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An Introduction
Mike Cassidy

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Biological evolution, the theory of natural selection and of common descent, is a triumph both of human reasoning and scientific undertaking. The biological discipline of evolution contains both a chronicle of human endeavour and the story of life on Earth. This book is concerned with living forms and how they developed from 'simple and unpromising beginnings'. It considers evolution as both process and product. The author, an experienced teacher and educator, employs a historical narrative, used to convey the idea of 'change with modification' and to emphasise the relevance of evolution to contemporary bioscience. Biological evolution has now become part of the scientific orthodoxy, and this accessible text will assist undergraduate students in the biological sciences within any ongoing debate.

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Preface

A textbook is more than a simple source account or provider of information. We live in an information age where factual description and scientific explanation are readily available on-line. And so, the textbook (particularly an introductory text such as this) should also convey ideas, stories, context and controversies as well as fulfilling its primary teaching role.

Inevitably, in discussing biological evolution, there will be overlap between academic disciplines (genomics, molecular biology, history of science, palaeontology, anthropology and zoology) but the outcome remains the same – evolution provides both a profound and true account of life on Earth. Evolution is an accepted fact supported by overwhelming evidence. Rules of scientific evidence apply here in the same way as they do in molecular, physical or chemical studies; and we can note that recent research into genomics and molecular phylogenetics is continuing to yield new insight into biological evolution. History though, if anything, teaches us not to be complacent; scientific principles can be re-examined, repurposed and redefined. It is my hope that this text will inspire the reader to explore further the intricacies of biological evolution and ultimately to understand the origins of ourselves and the world around us.

We learn effectively through stories. And the biological discipline of Evolution contains both a chronicle of human endeavour and the story of life on Earth. This book is concerned with living forms and how they developed from 'simple and unpromising beginnings'. It considers evolution as both process and product. An historical narrative is employed; used to convey how the idea of 'change with modification' developed and what evolution now means to contemporary bioscience. The topic of Evolution is taught in schools, colleges and universities (it has also been included in the UK National Curriculum for Primary schools) and its central role in the study of the Life Sciences is now well understood. Evolution of course provides a unifying theme, a scaffold on which to place our developing understanding of past and present biota.

In an age where students discuss the evolution of the cosmos or the evolution of the mobile phone it was thought appropriate here to use the more correct epithet, *Biological Evolution* as its title.

Biological evolution, the theory of natural selection and of common descent, is a triumph both of human reasoning and scientific endeavour. And although, for most of us, the story begins with Charles Darwin and Alfred Russel Wallace in the mid-

nineteenth century, the idea of biological change over time was not new. Through primitive animism and the later philosophies of the ancient world, the history of evolutionary thought takes in several millennia and several different world views. The Age of Enlightenment, including the Scientific Revolution of the seventeenth and eighteenth centuries, also had a profound influence on evolutionary thought.

Scientific advance may seem to appear rapidly in human history, but the reality is the 'fine tuning' of ideas and refinement of major concepts takes many generations. The same is true for biological evolution. The basic ideas of selection and modification were laid down by Darwin and Wallace, but over the subsequent 150 years or so new insight into both macro- and microevolutionary change has become evident. Not least of which are the syntheses of Evolution and Heredity together with Evolution and Development. The new sciences of genomics and bioinformatics are providing even further detail concerning the mechanism of change while advances in palaeontology, embryology, biogeography and geology yield yet more insight.

Through context (how and when ideas were first formed) and through argument and debate the text will both encourage exploration and provide an explanation for evolution. This book is intended as an introduction to the subject of biological evolution for the undergraduate student of biology (along with students of anthropology, psychology, genetics and allied professions). Its text is intended to be both comprehensive and detailed where necessary, but it is hoped that the narrative style and historical context will also appeal to anyone with an eye for a good story.

The book is structured in such a way as to introduce the main ideas initially and then explore details of mechanism ('how evolution occurs') and product ('what has evolution produced'). As far as possible, detailed mathematical accounts and complex chemistry have been omitted. For convenience, important technical terms are written in bold type while in-text citation and references have been kept to a minimum with both a 'References' and a 'Recommended Reading' section at the end of the book.

The book is arranged into 12 chapters. Early sections deal with a historical account of the major evolutionary figures and the evidence put forward to support their theories. The middle chapters look in detail at microevolutionary processes, while a 'macro' approach, the history, origins and progression of life on Earth, follow on. The final chapters on trends, debate and controversies explore recent advances in evolutionary science along with the cultural impact of biological evolution in the nineteenth, twentieth and twenty-first centuries. An analysis of this kind will inevitably explore the bigger issues of science and religion, communicating science and the misuse of scientific theory with evolution as its central theme.

Biological evolution has now become part of the scientific orthodoxy, but it is not, of course, without its detractors. It is hoped that this text will assist students within the on-going debate.

Acknowledgements

The book owes much to past students, friends, family and colleagues, in particular initial conversations with Dr Alec Panchen. My own thinking on the ideas and concepts of evolution has also developed profoundly through tutoring the next generation of biologists and biology teachers both at Warwick and Durham Universities.

I acknowledge, with gratitude, the help of staff at Cambridge University Press. Other colleagues have also assisted in reviewing chapters and allowing permission to use figures; their names (and my thanks) are found at the end of the book.

The completion of this book has been influenced of course by my family, for without them it would not have been possible. My wife and sons have been steadfast in their support; to Jacquelyn, Oscar and Athol for their assistance, perseverance and insight.

There are so many discerning books and inspiring communicators of evolutionary biology – I wouldn't know where to begin thanking them. But I do know that the scientific establishment is so much the better for their presence, and I hope that this text will assist the next generation of life scientists in promoting their own endeavours.

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

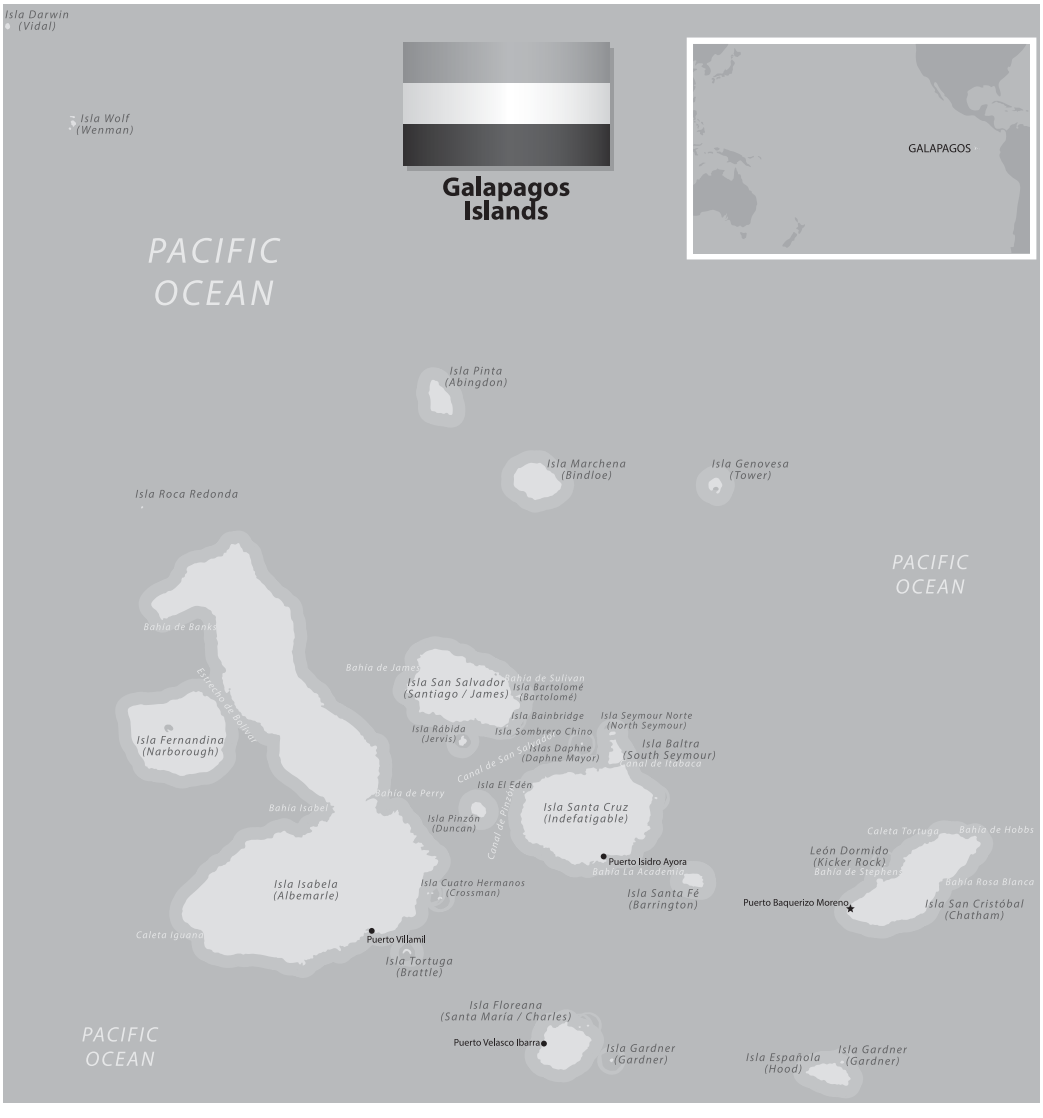


Figure 1.1 Sketch map of the Galapagos group of islands indicating the main sites referred to in the text. Credit vasosh / iStock / Getty Images Plus.

animal and plant life is mirrored by the diversity in habitat. And since emerging from the Pacific Ocean 'hot spot' around four and a half million years ago, organisms have populated these islands (arriving from the South American coast) providing a unique insight into adaptive radiation and the evolutionary process.

Radioactive dating has shown that the oldest islands are about 5 million years old, the youngest about half a million. The importance of the isolation of the Galapagos

from the South American mainland to the study of Darwin's finches is that it seems there was never any land connection between the two areas. If a common ancestral species of all Darwin's finches arrived from South America, it must have done so by chance – on floating mats of vegetation (which still detach themselves from coastal Ecuador today), by being blown off course or by other infrequent means. Thus, the founding population of the ancestral Galapagos finches presumably consisted of a small number of individual birds, with no doubt many casualties en route.

The environment of the Galapagos at first appears to the observer to be very inhospitable. Darwin's first impression of 'Chatham' was not favourable:

> Nothing could be less inviting than the first appearance. A broken field of black Basaltic lava is everywhere covered by a stunted brushwood which shows little signs of life. The dry and parched surface, having been heated by the noonday Sun, gave the air a close and sultry feeling, like that from a stove: we fancied even the bushes smelt unpleasantly. (*The Voyage of the Beagle*, 1845, Chapter XVII, 'Galapagos archipelago')

Similarly, David Lack (1910–1973) speaks of 'miles of dreary greyish brown thorn bush, in most parts dense, but sparser where there had been a more recent lava flow, and the ground still resembled a slag heap'. And yet the Galapagos have an enormously rich fauna, notably of birds, with many endemic species (unique to the island), and an equally rich marine life. A clue to the reason is the unique presence on the islands of a bird, whose group is more usually associated with Antarctica, the Galapagos penguin (*Spheniscus mendiculus*), the only equatorial penguin species. For islands on the equator the climate is often surprisingly cool and the sea conspicuously so. The explanation is the Humboldt Current which brings plankton-rich cold sea water up from the coast of Peru. The Galapagos climate is markedly seasonal. From roughly July to December, the Humboldt Current dominates, lowland air temperatures are cool and the rainfall slight. During this season, however, an inversion layer is created, and those islands with considerable highlands have those highland regions continuously wet, so they are covered in a rich green layer of plants. From January to June there is a warm, wet season in the lowlands with mostly clear skies but occasional heavy showers.

