to be interested in speciation; the division, in time, of one species into two or more and the mechanisms by which this occurs.
2. Taxonomists, interested in the classification and the hierarchical grouping of organisms, are concerned not only with constructing classifications but also with reconstructing the history of life (to which others including palaeontologists and molecular biologists also contribute).
3. Palaeontologists study fossils and explore life forms in different geological periods and can comment upon rates of evolution.
4. It is probable that most evolutionary biologists are preoccupied with the origin of adaptations – the reasons why adaptation is adequate rather than perfect and whether all the characteristics of organisms should be explained by natural selection.

To answer our question therefore (so, what is evolution?) we might say that evolution is a process of biological change – a theory that attempts to explain biodiversity together with an explanation in terms of differential reproductive success.

In addition to these lines of research there is a newly important branch of evolutionary theory, that of the evolution of development (or '**Evo-Devo**' as it is known to its practitioners). For many reasons current evolutionary ideas do not fully explain how the development of individual organisms evolved. But in recent years there has been an explosion of knowledge in the role of the genome in animal development and the application of this knowledge to evolutionary problems.

It should be clear from what has been said so far that not only are there several sets of data that can be explained by evolutionary theory, but there are also several types of explanation. Together these represent the multifaceted discipline of evolutionary biology.

Change and Species Formation

In studying evolution, one is inevitably exploring biological change, the formation of new species together with the extinguishing of others.

But change and dynamism appear to be features of the world in which we live. Over its four billion or so year history the Earth has undergone profound change in terms of its geology, its atmosphere, the landscape, the climate and its constituent biota. Indeed, change in the abiotic (non-living) world often precedes or even dictates change in the biotic. Further proof, if needed, that all aspects of the natural world are interwoven

Perhaps a more cogent argument arises when scientists look beyond our own planet for signs of life. This new science of **exobiology** (also referred to as Astrobiology) needs to consider how extraterrestrial life might present itself. It presumably will need to secure an energy source and it will need to carry out various processes including coordinated activity and reproduction, but importantly (for the argument presented here) life will be seen to *evolve*. Evolution, or hereditable biological change over time, is now generally seen as one of the handful or so major characteristics of living things. Professor Gerald Joyce at the Salk Institute in the United States is an astrobiologist and an expert in the field of in vitro evolution (recreating the biomolecules of early life). Perhaps he has provided us with the best definition of life:

A self-sustaining chemical system capable of Darwinian evolution

One of Charles Darwin's greatest achievements is to suggest a mechanism for the observed biological change over time – and that is **natural selection**. His theory of natural selection is both simple and elegant. Yet it is not reducible to the conventional rules of physics and chemistry. In this respect the biological sciences may be considered as inhabiting two epistemological 'spaces'; on the one hand, the sciences of genetics, physiology, medicine and neuroscience (disciplines that are reducible to physical laws) and on the other, behaviour, community ecology and evolution which are not. Evolution it is argued belongs to this latter branch of whole organism biology where possible **emergent properties** arise and different research paradigms are needed.

Natural History and Classification

Organising our knowledge of the natural world and naming objects is a characteristic of human societies. Allied to this peculiarly human activity is the search for order and a desire to explain the world as it appears to us. The biological discipline dealing with the classification or grouping of organisms is known as **taxonomy**; this forms part of a more general speciality known as **systematics** (a study of the types and diversity of organisms). Confusingly, some biologists – mostly botanists – refer to a classification as a 'taxonomy'.

Nomenclature (the naming of organisms) is a highly prescribed business. Before organisms can be classified, it is essential to have an agreed naming system.

This applies not only to the naming of species but because classification of organisms is always expressed as a hierarchical structure ('groups within groups'), there must also be rules about the naming of higher ranks. The whole system is policed by various International Commissions, most notably one for Zoology and one for Botany. Until the early 1960s methods for classifying organisms were ill-defined despite the fact that systematists claimed they were producing 'evolutionary classifications'. Methods were largely intuitive. But then there arose not one, but two methods of classification, both claiming to be uniquely objective. They are known as **phenetics** (originally called 'numerical taxonomy') and **cladistics**. Their practitioners often became bitter rivals, while both poured scorn on the easy-going and intuitive evolutionary taxonomists. The dust has now settled, and methods related to both phenetics and cladistics are in use for different taxonomic purposes.

Natural history as an academic enterprise has a long and distinguished history in the United Kingdom. The oldest biological society in the world, The Linnaean Society of London, was founded in 1788 to honour the botanist (Carl Linnaeus), his works and his legacy – his efforts in systematising the living world.