Before moving on to talk in detail about those finches, there is one more important point to be made. The birds are not quite unique to the Galapagos Islands. About 300 miles (500 km) southwest of Costa Rica in Central America, and nearly twice that distance northeast of the Galapagos, there is a small (47 km^2) island called Cocos (situated on the Cocos plate). Like the Galapagos, it is a volcanic island, but in other respects it is very different. There is no seasonality: the whole island experiences heavy rainfall throughout the year and consequently is covered by dense rain forest. There are only four resident land birds on Cocos Island. One of those is a 'Darwin's finch'!

The vice governor's comments about each island having its own type of tortoise extends also to other animals such as lava lizards, birds and various land snails. Each of these animals appears to have distinct forms unique to the different islands. Thus, one can postulate that the ancestral mainland 'castaways' that first arrived settled the

various islands and therein adapted to their own unique environmental circumstances. So, tortoises on islands with lush vegetation developed high domed shells to move more easily (tracks made by tortoises in this dense vegetation are easily seen from the air), whereas those tortoises living where vegetation is poor acquired long necks and peaks at the front of their shells to allow them to reach up to the dominant plant (in this case the prickly pear cactus). In a similar vein, land snails in arid areas developed a small mouth (to avoid excessive water loss) and long, conical shells, while those snails in wet areas acquired wide mouths and globular shells. All of this points to a phenotypic plasticity and a rapid radiation of within-species forms adapted to its own environment and providing the potential for future speciation. But perhaps the most iconic example of island radiation and brisk speciation is the finches.

Current reckoning is that there are 14 species of finches on the Galapagos. Darwin landed on four of the islands during his five-week stay (although he saw many more as the *Beagle* criss-crossed the archipelago). He collected specimens from the four islands but attached so little importance to inter-island variation that he mixed up the specimens from the first two islands (Chatham and Charles) that he visited. Darwin did not even recognise that all the species formed a closely related group until the *Beagle* specimens had been studied by the Zoological Society's ornithologist John Gould. Gould explained to Darwin that all the Galapagos finches in the Beagle collection formed a group of species more closely related to each other than to any other birds. Darwin's conversion to transmutation seems to have occurred soon after this explanatory meeting with Gould in mid-March 1837. Nevertheless, there is no account of the finches in the *Origin of Species* of 1859, although Darwin does say of them in the second edition of his account of the voyage (1845), 'One might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends'.

The Galapagos finches are small and mostly dull-coloured birds, little more than a sparrow size. The most striking feature of the whole group is the variation in the size and shape of the beak. The large ground finch *Geospiza magnirostris* has a massive parrot-like beak and a large heavily muscled head to support it. At the opposite extreme the little warbler finch, *Certhidae olivacera*, has a slender probing beak like that of a warbler! (Figure 1.2). Amazingly it took until the 1940s for general agreement that these beak shapes were adaptive, despite numerous early studies. This agreement resulted from the publication of an important book by David Lack, which popularised the phrase *Darwin's Finches* as its title (Lack, 1947).

The Finches

In the classification of organisms, the **species** is regarded as the fundamental taxonomic unit, and definitions of species (the 'species concept') have been a matter of vigorous debate since before Darwin's time. Thus, any evidence bearing on the origin of a new species (or better still a whole series of new species) would be cogent evidence for evolution. The species concept is discussed in Chapter 6, but in general terms species are groups of freely interbreeding individuals separated from other

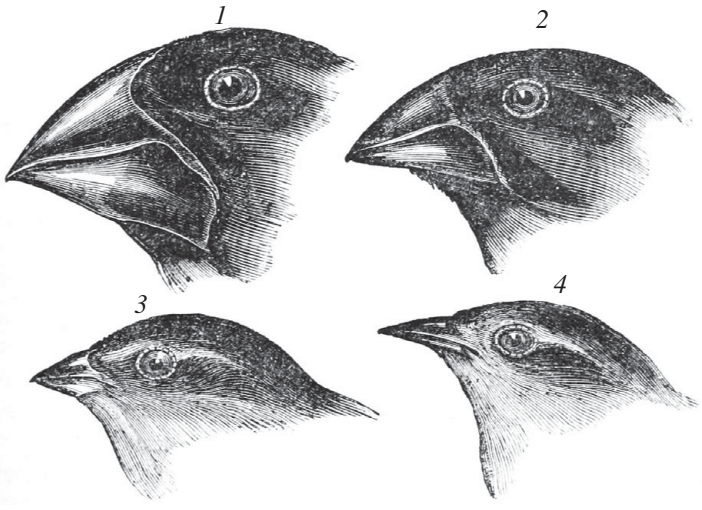


Figure 1.2 Woodcut of Darwin's finches. As drawn by John Gould.

groups by failure to interbreed. In a classification species are gathered together into **genera** (singular **genus**), but genera are to some extent arbitrary and subject to personal taste; there is little discussion, if any, about 'the genus concept'.

It is thought that there are 14 species of Darwin's finches on the Galapagos Islands, plus the one on Cocos Island. Not surprisingly large islands tend to have more resident species than smaller ones. Opinions vary as to the number of genera that should be used to group the finch species, but six genera are a generally acceptable number. They are as follows:

1. ***Geospiza*: the ground finches**
   - o Large ground finch – *Geospiza magnirostres*
   - o Medium ground finch – *G. fortis*
   - o Small ground finch – *G. fuliginosa*
   - o Sharp-beaked finch – *G. difficilis*
   - o Large cactus finch – *G. conirostris*
   - o Small cactus finch – *G. scandeus*

There is strong evidence, and general agreement, that the ground finches form a natural group. All are related to one another more closely than to any other species of Darwin's finch. Technically the genus Geospiza is a **monophyletic** group, that is, the group consists of ancestral species and all their descendants.

2. ***Camarhynchus*: the tree finches**
   - o Large tree finch – *Camarhynchus psittacula*
   - o Medium tree finch – *Camarhynchus pauper*
   - o Small tree finch – *Camarhynchus parvulus*

The tree finches, as their name suggests, live much more in trees than do the ground finches. The tree finches are found more in the highlands and feed largely on insects.

3. ***Cactospiza*: the woodpecker finches**
   - Woodpecker finch – *Cactospiza pallida*
   - Mangrove finch – *Cactospiza heliobates*

The woodpecker finch is famous for not only using tools, but also for modifying them to its purpose. The behaviour was discovered in 1919 and has been observed frequently since. The bird uses a cactus spine, or a twig, often broken off by the bird itself, as a probe held lengthwise in the beak to winkle out grubs, etc. from cracks in bark. It also climbs up and down vertically like a woodpecker. The mangrove finch has also been observed in tool use. The former is a mostly highland species, the latter is found only in the mangrove swamps of Isabela.

4. ***Platyspiza crassirostris*: the vegetarian finch**

The only species in its genus; it lives in trees mostly in the highlands. Feeds on fruit, leaves and buds.

5. ***Certhidea*: the warbler finches**
   - The green warbler-finch – *Certhidea olivacea*
   - The grey warbler-finch – *Certhidea fasca*

The warbler finches feed mostly on insects, even in flight. *Certhidea olivacea* is found in the central, high islands (Santa Cruz and Santiago). *C. fusca* is known to occur in four lower more peripheral islands. Darwin did not accept that the warbler finch was any close relation of the others until convinced by Gould.

6. ***Pinaroloxias inornata*: the Cocos finch**

The single species from Cocos Island is small (13 g) with a slender, slightly curved beak like that of the warbler finch.

Despite uniformity in appearance, a study has shown that individual birds are specialist feeders with a large variety of ways of life in the rain forest. Specialities include searching for insects in leaves and in branches, looking for crickets and grasshoppers among dead leaves and collecting nectar.

Classification and the Galapagos Finches

Before any scientist can study objects, or phenomena, they must organise them some way. Ever since the days of the ancient Greeks, the most useful way of doing this has been to produce a **hierarchical classification**. Hierarchies come in two principal sorts. Both share the feature that they are defined by a series of **ranks**. The first is an **exclusive hierarchy**; an example here might be military rank. The second an **inclusive hierarchy** such as a taxonomic rank.

The term ‘rank’ perhaps needs explanation; in the words of the evolutionary biologist Ernst Mayr (1904–2005): ‘Military ranks from private, corporal, sergeant, lieutenant, captain up to general are a typical example of exclusive hierarchy. A lower rank is not a subdivision of a higher rank; thus lieutenants are not a subdivision of captains’.

In contrast though, a biological classification is an example of inclusive hierarchy. With Darwin’s finches, a single genus usually (but not always) includes several species. Then genera are grouped together in families and so on, at an ever more inclusive series of ranks (a set of nested groups). Biological classifications are usually also irregular – as an example, some genera have many species, others only one. By convention the hierarchy is also divergent; no species can belong to more than one genus.

In his book *Darwin’s Finches* (1947), David Lack not only presents a written classification of the birds (with discussion of the priority of the whole grouping within higher ranks) but also draws up a diagram looking like a family tree, with individual species at the end of each branch. He describes this diagram as ‘an evolutionary tree’, thus drawing an important theoretical conclusion, which is by producing a (correct) classification one is producing not just a diagram of that classification but also of the *pattern of descent*: an inclusive irregular classification is best explained as a **phylogeny**. Lack drew on previous work in drawing up his diagram; his classification was principally based on not only comparison of the appearance of the birds, but also of their ecology and behaviour such as song. If, however, one could use some completely different method and different data to classify Darwin’s finches and the new method produced the same result, then one could feel that the classification was ‘correct’. It would also show that the classification was in some way real and not just a convenient grouping of data. A ‘real’ classification based on natural groupings (birds, fish, insects, etc.) has been referred to as a **natural classification**, whereas a classification of convenience (all the waterfowl, all the yellow flowers) has been called an **artificial classification**.

Since Lack’s time, there have been numerous studies of Darwin’s finches, notably those of Robert Bowman from the 1960s to the 1980s including studies of beak function and song, which are outstanding not only as a series of works on the finches, but also as a thorough study of the ecology and evolution of animals. We can also note the research of husband and wife team Peter and Rosemary Grant (with a succession of colleagues, assistants and research students) from the 1970s to the present day.

In recent years the finches have been reclassified using techniques derived from biochemistry and molecular biology. In the 1970s and 1980s attempts were made at reclassification using the electrophoresis of proteins. But this method in general was not able to distinguish between individual species in such a closely related group of birds. With the 1990s came the use of **DNA sequencing**. Deoxyribonucleic acid (DNA) is the genetic material in all animals, present in the nucleus of all cells as the famous double helix, but also present as a single strand in the numerous mitochondria, the tiny power-houses of the cell, scattered through the cell cytoplasm. The genetic code itself consists of four bases (A: adenine, C: cytosine, G: guanine,

T: thymine), an alphabet of four letters, anchored along the DNA molecule. But if two species of birds (or other organisms) diverge from one another over evolutionary time, **point mutations** can occur so that in one or both cases, one base is substituted for another at any site. The longer that two bird species have had a separate history, the more mutations are likely to occur, so that mutation number becomes a measure of elapsed time.

Both Galapagos finches and Hawaiian honeycreepers have been used to study adaptive radiation. Honeycreepers (see Figure 1.3) such as Apane (*Himatione sanguinea*), L'iwi (*Vestiaria coccinea*), Amakihi (*Hemignathus virens*), Akiapola (*H. wilsoni*) and the Nihoa finch (*Telespiza ultima*) also show the (relatively rapid) beak radiation of endemic island birds from a common ancestor.

The hope is, that in comparing the DNA base sequence of one species with another, a 'molecular clock' will prevail, i.e. that the number of base differences in any sequence from two birds will be directly related to the time since the two diverged. This will not be true if the length of DNA has some vital function but might work for lengths of DNA of no known function.

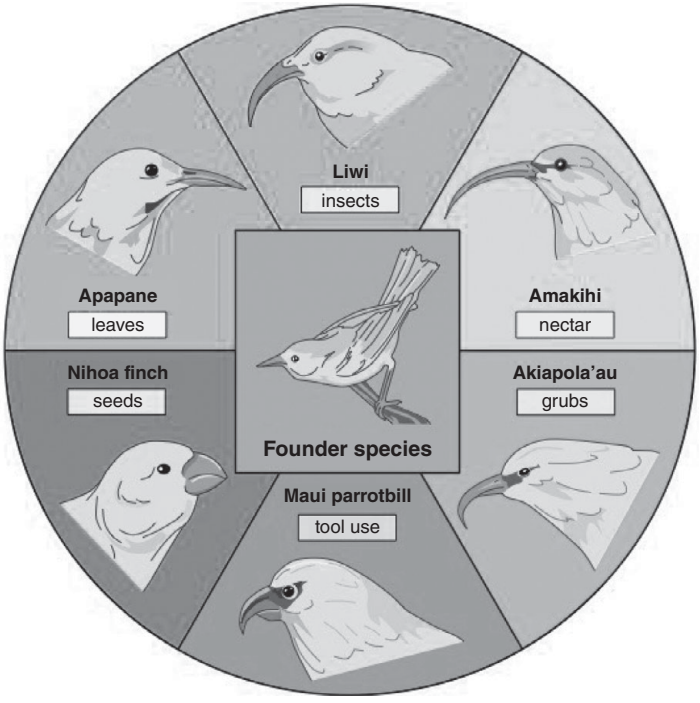


Figure 1.3 The adaptive radiation of beak forms in Hawaiian Honeycreepers. The following have kindly allowed permission to use their photographs or images within this book: Brent Cornell (BioNinja) https://ib.bioninja.com.au/standard-level/topic-5-evolution-and-biodi/52-natural-selection/adaptive-radiation.html

Once again, the results with DNA sequencing of Darwin's finches were short of convincing, but it became clear that the six ground finches were a natural closely knit group and that the warbler finches, comprising two species, had separated from all the others before the others had separated.

In these studies, pursued by members of the Grants' 'school', both nuclear and mitochondrial DNA were used, but in the 1990s a new molecular technique came into use. In the nuclear genome there are frequently considerable lengths of repeated short (2 or 3) base motifs (e.g. . . .CACACACA. . .) of no known function. This is called 'microsatellite DNA'. Mutation consists of the addition or deletion of individual motifs (a single CA, for instance). So what characterises the **microsatellite DNA** of a bird is not one or more point mutations of single bases, but microsatellite length. Comparison of one microsatellite length from each bird would be of little help, but large numbers of these microsatellites are available from any individual and the whole set characterises that individual (a similar technique is used in so-called genetic fingerprinting for forensic purposes).

In 1999, Petren, Grant and Grant were able to publish a phylogenetic tree of all species of Darwin's finches, including the Cocos finch (Petren et al., 1999). In many ways the satellite tree corroborates Lack's tree and the ordering into genera as listed above. But there are important differences of pattern and interpretation, to some extent foreshadowed in the results of DNA sequencing. One is the separation of the vegetarian finch, which branched off the main stock before the ground finches and the tree finches (including the woodpecker finches) separated from one another. A second inference is that the Cocos finch is not the first to diverge from the Galapagos finches – one of the warbler finches has that honour. Therefore, the ancestors of the Cocos finch almost certainly colonised Cocos Island from the Galapagos and not from the South American mainland. And lastly, and perhaps most importantly, the warbler finches themselves are only distantly related to one another. *C. olivacea* was the first to diverge from the whole stock, then the Cocos finch, and then the other warbler finch, *C. fusca*. **All this happened before all the remaining species became distinct**. This leads to a most important conclusion. The resemblances between the two warbler finch species are not indicators of closeness of relationship and must therefore be primitive for all Darwin's finches. They therefore probably give us a good idea of the appearance of the first-ever Darwin's finch and are a guide to our search for the bird species most closely related on the South American mainland. Lack did not know that there were two species of warbler finch (although he did know that 'it' was divisible into several possible subspecies). He correctly suggested early divergence from the main stock but thought that the ancestor of the whole group would be like one of the ground finches, with black male plumage and a crushing beak.

In 2014 Skinner et al. explored epigenetic inheritance in five species of Darwin's finch (see Figure 1.4). Epigenetic inheritance (more accurately transgenerational epigenetic inheritance) reflects the concept of heritable changes in which the physical structure of the DNA remains unchanged. The accepted model of course is that genetic mutation (established over time) generates the heritable phenotypic variation upon which natural selection acts. However, using erythrocyte DNA, this study explored

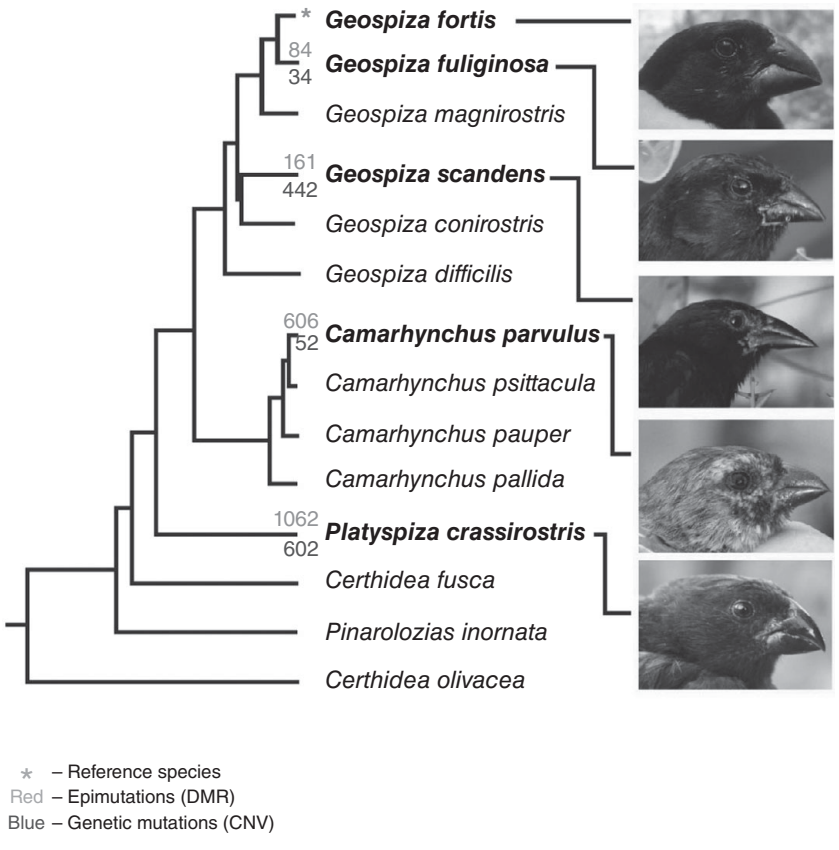


Figure 1.4 Numbers of genetic and epigenetic mutations in relation to the phylogeny of the Galapagos finches (reproduced from Skinner M. K., Gurerrero-Bosagna, C., Muksitul Haque, M. et al. (2014) Epigenetics and the Evolution of Darwin's Finches. *Genome Biology and Evolution*, 6, 1972–1989, by permission of Oxford University Press). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

the possibility that epigenetic changes can accumulate producing the 'clay' upon which natural selection may introduce change.

Blood samples were taken and analysed from five species of finch collected from Santa Cruz island in 2009. Genetic mutations were identified through use of gene duplication and deletion, while epigenetic variation was explored through differential DNA methylation analysis.

The phylogenetic tree in Figure 1.4 follows Lack's physical traits reinforced by Petren, Grant and Grant's microsatellite data. Epigenetic mutations (epimutations) are shown numerically (in red) along with copy number variation (genetic mutations) in blue. There were generally more epigenetic mutations than genetic ones indicating that epimutations may be a major component in evolutionary change. There was also a significant correlation between the number of epimutations and phylogenetic

distance – perhaps suggesting that epigenetic change accumulates over long periods of evolutionary time (1–3 million years).

The relative importance of genetic and epigenetic inheritance remains a subject of considerable debate.

Darwin's Finches and the Origin of Species

A reconstructed pattern of evolution (as drawn by Lack for Darwin's finches) is known as a phylogeny. Two historical processes must have contributed to that phylogeny. Any evolutionary change in time – in anatomy, behaviour, development or molecular constitution – is known by the term **phyletic evolution**. If phyletic evolution had not occurred in the history of life, then all living things would look like their first ancestors. The second evolutionary process (or 'mode' of evolution) is '**speciation**', the splitting in time of one species into two or more. If no speciation had occurred in the history of life, there would be, assuming a single common ancestor, only one species of living thing on Earth!

As we shall see later, there is still some dispute about the nature of speciation, particularly in animals. We have already seen that animal species are separated from one another by some sort of barrier, physical, behavioural or physiological, such that members of two different species do not normally interbreed with one another. This applies even in the case of two closely related (sibling) species occupying the same area, such as two species of Darwin's finches living on the same small Galapagos Island. At some stage in their joint history a barrier to free interbreeding must have occurred. It has long been the claim of the evolutionary biologist Ernst Mayr that for that barrier to arise, splitting one species into two, there must have been an **allopatric** phase with the two, incipient species separated geographically. During the period that the two, incipient species are separated, differences in structure, behaviour, physiology, etc. evolve either in response to their different environments or by chance. If in the future the two species come to occupy the same habitat, the barrier to interbreeding will be enhanced by **natural selection** – Darwin's great theory of the mechanism of evolution (see 'The Galapagos Islands and Natural Selection'). Hybrids will either not be produced or will be at a competitive disadvantage to the pure-bred members of what are now separate species.