Elsewhere in Britain natural history became more organised with the standard works on identification produced. These included John Ray's *Catalogus Plantarum Angliae* and Martin Lister's *Historiae Animalium Angliae*, both published in 1678. It was in Plant Science or Botany that the discipline of natural history was first formalised. This is not surprising given the relevance of plants and plant products to the early study of medicine. The Society of Apothecaries based in London not only initiated the famous Physic garden at Chelsea but also promoted field trips into the local countryside. The earliest of these excursions was in May 1620 (the date of the voyage of the Mayflower to the New World). The Aurelians, as the lepidopterists (butterfly hunters) of the day like to call themselves, were another early specialist society.

In the mid-eighteenth century, natural history was more of a fashionable subject than a scientific one. It was perhaps the Victorians in the nineteenth century who forged natural philosophy to become the precursor of the more academic disciplines of Biology and Geology. Charles Darwin's seminal work (*Origin of Species*) in 1859 interestingly provided a unifying theory for both the plant and animal sciences.

In 1866 a Chair in Zoology and Comparative Anatomy was created at Cambridge University, and the Education Act of 1870 brought a breakthrough in the teaching of Elementary Science. Indeed, there was such a shortage of teachers that the eminent zoologist Thomas Henry Huxley was asked by the government to set about providing a 'crash course' for teachers in botany and zoology.

There are many clubs, associations and learned societies that have contributed to our knowledge of the natural world. Both amateur and professional biologists are employed in the study of flora and fauna, local and national. It is upon this knowledge base, prepared by the natural historian, that the modern disciplines of taxonomy, ecology, ethology and (ultimately) evolutionary biology are founded.

An early example of a natural historian exploring evolutionary theory is that provided by Canon Henry Baker Tristram, born in 1822. 'The great Gun of Durham', as he was known, was an authority on birds in Durham, Northumberland and Palestine. As president of the British Association and Canon of Durham University's College, Tristram (described as 'a close observer and diligent collector') was one of the first people to accept, in print, Darwin's theory of evolution. This he did in an article in 1859 (less than one year after the publication of Origin of Species) in the '*Ornithology of North Africa*':

> Writing with a series of about 100 Larks of various species from the Sahara before me, I cannot help feeling convinced of the truth of the views set forth by Messrs. Darwin and Wallace in their communication to the Linnaean Society . . . it is hardly possible I should think to illustrate this theory better than by the Larks and Chats of North Africa. (*The Ibis*, Volume 1, 1859)

Tristram then proceeds to discuss 'gradual modifications of colouration and anatomical structure' where 'in the struggle for life . . . a very slight change for the better . . . would give the variety that possessed it a decided advantage over the typical or other forms of the species' (Tristram, 1859: pp. 429–430). These views were also expressed in his Presidential address to the Tyneside Naturalists Field Club. This was a brave act coming from an Anglican churchman, but indicative of the growing acceptance of evolutionary theory.

Exploring the Development and Progress of Life on Earth

Reconstructing the history of life is usually regarded as the task of evolutionary biologists in general and palaeontologists, whose discipline takes in aspects of both biology and geology. Essentially, palaeontologists collect and prepare (that is clean up) fossils and then try to make valid statements about the anatomy, ecology and even behaviour of the organisms their specimens represent. Most palaeontologists are taxonomists and attempt to say something about the historical significance of their fossils by including them in a classification that also embraces living species.

A further category of evolutionary biology is that of the 'adaptationists' (there does not seem to be a suitable collective noun). Many are particularly interested in the evolution of behaviour (including human behaviour) and term themselves 'behavioural ecologists' or 'sociobiologists'. Their principal preoccupation is with testing or applying Darwin's theory of natural selection to the anatomy, behaviour and ecology of animals.

One thing Darwin could not do was provide a valid account of heredity – the mechanisms by which the characteristics of one generation are passed on to succeeding generations. No one could blame him for that as the work of Gregor Mendel (and hence the beginning of modern genetics) was only 'rediscovered' in the year 1900. At first a number of scientists believed that Mendel's conclusions refuted Darwin's theory of natural selection. The two theories were happily reconciled in the late 1930s and early 1940s in the so-called 'Synthetic Theory' of evolution. This new synthesis (the **Synthetic Theory** or **Modern Synthesis**) proposed that variation was brought about by random events and that populations evolve by means of changes in gene frequency (e.g. those brought about by natural selection). The Synthetic Theory is sometimes called 'Neo-Darwinism', the revival of an older term with a somewhat different meaning.

Evolutionary change can occur both above and below the level of species. Genetic change within a population, or below the species level is referred to as microevolution (that is changes in gene frequencies, mutation etc.). It is possible to demonstrate microevolution. Macroevolution, on the other hand, is evolution above the species level, including speciation. Its phenotypic changes affect the lineage of organisms and the ultimate appearance of higher groups (for example, the evolution of insects and the appearance of land plants). Macroevolution takes place over a much larger time scale and its progress is inferred using various lines of evidence, fossil appearance, radiometric dating, chemical analysis and degrees of relatedness.