Darwin's finches have long been regarded as ideal exemplars of allopatric speciation (isolated by a physical barrier). A little thought will demonstrate that there are two ways in which part of a single species can be separated from the rest:

1. If the range of a species is divided by some geographical event, such as the opening of a seaway or the origin of a mountain chain, free communication between members of the species on either side will cease. This is a *vicariance event*.
2. If on the other hand a sample of the population crosses a preexisting barrier, either voluntarily or by chance (wind-blown, or the floating mats of vegetation referred to in the section 'The Galapagos Islands and Darwin's Finches: A Case Study', for example), then this is a *dispersal event*.

The islands were never connected to the South American mainland, from which they are far distant. They are also volcanic, so uninhabitable when first formed. But

dispersal from the mainland to the islands is certainly possible if one considers that the major Galapagos fauna are birds and reptiles (mammals are rare):

- Birds of course can fly. Many of the coastal nesting birds (e.g. albatross) are strong, long-distance flyers. Others could have been aided by prevailing winds.
- Reptiles are particularly hardy animals and could theoretically survive for many months on floating vegetation mats.
- Mammals are much more vulnerable to water loss and lack of food and therefore less likely to survive long sea journeys.

But the first dispersal event – South America to the Galapagos – does not explain the existence of ***14*** species on the islands. The finches are one of the best-known examples of **adaptive radiation** occurring due to allopatric speciation. Grant envisages:

1. The ancestral birds arriving on San Cristobal (Chatham).
2. Then after their adaptation to that island, a few birds 'island-hopping' to other islands to which they and their descendants became adapted.
3. The third and critical phase is when some island-hopping birds arrive on an island already inhabited by a finch population that has adapted to a particular way of life on that island. The new arrivals, if they survive, may have a different way of life and if breeding between the two stocks is inhibited, they will constitute sibling species descended from a common ancestor.

The whole process depends on many islands, at least slightly different in their environmental demands, and the rarity of island-hopping events over many generations. Without a sufficient time-frame, the bird stocks will not be sufficiently different for an interbreeding barrier to be formed – they will still be the same species. When the two stocks are established, reinforcement occurs. **Reinforcement** is due to any factor that causes the two species not to interbreed, and to occupy different ecological niches. The whole process can be summed up as divergence in allopatry and reinforcement in **sympatry**. Sympatry is where two or more species overlap as they diverge.

Thus, the theory of **adaptive radiation by allopatric speciation** implies that each species arose by differences in allopatry, presumably on a different island, and then **reinforcement in (subsequent) sympatry**. As a corroboration of this theory, evolutionary biologists point to the Cocos Island with its single finch species. There was no scope there for differentiation in allopatry after the ancestral birds had arrived.

It is a characteristic of good science that however firmly established a grand theory is, scientists themselves will question it. Newton's mechanics were eventually superseded by Einstein's relativity. Therefore, can we question the scenario of an adaptive radiation of Darwin's finches on the Galapagos Islands? The answer is yes, of course, but in this case that questioning will lead to a deeper understanding of the historical process, rather than destruction of the theory.

(1) Until recently it was thought that no Galapagos island had ever been nearer to the South American mainland than those still existing. But in 1992, geologists discovered a series of seamounts (undersea extinct volcanic mountains) between

the Galapagos and the mainland. Some of these underwater hills had cobbles indicating coastal erosion – they once protruded above the sea. So at least some island hopping between South America and the Galapagos might have occurred.

(2) For the extreme allopatric model, inter-island flight should be a rare event, but occasional vagrant species are seen on islands where they are not regarded as resident, and in recent years (1982–1983) the large ground finch has coloured the small island of Daphne Major.

(3) One case is known of the apparent beginnings of sympatric speciation, an island population dividing itself into two. The Island was Genovesa, small, remote and flat. The large cactus finch is resident on Genovesa and has been intensively studied by the Grants. They started their work there in 1978 after a severe drought in 1977. Male birds were heard to sing one of two distinct territorial songs, A or B. The nestling birds have one of two beak colours, yellow or pink. A males had 36% offspring with yellow beaks (and 64% with pink!), whereas B males had only 18% yellow. There was also a significant difference in bill length between adult A and B birds, correlated with different feeding habits. Type A birds fed on the flowers or hammered open the fruits of the prickly pear cactus, while B birds tore open the cactus pods searching for insects.

There seems little probability that either A or B birds had arrived from elsewhere. The nearest population of the large cactus finch to that on Genovese is the only other one known, and is on the distant island of Espanola about 200 km away. There is no evidence of any other population ever having existed between the two. In subsequent years, the correlation between song type and beak length disappeared and there was no evidence that females of type A parentage mated for preference with type A males (**assortative mating**). Nevertheless, the division of the population in 1978 suggests the initial stage of sympatric speciation.

(4) There have been many cases recorded of hybridisation between different species of Darwin's finches, even those belonging to different genera. Over a period of 16 years, the Grants and their associates have conducted very detailed studies of the finches on the small crater island of Daphne Major. They discovered that the medium ground finches regularly hybridise at a low level with both the small ground finch and the small cactus finch, and that the hybrid offspring appear to be at no disadvantage, sometimes even flourishing more than pure-bred birds. This seems at odds with the idea that two sibling species in sympatry should evolve away from one another as the final stage of speciation. It also poses the question, too complex to deal with here, as to whether the six species of ground finches are in fact good species.

The Galapagos Islands and Natural Selection

It was Charles Darwin's great achievement not just to suggest that evolution had occurred (and give cogent reasons for accepting this) but also to propose a *mechanism* that could produce evolutionary change. His theory of natural selection proposed such

a mechanism, answering in part the question, how can evolutionary change, phyletic evolution, occur, and how is it that living organisms adapt to changes in their environment? Natural selection is a theory of adaptive change. And yet, as we have seen, it was not generally accepted that the differences in size and shape of the beaks in Darwin's finches were adaptively significant until the publication of Lack's book in 1947.

Darwin thought that natural selection, and thus adaptive change, was extremely slow and thus not open to observation. A study by Peter Boag and Peter Grant, published in 1981, showed that significant change can occur within a single generation. In 1977 the rains failed on the island of Daphne Major, resulting in very high mortality in the population of the medium ground finch, *G. fortis*, and no breeding. The birds that survived into 1978 were considerably larger than those that died (immediately showing the sex ratio, roughly equal before, of six males to one female). Seeds are the main food of *G. fortis* and in the drought year were in very short supply. This was particularly the case with the small seeds that were their staple. Only large birds with relatively deep beaks could open the seed cases and crush the seeds of the plant *Tribulus*. There was another plant with smaller seeds available, but this produced a sticky latex, gumming up the unfortunate bird.

Thus, selection for the ability to eat large tough seeds resulted in a change in mean beak depth, but this would not result in evolutionary change, unless the difference were heritable. To show that this was the case the beak depths of later offspring were plotted on a graph against the mean beak depth of each offspring's parents demonstrating that beak depth is indeed heritable. Adaptive beak depth can result from natural selection.

A few years later the direction of selection was seen to reverse. In December 1982 the islands were hit by the effects of one of the most severe El Niño events of the twentieth century. The rains on Daphne Major continued to the end of summer and throughout the period *G. fortis* went into a breeding frenzy, each breeding pair, including some born in the same year, producing several broods. The population rose by some 400%. After the rains there came a population crash. But this time it was large birds (especially males) that were selected against. The reason is uncertain: there was in this case a surplus of small seeds relative to large, and it was suggested that, beak size or not, large birds simply needed more seeds, thus involving more searching to keep going. Also, it is said that the large beaks are less useful in the young before the beaks harden.

The sensational changes in one generation resulting from both events on Daphne Major impressed evolutionary biologists, but the Grant team themselves noted that what they had described was a case of **stabilising selection**. The birds on Daphne Major could react rapidly to climate change, but over the years, body and beak size fluctuated about a mean. There was no evidence of selection producing phyletic evolution – sustained directional evolutionary change. For natural selection to produce such change, there has to be new genetic information on which selection can act. We will discuss the origin of such information (known as **mutation**) in Chapter 3.

The Galapagos Islands therefore provide a powerful endorsement of Darwinian evolutionary theory along with an outstanding outdoor laboratory in which to study natural selection. The rate of evolution is rapid; in just under four million years there has emerged an amazing diversity of form arising from the animals and plants flying, floating, hitch-hiking or swimming there. Population sizes have become extraordinarily large in some cases, for instance in the unique marine iguana. Why should this be so?

One possible answer is in the relative lack of predators on the island. Snakes are small and ineffectual against all but the smallest reptiles. The Galapagos hawk is limited by nesting sites, and among the invertebrates the large (20 cm) centipede *Scolopendra* is a formidable adversary for other invertebrates but it rarely troubles the islands' vertebrate population. Large jungle predators from the South American mainland (mainly mammals such as the jaguar) just could not make the journey. Also, visitors to the island frequently note how tame all the animals are. Such 'island tameness' is typical of those creatures not subject to extensive predation pressure.

It is suggested that a lack of predators coupled with smaller size and rapid reproduction (energy can now be diverted into reproductive success) has spurred the evolutionary trajectories of the Galapagos communities.

Perhaps disconcertingly, a point was made of featuring data that might conflict with orthodoxy. Does the discovery of seamounts to the east of the present archipelago cast doubt on the accidental dispersal of ancestors to the Galapagos? Does inter-island flight occur too frequently for the allopatric scenario to be valid? Does hybridisation between apparent species refute their states as good species? Could incipient sympatric speciation, as seen in the large cactus finch on Genovesa, go to completion? I suspect that the answer to all these questions is 'no', but they must be asked. Progress in science is made by the recognition of data that appear to contradict established theories, by debate between theories and by continuous, ruthless questioning.

Humans pollute – we can degrade the environment, but we also conserve. The last remaining giant tortoise on the island of Pinta, *Chelonoidis abingdonii*, was discovered in 1971 and relocated to the Charles Darwin Research Station on the island of Santa Cruz. Named 'lonesome George', this male Pinta giant tortoise was the very last of his kind. Attempts to locate other Pinta tortoises or mate him with females from closely related species all failed (although interestingly clutches of eggs were produced from such matings but none were viable). Sadly, Lonesome George died in 2012. The death of the 'last of his kind' was, of course, a blow but also a 'wake-up call' to conservationists globally. George's death (at the relatively young age of 80 years or so) has reawakened conservation efforts both in the Galapagos and elsewhere resulting in a finding in 2015 that a closely related species, *C. donfaustoi*, had a 90% DNA match to that of George.

2 Reviewing the Evidence for Evolution

Evolutionary change has created biological lineages, all interrelated. And it is the role of the biologist both to describe the pattern of change and explain how our current biological diversity came to be. By observing present-day phenomena, we can see that:

- animals and plants are grouped in a meaningful way in that they seem to form 'natural groups' (birds, fish, conifers, etc.),
- there is a distinct **heritability** within living things (put simply, 'like begets like'/ offspring resemble their parents),
- an adaptation exists between an organism and its environment (living things seem to be well 'fitted' to the environment in which they live),
- we observe 'curious rocks' that resemble living things that no longer exist (ammonites in mudstone or leaf impressions in coal) – we call these **fossils**.

Darwin's theory of evolution by natural selection remains the strongest argument in the explanation of all the above phenomena. It overturns Aristotle's 'fixed' view of nature and replaces the notion of a preordained world. Modern science, from the sixteenth or seventeenth centuries onwards, replaces conjecture with evidence and dogma with reasoned argument.

We live on a dynamic and rapidly changing planet, and we believe that living organisms also have changed – either in response to a fluctuating physical environment (and the opportunities or threats that affords) or to interactions between types of organism occupying those environments. But this point cannot be assumed or simply inferred; ***evidence*** is required.

Over the years, several lines of evidence have been presented.

Homology and Comparative Anatomy

By comparing animals and plants it is possible to infer relationships from their body structures. The feathers of birds, the milk of mammals, the organisation of sepals and petals in flowering plants all provide clues to their 'connectedness'. But a closer examination reveals greater depth. The organisational plans (or '*Bauplan'*) of the various animal phyla reveal the potential for a common ancestor from which all members of that group are derived. These organisational plans (the type and arrangement of bones, common physiologies or behaviours) are the *homologies* on which this

section is based. The evidence they provide for evolution is indirect but overwhelming both in its logic and in its congruence with other lines of proof.

If evolution was proposed by Darwin and Wallace to explain classification, then logically the existence of natural classification should not be cited as evidence for evolution. However, the *pattern* of evolution is important and fundamental to both classification and reconstructing evolution. Central to this notion is the concept of **homology**.

The concept of homology predates that of evolution by hundreds, possibly thousands of years (being traced back to Aristotle in the fourth century BC). In 1555 Pierre Belon included a famous diagram (Figure 2.1) in his book of birds. He illustrated a human skeleton and that of a bird opposite one another, labelling in each what he considered to be corresponding bones. This correspondence, showing unity of plan, is a demonstration of homology. Put simply, homology refers to the basic similarity in structures observed in dissimilar species. The reason for homology is that these (dissimilar) species had a common ancestry and a basic structural pattern that has been preserved along the lineage.

Let us take a standard example of homology, the pentadactyl (or five-fingered) limb of tetrapod (four-legged) vertebrates. In all but the very earliest tetrapods the limbs appear to be derived from a common pattern (Figure 2.2). There is a single bone that

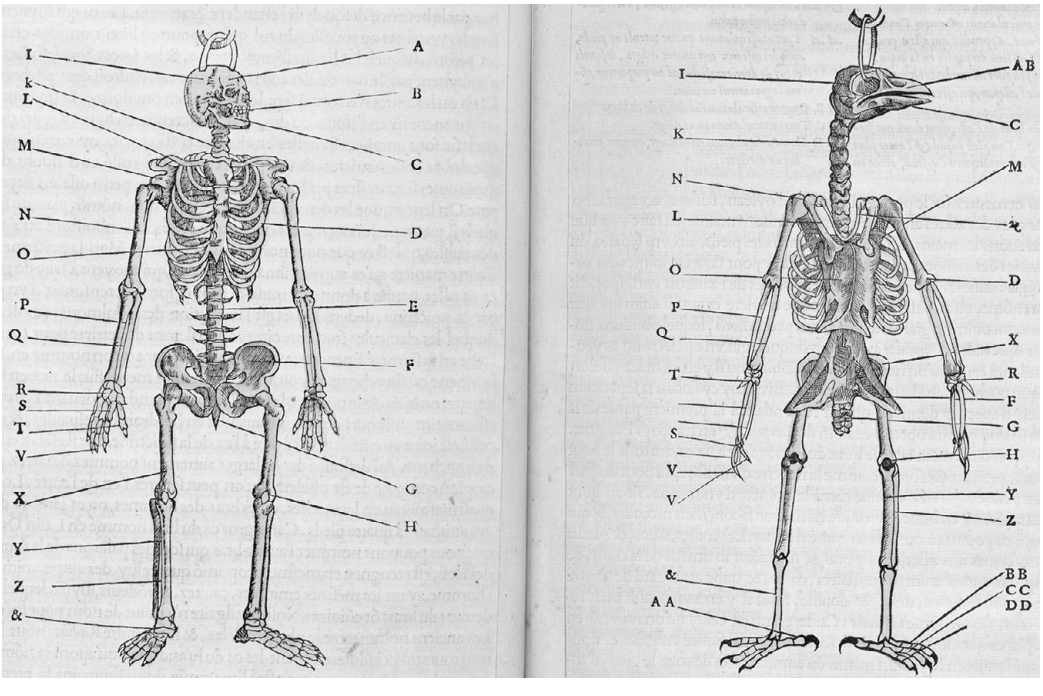


Figure 2.1 A comparative anatomy of birds and Man from Pierre Belon's (1555) book, *The Nature of Birds*.

articulates with a limb girdle; that bone then articulates with two parallel bones followed by the bones of the wrist or the ankle. Finally, hand and foot each bear five digits. This pattern then appears to have been modified to serve a range of functions in different tetrapods. For example, reduction to a single toe on each foot in the case of horses, or two toes (cloven hooves) in deer, antelopes and related animals. But the individual bones of the pentadactyl limb are homologous with one another (resemblance indicating common ancestry). The humerus of a horse is homologous with the humerus of a bat, although their functions relative to locomotion are very different (they are, of course, related to the same vertebrate ancestor). The whole forelimb of a horse is adapted for galloping, that of a bat for flight, but both appear to be derived from the common vertebrate plan of the pentadactyl limb. **Homology** therefore represents the state of affairs where a resemblance in body structure or morphology is the direct result of the organisms possessing a common ancestor and therefore acquiring similar structures (albeit often adapted now for different purposes). We can take the argument further by comparing the forelimb of a bat with that of a bird, the only other living vertebrate group capable of powered flight, and then ask is the forelimb of a bat homologous with that of a bird? The answer is 'yes and no'! They are homologous as pentadactyl limbs, but not as wings, as should be clear from their structure. In birds the aerofoil surface of the wing is formed by flight feathers, and the bones of the hand, including the digits, are fused and reduced. In a bat the aerofoil

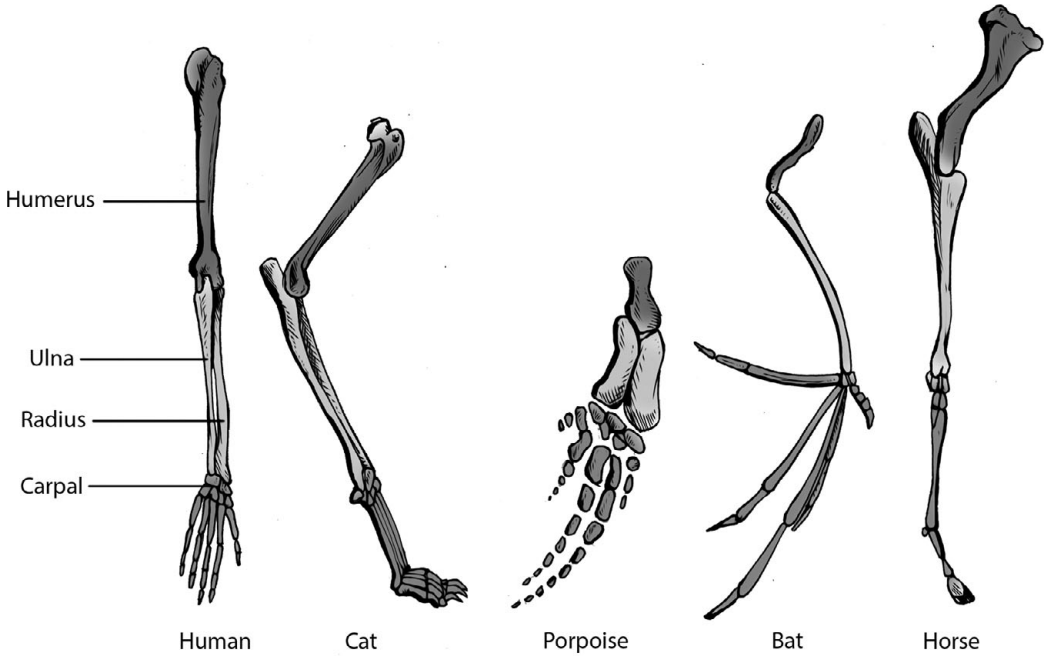


Figure 2.2 Homology as evidenced by the pentadactyl limb in vertebrates. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

surface is formed by skin stretched over very elongated fingers and all five digits are present. If we now introduce a third animal for comparison, a house fly, also capable of powered flight, we can ask if the forewing of a house fly is a homologue of the wing of either a bird or a bat. The answer is a resounding 'no'! And yet the fly's wing subserves the same function as that of a bird and a bat – the means of powered flight. All three wings are **analogous**, that is they serve the same *function*. **Analogy**, a resemblance or superficial similarity, is common in nature as we see organisms arriving at the same 'solution' for the same biological problem (locomotion in water or seed dispersal in plant for instance).

To return to the bird and the bat, their forelimbs are homologous as pentadactyl limbs, but analogous as wings. They have the same basic structure but are adapted in different ways for the same function. The great British comparative anatomist, Richard Owen, defined analogy and homology in 1843 as follows:

Analogue: A part or organ in one animal which has the same function as another part or organ in a different animal.

Homologue: The same organ in different animals under every variety of form and function.

Many biologists treat analogue and homologue as though they were mutually exclusive, but it is clear from Owen's definitions that this was not his intention, nor is it proper usage today. A third term to describe non-homology is therefore necessary and was proposed by Ray Lankaster in 1870. It is **homoplasy**, a general similarity not due to common ancestry. The wing of a house fly is both analogous and homoplastic to that of a bird. There is no structural suggestion that both are modified from a common source. The most common cause of homoplasy is often convergence of DNA mutations. As a point of information, the different beak sizes of Darwin's finches appear to be the result of change in one, or just a few, genes; thus, substantial adaptive radiation can be the result of relatively little genetic change.

Of our three flight-powered animals the bird and the bat share many features as tetrapod vertebrates, including a forelimb which is a modified pentadactyl limb. But this character, to have a forelimb modified as a wing, is not a general feature of the lowest-ranking group to which they both belong (the Amniota). They are, however, much more closely related to one another than either is to the house fly. What we have here is a very small inclusive hierarchy of homologies. There are many more shared homologies between bat and bird, than between both of these and the fly.

Thus, inferences of homology are the basis of classification. An order of precedence should now read:

Data (i.e. 'characters') → inferences of homology → classification → reconstruction of phylogeny (i.e. evolution).

In more modern terms, homologies used to define groups in classification are known as *taxic homologies*. But there is another category of homologies that can be used as evidence for evolution. It is *transformational homology*. As an example, we can take the three small bones that conduct sound from the ear drum to the inner ear in mammals.

They form a chain, with the malleus (hammer) linked to the ear drum and followed by the incus (anvil), and the stapes (stirrup) which connects to the inner ear, where the organ of sound reception is situated. Comparative anatomy and embryology show that the malleus and anvil are homologues of the two bones (or cartilages) that form the jaw joint in all vertebrates except mammals. These are the quadrate at the back of the upper jaw and the articular for the lower jaw. In tetrapods the stapes is also an ear ossicle, but in fishes it is a bone (or cartilage) suspending the jaw joint from the braincase. So, the malleus and incus are transformational homologues of the articular and the quadrate, respectively.