By the mid-1960s it became possible to study evolution at the molecular level. In studying proteins, it became apparent that there was a greater diversity of molecular form within populations than previously imagined. Techniques such as gel electrophoresis confirmed the amino acid sequences of these molecules, while rates of change led to the suggestion of the possibility of 'molecular clocks'. Motoo Kimura (1924–1994), a Japanese population biologist, hoped to combine the discipline of population genetics with the newly emerging molecular data. What emerged was a realisation that the observed variation within groups was too large to be explained simply by natural selection. He therefore proposed an alternative hypothesis, that of the **Neutral Theory of Evolution**. In this he postulated that molecular evolution was driven not necessarily by Darwinian natural selection but by random, non-adaptive changes within the genome.

Results of molecular studies have proved to be increasingly important in understanding the evolution of life on Earth, while the neutralist–selectionist debate has proved to be a useful focus for studies of molecular evolution.

To summarise, therefore, ***the Earth is a rationally ordered physical and biological system in which changes occur***.

In the mid-seventeenth century James Ussher, the archbishop of Armagh, stated that the Earth was created the night before Sunday 23 October in the year 4004 BC! He did this by carefully measuring biblical genealogies. By 1800, however, geologists had demonstrated that the Earth must be older (for instance by calculating the length of time it takes for an object with the mass of the Earth to cool down). And Darwin, like his mentor the geologist Charles Lyell, believed in the **Principle of Uniformitarianism** (an agreement that processes we see in the present day also occurred in pretty much the same way as they did in the past); both Darwin and Lyell believed in a continuous, gradual geological change. The continuity of geological events on Earth is mirrored by Darwin's thoughts on organic evolution – a classic expression of this Principle of Continuity.

Famously, in 1831 her Majesty's ship 'Beagle' sailed from Devonport with the young naturalist Charles Darwin on board. And, as we now know, studies on the habits of the cuckoo, extinct quadrupeds, distribution of land shells and birds of the Galapagos Archipelago all contributed to his landmark text *Origin of Species* some 30 years later.

The Galapagos Islands and Darwin's Finches: A Case Study

The Beagle's orders were to survey and map the coastline of southern South America, then, following the Galapagos visit, to sail west via Tahiti, New Zealand and Australia, making astronomical and other observations. Darwin's brief was, as guest naturalist, to study the geology and natural history. He landed home at Falmouth on 2 October 1836, nearly five years after the Beagle's departure. Darwin recorded that 'in July (1837) I opened my first notebook for facts in relation to the *Origin of Species*, about which I had long reflected, and never ceased working on for the next twenty years'. His great work on evolution, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, was not published until 1859.

The Galapagos Islands, over the many years since Darwin's visit, have acquired an almost mythical status in accounts of the development of his theory. Some popular myths have Darwin's conversion to 'transmutation' (i.e. evolutionary change) occurring suddenly during his five-week stay on the Galapagos, but there is no evidence of this other than an ambiguous note written as he prepared a catalogue of his bird specimens from previous ornithological notes, nine months after leaving the Galapagos. He was referring to the mockingbirds (*Mimus parvulus)* collected from four of the islands: the specimens from Chatham and Albemarle he says appear to be the same, but the other two are different. On each island each kind is *exclusively* found; habits of all are indistinguishable.

> When I see these islands in sight of each other, and possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure and filling the same place in Nature, I must suspect that they are only varieties. If there is the slightest foundation for these remarks the zoology of Archipelagos – will be well worth examining, for such facts would undermine the stability of Species.

Darwin had also been told by the English vice governor of the Galapagos that the giant tortoises (*Chelonoidis nigra*) differed consistently from island to island but took little notice and did not collect museum specimens of the tortoises while there. The only tortoises collected by anyone (except for two babies kept as pets) were eaten by the Beagle crew and the skulls thrown overboard! Indeed, because of their size, hardiness and longevity, the tortoise population on the islands would be decimated by pirates and whalers who embarked onto the islands for shelter and provisions. It is reckoned that more than 100 000 of these lumbering reptiles (the megafauna of the Galapagos) were removed by seafarers.

The Galapagos archipelago comprises 16 volcanic islands of differing ages with varying landscapes (Figure 1.1). The younger islands like Fernandina in the West are inhospitable with harsh, arid landscapes of volcanic ash and lava flows and little vegetation. The older islands like Santa Cruz to the East are clothed in vegetation and are the centre of the Galapagos' famed biodiversity. The oldest islands like Espanola, around 4 million years old, are sinking into the ocean with erosion reducing the landscape to a flattened coastal remnant. The significance of this is that the diversity in