Such transformational homologues are inferred by the principle of connections proposed by the French comparative anatomist Étienne Geoffroy St-Hilaire (1772–1844). Homologues in two animals might look very different and serve very different functions, but they can be recognised by their connection to surrounding structures and their general topology within the respective organisms. We shall see below that transformational homology can be combined with the fossil record to provide powerful evidence for evolution.

For completeness we should note another type of homology, which was very much the focus of attention at the turn of the eighteenth/nineteenth century. It concerns homology within a single organism and was named '*serial homology*' by Owen. In a centipede all the many body segments, after the specialised head region, are remarkably similar and are clearly built on a common plan – each is a serial homologue of all the others. The same serial homology applies, but rather less so, to the body segments of a vertebrate. Each segment possessing a vertebra, a pair of ribs, a pair of spinal nerves and segmented muscles. But what has happened at the head end? It was suggested by the great German writer Johann Wolfgang von Goethe (1749–1832) that the vertebrate skull consisted of (probably four) modified vertebrae. This was accepted by many anatomists including Owen but is not generally believed today. Another theory of Goethe's is however accepted. In 1907 he suggested that for the parts of a flower, each of the sepals (collectively the calyx), petals (corolla), stamens and pistils, could be regarded as a modified leaf. Such homologies are now known as *iterative homologies* as they are not necessarily arranged in serial order.

Embryology

As with the study of comparative anatomy, a comparative study of animal embryos reveals similarities in form that puzzled early biologists. It was Charles Darwin who reconciled these strange and yet similar developmental processes under the unifying theme of biological evolution. Once again, the argument is indirect but compelling.

During the eighteenth century, and in the first half of the nineteenth, the majority opinion among naturalists was *not* that the natural order of organisms was a tree-like inclusive hierarchy, but rather a linear series, a ladder or 'scala naturae'. This 'Ladder of Nature' or 'Great Chain of Being' was pictured with Man near the top and going down through 'higher and lower' animals to plants at the bottom along with inanimate objects such as rocks and pebbles (Figure 2.3).

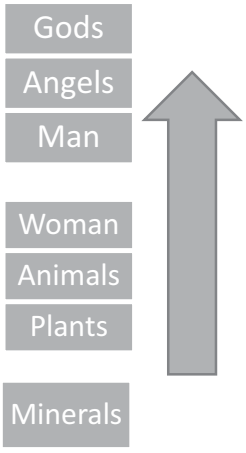


Figure 2.3 Aristotle's 'Great Chain of Being' or '*Scala'*.

In human development, the growing embryo was thought to climb the scala naturae individually (or at least the upper vertebrate part of it). Thus, the individual developed through stages corresponding to fish, amphibian, reptile and mammal before birth. The person who demonstrated that this was false was Karl Ernst von Baer, who in 1828 showed that the pattern of embryo development was not through a linear series, but one of *divergence*.

> Each embryo of a given species instead of passing through the stages of other animals departs more and more from them. Fundamentally therefore, the embryo of a higher animal is never like (the adult of) a lower animal, but only like its embryo.

Here then there appears another irregular divergent hierarchy that could be used as a basis for classification. According to von Baer, the early embryos of two different species share many of their characters but diverge by acquiring more and more specialised characters as they develop. High-ranking characters develop first, successively lower ones later. This is not universally true: a hen's egg has many special features (adapting it to be free of standing water) that develop before features characterising all tetrapods, and other embryos may have features that ensure their survival, but in general terms von Baer's Laws give a truer picture of ontogeny (individual development) than the scala naturae.

A rather appealing (though incorrect) hypothesis concerning animal embryos and evolution is Haeckel's 'biogenetic law', sometimes referred to as his 'Theory of Recapitulation'. The similarity between 'higher' vertebrate embryos (see Figure 2.4) is explained as the animal somehow recapitulating its evolutionary history. Ernst Haeckel, a German evolutionist and contemporary of Charles Darwin, noted the resemblance between animal embryos and the adult form of its ancestors, while German *Naturphilosophie* at that time saw deep bonds between individual

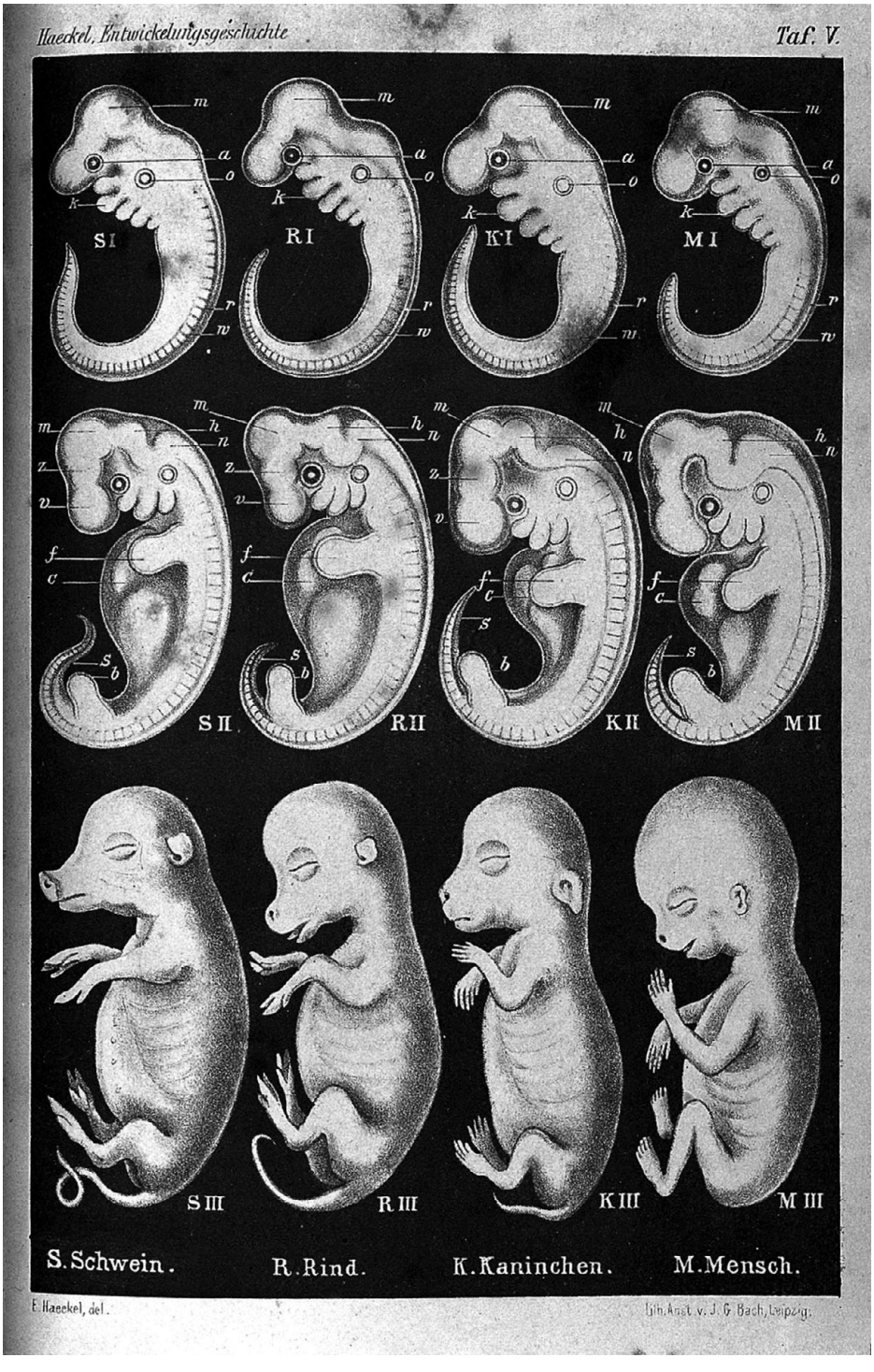


Figure 2.4 Comparison of vertebrate embryos noting their similarity, (Pig, Cow, Rabbit, Human).

development and the organisms' evolutionary development – as exemplified in Haeckel's phrase 'ontogeny recapitulates phylogeny'. Haeckel's Biogenetic Law (Haeckel, 1866) is one of several recapitulation hypotheses. The resemblance between embryos, he argues, is that the animals are 'replaying' their phylogenetic history.

Stanley Hall in the United States took this idea into the realm of developmental psychology arguing that children go through early stages of development paralleling their evolutionary development, and biologists Ernst von Baer and Louis Agassiz were strong advocates of this type of biological progress. It is not clear whether Charles Darwin was influenced by this type of German metaphysical thinking, but the general opinion is that he was rather wary of ascribing a distinct biological progress to his findings. In Darwin's eyes progress came about naturally and organically through the process of selection. Ernst Haeckel proposed his biogenetic law after reading Darwin's *Origin of Species*. However, where Haeckel attributed embryonic similarity to extant species resembling the adult forms of their ancestors, Darwin suggested the embryos of current forms look similar to those of their ancestors because they all *shared a common ancestor*.

Haeckel's Theory of Recapitulation has largely gone out of fashion since it became clear that embryos do not resemble the *adult* forms of their forebears, rather they resemble their ancestor's *embryos*. Similarly, there is no fixed relationship between embryo and adult form; not all characters are seen in the embryo, and in some groups, like the plants, all traces of their ancestry are lost during development. But although recapitulation does not provide an explanation, there are legitimate grounds for inferring that the resemblance we see between embryos is the result of a shared ancestry and therefore provides strong evidence for evolution along the lines of embryological homologies.

Vestigial Organs

One transformational homology was cited by Darwin as evidence of evolution, that of vestigial organs. The hip girdle and hind limb of whales are entirely embedded within the body yet are clearly homologues of the functional back legs of other mammals (Figure 2.5). Similarly, the baleen or 'whalebone' whales, such as the blue whale, lack teeth. The baleen whales feed by filtering sea water to retain plankton through a series of long narrow plates of baleen, made of keratin, the stuff of hair and fingernails. Yet the embryos erupt apparently functionless teeth which are soon lost. Primitive snakes such as the boa constrictor also have reduced hind limbs (although they have lost their forelimbs altogether). The hind limbs appear externally merely as spurs, either side of the vent. **Vestigial traits** are a feature of a species that once had an adaptive purpose in the ancestor of that group but have now either lost their use, as in the case of the human coccyx, or have been coopted for a new use such as the early vertebrate jaw bones now found in the inner ear. Structures such as tiny hind limbs in snakes, non-functional eyes in cave-dwelling fish and air sacs in the limb bones of flightless birds are vestiges of a former, ancestral, lifestyle.

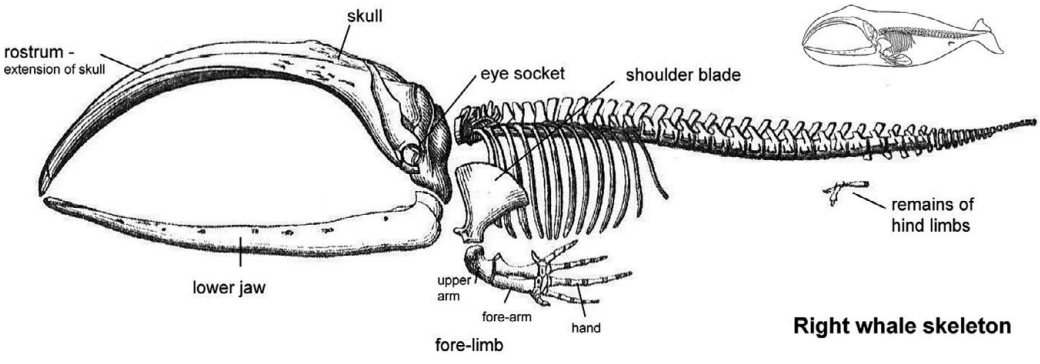


Figure 2.5 Whales possess limb bones similar to that of hooved mammals.

An example of what Darwin confusingly called 'rudimentary organs' is the useless wings of some beetles. In beetles the forewings, present in most insects, are modified as hard wing cases not used in flight but opened down the midline so that the hind wings can operate. But in some species of so-called ground beetles the wing cases are, in Darwin's phrase, 'soldered together' so that the hind wings, still present, are useless for flight. In this case there seems no possible explanation other than that the ground beetles are descended from flighted ancestors.

Another extraordinary case involves the recurrent laryngeal nerve of mammals. This nerve is a branch of the vagus nerve. The vagus emerges from the brain near the back of the skull. The recurrent laryngeal branch then runs along the neck, loops around the dorsal aorta (the large blood vessel that carries blood from the heart for distribution round the whole body except for the head and neck) and then redoubles back towards the skull, providing the nerve supply to the larynx. If the human recurrent laryngeal ran straight from the skull region to the larynx it would be centimetres shorter – the recurrent laryngeal of the giraffe would be several metres shorter! The reason for this apparently wildly inefficient piece of wiring is clear if one looks at the situation in fish, who have no neck. The dorsal aorta of mammals is the homologue of the fourth (from the front) of a series of blood vessels supplying the gills. Numbers 1, 2 and 5 have disappeared in the adult mammal: number 4 is the dorsal aorta and number 6 the pulmonary artery taking blood to the lungs. In the embryo mammal numbers 4 and 6 are connected and the recurrent laryngeal loops behind the connection (the ductus arteriosus). The ductus degenerates in the new-born mammal, but the nerve continues to loop behind the ligament that is its remnant and thus around the aorta. In fish the nerve goes straight to its destination.

In each of these cases of vestigial organs one is compelled to see the anomaly as a remnant of an ancestral condition – **phyletic evolution** (the divergent development of two or more daughter species from a single parent species) has occurred. But a note of caution is necessary. To take a previous example, many cave-dwelling organisms, such as shrimps, fish and the blind cave salamander *Proteus*, have degenerate eyes or none at all. But all have close open-air relatives with eyes normal for their group.

Proteus (the Olm), which occurs in caves near the eastern Adriatic coast, is also **neotenous**, that is, it lives in a permanent larval condition, with feathery external gills and limbs with reduced digits – three at the front, two at the back. It thus seems probable that the eyes are vestigial – they develop so far and then degenerate. But in other cases, it may be more difficult to decide which way to read the series. All such cases are evidence for evolution, but one needs to know which way to read the transformational homology.

In answer to 'special creationists', who claim that a complex coordinated organ such as the human eye could never have evolved by natural selection, the evolutionary biologist Richard Dawkins has presented a compelling scenario, with each stage better adapted for vision than the one before. Many protozoans (single-celled organisms) have an eye-spot of one or a few light receptors, and so do some animals, with in this case several light-sensitive cells. In some cases these cells are partially shielded, so that not only is the creature aware of light and darkness but, by movement of the shadow, the direction of the light. Next, we move to the light cells situated in a hollow cup and omnidirectional detection. A deep cup with a small aperture gives a poor, dim and fuzzy, pinhole camera effect. Decrease the size of the pinhole and the image is sharper but dimmer; increase it and the brightness improves but the image worsens. Oddly the living marine mollusc Nautilus has only reached this stage, while the related octopuses and squids have evolved the solution, a lens; though their eye is very different in construction and embryology from the vertebrate eye.

Animal 'vestiges' are still used by creationist thinkers to try and disprove evolution. Why, they argue, has an animal (or plant) evolved a useless feature? Alternatively, some argue that vestigial features do have a function (possibly one not discovered yet) and that the biologist is hopelessly trying to find an evolutionary antecedent. In other words, a trait cannot be vestigial if it still has a function. But what is missing in these arguments is that evolutionary theory does not say that a vestigial organ has no function – the point is '*it no longer performs the function for which it evolved*' (Coyne, 2009).

The point of this digression is to pose the question, how, when faced with a poorly developed structure in an animal relative to its near relations, do you tell whether it is vestigial or not yet fully developed ('rudimentary'!)? The answer again is to look at the classification. A blind, cave-dwelling creature with poorly developed eyes (or no eyes!) is likely to show a degenerate, or vestigial, character, if open-air forms, who are also members of the group to which it belongs, have fully developed eyes. Another possible explanation of a strange vestigial feature is the 'throwback', the reappearance of a character once lost. It is said that Julius Caesar for instance once rode a horse with feet 'almost human'. And both sperm whales and humpback whales may be found with 'projecting rudimentary hind limbs'. The reappearance of a previously functional characteristic is known as an **atavism**.

Vestigial traits occur naturally within a population whereas atavisms are often spontaneous (but still they shed light on evolutionary history). The existence of hen's teeth is perhaps a myth but in 1980 it was demonstrated that grafted mouse mesenchyme tissue could induce dentine formation in chick enamel suggesting that genes might be conserved unaltered for millions of years yet remain inactive.

The Fossil Record

The usual assumption is that the fossil record is *the* evidence for evolution. It certainly represents evidence of a change in the totality of living things (the biota) over time. But to make the case most forcefully, one needs to produce a logical argument in several steps. In this section the assumptions will be itemised and the argument (that the fossil record is evidence for evolution) presented in full:

1. that fossils are evidence of once-living organisms and not some parallel phenomenon;
2. that fossils in their stratigraphic setting (i.e. their sequence in the rock strata) constitute a historical record;
3. that extinction is a real phenomenon;
4. that there is progression in the fossil record, i.e. that the record shows a succession of biotas through geological time, such that individual species in the record are clearly related to those that come before and after them, without being identical;
5. that, despite known major extinction events, the fossil record is not interrupted by any catastrophic event that is known to have wiped out all existing life; and, furthermore, that the first appearance of any fossil group (from species upwards), and their disappearance from the record, do not always coincide with known major extinction events; *and therefore*
6. that any apparent progression (which need not imply improvement, just change) is more plausibly interpreted as phyletic evolution than as 'catastrophism' (i.e. the extinction of the whole biota to be replaced by a newly created one).

The argument regarding the use of fossils is explored further below. The same number order is employed.

1. The term 'fossil' is used to label any specimen preserved in a rock stratum, or other ancient material such as amber, that constitutes evidence of a former living thing or things. Some fossils seem to us today to be easy to interpret. Fossil mollusc shells, bivalves or snail-like, are so like living forms, and sometimes of the same species, that their interpretation seems obvious. But two things must be borne in mind. Firstly, as was written by a philosopher of science, D. B. Kitts, in 1974: 'fossils by themselves tell us nothing; not even that they are fossils' (Kitts, 1974). Directly or indirectly, fossils are always interpreted by comparison with living organisms. Secondly, fossils have not always been interpreted as the remains of once-living organisms. During the seventeenth and eighteenth centuries there was a vigorous debate between those who advocated the modern view and those who believed that fossils represented a parallel creation, never alive but simulating living things. In the 1660s a Dane (Nils Stenson) offered two reasons for interpreting fossils as once living. He looked at the common 'tongue stones' (petrified shark teeth) of northern Mediterranean strata and noted that they were closely similar, in both external form and interior construction, to the teeth in living sharks. His second criterion was that the fossil teeth embedded in rock had impressed their form on the surrounding rock

sediment. They were therefore formed before being buried in the sediment. They had not 'grown' by some means within the sediment itself. But those who doubted the nature of fossils had their reasons. Finding fossils of creatures no longer alive implied extinction, which cast a slur on God's creativity – He would not create organisms only to scrap them. They were also disturbed at finding fossils of marine shells high in mountains – now known to be due to tectonic movements within the earth.

2. Historical geology, as taught to all students of the subject, depends heavily on two principles, the **principle of superposition** and the **principle of correlation**. The first is delightfully simple, but all important. In an exposed sequence (a 'section') of sedimentary rocks (those formed by deposition of preexisting particles), such as sandstone or mudstone, unless the section has been radically disturbed, the oldest will be at the bottom. The second principle is used to judge the relative ages of strata throughout the world. If a stratum in one part of the world has a fossil biota the same as or close to that of a stratum elsewhere, then the two strata are of approximately the same age. The converse does not apply: two strata from different localities with very different biotas are not necessarily of significantly different ages: they could be of the same age but represent very different environments – one marine and one freshwater for instance.

   Since the middle of the eighteenth century, geologists have painstakingly been reconstructing the sequence and thus relative ages of strata throughout the world, and the work continues to this day, so that we now have considerable knowledge of the relative ages of sediments worldwide and thus of the sequence in the fossil record of any group of organisms in which we are interested, together with a hierarchical classification of stratigraphic time, dividing the whole Earth history into aeons, divided into eras, divided into periods, divided into epochs, divided into stages. And so, fossils found at different levels in the sequence can be placed in time relative to one another.

   Some of those who choose not to accept that evolution has occurred deny the historical nature of sedimentary dating. But those people now have to confront the acceptability of modern physics as well as all historical geology and systematic biology. During the twentieth century a number of techniques were developed for radioactive dating, using measurement of the rates of decay of radioactive elements to give the ages in years of rocks and directly or indirectly of fossils.

3. As we saw above, pious scientists in the seventeenth and eighteenth centuries had great difficulty in accepting the reality of extinction. To them fossils were either a parallel creation, probably never alive, or, alternatively, creatures known only as fossils would one day be found alive as the world became more fully explored. Most fossils then known were of marine animals, and it was easiest to believe that someday they would turn up from the depths. But at the end of the eighteenth and the beginning of the nineteenth century, large fossil mammals, mammoths, ground sloths and others were discovered in both the Old and the New World. It was very unlikely that such conspicuous land animals had been overlooked as the Earth became better known. Many of these had been described as fossils by Georges

Cuvier (1769–1832), the founder of systematic vertebrate palaeontology, and it was he who convinced the scientific world of the reality of extinction.

4. It is also Cuvier, with his fellow French geologist Alexandre Brogniart, who share the credit with an Englishman, William Smith (1769–1839), for establishing the principle of correlation (see above) for the relative dating of fossils. Thus, in a rock section, if each stratum has its own distinctive suite of fossils, it can be assumed that those in a lower stratum had become extinct before the preservation of those in the stratum above. A good example is the series of ammonite zones to be found at the beginning of the Jurassic period in the rocks of the north Somerset and south Dorset coast. But unless the biota of the world has been steadily diminishing since the earliest fossil record, all the new fossils characterising a zone must have come into existence at or before the beginning of that zone. There has been change (or 'progress') in the fossil record throughout, with one biota replacing the immediately previous one.
5 and 6. Two obvious explanations suggest themselves for the progression. Cuvier and other early nineteenth century palaeontologists believed that the history of the Earth was to be a series of catastrophes that wiped out all living things and that after each catastrophe the biota was re-created with slightly different animals that survived until they themselves were wiped out.

The other explanation was that the younger biota arose from the older by phyletic evolution and speciation. Two arguments favour evolution; firstly, there is no probable explanation of the whole series of creation events that would be needed, nor is there any evidence of such a creative event. Secondly there has been a small number of major extinction events in the history of the Earth (of which the most famous, but not the most catastrophic, was that at the end of the Cretaceous Period, ca. 65 million years ago – extinguishing all the remaining dinosaurs – but see below!). But there is no evidence of any extinction event that wiped out all the biota. Furthermore, there is what is known as a 'background rate' of extinction. Fossil species become extinct (and new species appear) regularly in the record, not just coinciding with major extinctions.

This second point was made forcefully by the geologist Charles Lyall (1797–1875) in the third volume of his *Principles of Geology* (1833). He set out to divide the era from the Cretaceous extinction to the present day into four epochs. But rather than using the classical correlation methods of Smith and Cuvier, Lyall used a statistical technique. Using a vast data base of living and fossil mollusc shells, he defined each epoch in terms of the percentage of fossil shells found that were still known alive today – Eocene ca. 3%; Miocene ca. 20%; Older Pliocene 33–50%; Newer Pliocene ca. 90%. Thus, while many new species must have evolved since the beginning of the Eocene, there could have been no time at which an extinction event wiped out the mollusc fauna, contrary to Cuvier and Briognart's study of the same era.

Thus the 'catastrophism' of Cuvier and others can be rejected, and change from one stratum to another in the fossil record is evidence of evolution.

One category of fossils has always been of interest to evolutionary palaeontologists. It consists of extinct organisms that span the difference between what are now

distinct taxonomic groups. The most famous of such fossils is Archaeopteryx from the Upper Jurassic of Southern Germany. Some half a dozen skeletons are known, preserved in the fine lithographic limestone of Solnhofen region. Archaeopteryx is usually presented as a 'missing link' between reptiles and birds but should more correctly be thought of as a bird that has retained primitive reptilian features. The most important bird feature is the presence of beautifully preserved feathers; not just contour feathers surrounding the body, which may have been present in some dinosaurs found in China, but true flight feathers on the wings, so diagnosed because they are asymmetrical with an off-central shaft and arranged as primaries and secondaries as in living birds. Otherwise Archaeopteryx is very much like small carnivorous dinosaurs. It has teeth in its jaws (seen also in later fossil birds); there is no massive sternum for the origin of flight muscles, and the long bones are solid rather than hollow as in birds. Its 'hands' retain three long flexible fingers with claws, and there is a long tail of vertebrae but fringed with feathers. However, the legs are more like those of living birds. To sum up, Archaeopteryx is not only a feathered dinosaur, but also a 'stem-group bird', demonstrating that birds are in fact a subgroup of dinosaurs.

Fossils and Phylogeny

Having demonstrated in general terms that the fossil record embodies evidence for evolution, two examples of individual evolutionary series are now presented. The first involves the evolution of an anatomical structure, using the concept of transformational homology, and the second an evolutionary series of animals.

For the example of transformational homology, we can take the three ear ossicles of mammals (see Figure 2.6) and trace their history in the fossil record. There is, first, evidence of the homology of the quadrate and the incus, and of the articular and the malleus from the embryology of mammals. In the foetus of primitive placental mammals, such as the hedgehog, the malleus can be seen developing in continuity with Meckel's cartilage; the cartilage then forms the axis of the lower jaw in vertebrates. Only later does the malleus become separate. The incus is then loosely attached to the malleus, and the stapes to the incus. There is also a ring-shaped bone, the tympanic, that holds the mammalian ear drum, into which the malleus inserts. Marsupial (pouched) mammals, such as the kangaroo, are, in most structures, more primitive than placentals such as the hedgehog. The baby kangaroo is also borne at a very early stage of foetal development, so that when the newly born 'Joey' suckles its mother, it is the primitive reptilian jaw joint that is used. The young kangaroo swaps from the primitive quadrate-articular articulation to the diagnostic mammalian one in the early days of its life.

Turning to the fossil record, the first creatures showing any diagnostic mammalian features occur in the Carboniferous period, some 315 million years ago. The first mammals with all the diagnostic characters appear in the Upper Triassic just over 200 million years ago. Between these there is a rich record of what are technically known as stem-group mammals. These do not constitute a single lineage from the

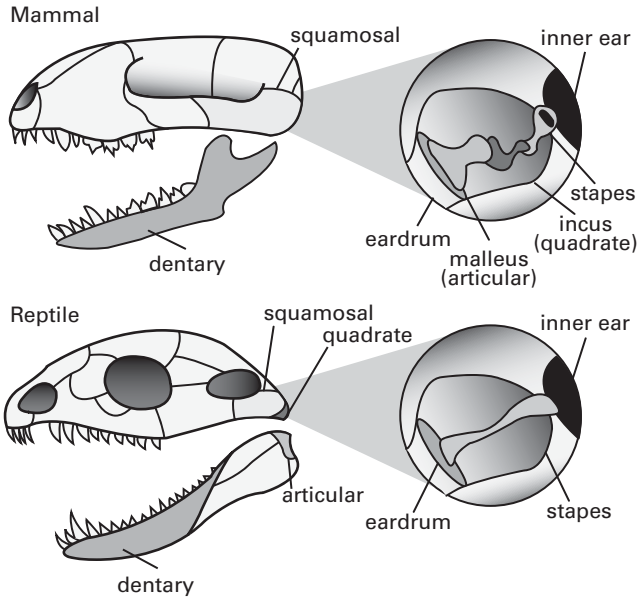


Figure 2.6 Evolution of the auditory ossicles (ear bones) of mammals from the jaw. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

most primitive stem-group mammal to the earliest true mammal, but a rich bush-like pattern. Nevertheless, it is possible to see every stage in the evolution of the middle ear of mammals from the jaw region of early tetrapods. The quadrate (incus) is reduced in size and loosens in the skull. The malleus (articular) is similarly reduced. A jaw bone called the angular is converted into the tympanic, while other lower jaw bones are lost leaving only the dentary, the sole lower jaw bone of mammals, which grows back to form the jaw joint with the top of the skull (Figure 2.6). Note how in the reptile the quadrate and the articular still form part of the jaw (again strong evidence for homology and for similar ancestry).

Once evolution was accepted among at least some palaeontologists in the late nineteenth century, it was assumed that by searching the fossil record, one could find direct evidence of phyletic evolution in the form of series of fossils through time representing ancestor–descendant sequences. The simple idea of the scala naturae turned into evolutionary history.

Probably the most famous example of this was the evolution of the horse. About 55 million years ago the earliest known member of the horse family (*Equidae*) flourished in the early Eocene epoch. Usually known as 'Eohippus' it is more correctly known as *Hyracotherium*. There are many species, the smallest of which is about the size of a domestic cat. Today there is only a single horse genus, *Equus*, that includes domestic and wild horses, asses and zebras. It was natural that when a number of apparently intermediate forms were found that the whole collection should be

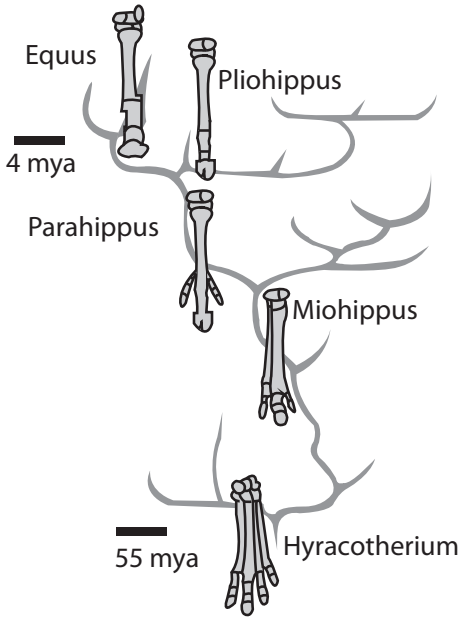


Figure 2.7 Evolution of horse limbs.

arranged in a linear series, not only to demonstrate the evolution of modern horse characters but as an actual ancestor–descendant sequence. But, in fact, it is now known that the history of the horse family shows a much more complex pattern. There was not just a single evolutionary line from 'Eohippus' to *Equus* but a branching 'bush' with, notably, a great radiation of browsing horses with low-crowned molar teeth, coexisting with early grazing horses with high-crowned molars with self-sharpening vertical plates of dentine, enamel and cementum, the present condition. One of the main differences between 'Eohippus' and *Equus* is that the former has four toes on the forelimb and three on the hind, while *Equus* has one on each. The reduction in toes is seen in Figure 2.7 along with the (predicted) transitional forms.

Nevertheless, there must have been a line of descent from *Hyracotherium* or something closely related to it to the living genus, and if one could demonstrate the acquisition of the characters of *Equus* in sequence through time, it would provide powerful evidence of phyletic evolution in the horse family. One can never be sure that one has an ancestral sequence in the fossil record, but one can, given the evidence, reconstruct the timing of those ancestors by classifying the actual fossils. As a very simplified example, Figure 2.8 represents the classification of just seven extant (or living) horse genera, using the states of just four characters: body size, number of toes on the fore-foot, the presence of high-crowned teeth and the presence of a postorbital bar. Now if the pattern of classification (a **cladogram**) is regarded as a tree, in other words the pattern of evolution, each branch-point or node represents the ancestor of all

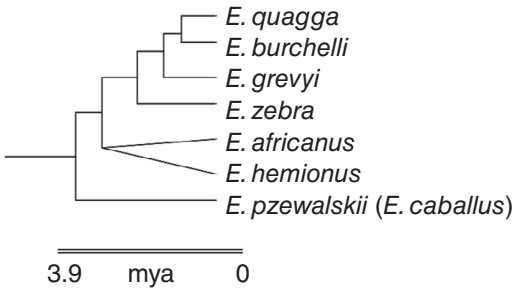


Figure 2.8 Cladogram showing the seven, living species of *Equidae* (genus *Equus*).

the branches that descend from it. Using complete mitochondrial sequences, Vilstrup et al. (2013) explored modern equids showing relationships, for instance, that zebras are "monophyletic within the genus", that is they share a common ancestor.

Biogeography

Biogeography (the geographic distribution of animals and plants) is not random but a result of both environmental and evolutionary factors. Yet the evidence from geographical distribution was instrumental in the work of Charles Darwin. He provided examples from Australia, South America and South Africa, all of which provide similar environments yet dissimilar flora and fauna. Darwin also drew attention to animals and plants on islands. They generally have a flora and fauna less rich than the mainland nearby and several species **endemic** (that is unique) to that location.

A major question for nineteenth century biologists though was how these animals and plants managed to get dispersed at all. Darwin himself spent many years conducting experiments on how snails and seeds could withstand saltwater and may be carried by floating matter or transported on the feet of birds. An alternative hypothesis was proposed by Darwin's close friend, the botanist Joseph Hooker. He explained that plant and animal distribution might well have been affected by land bridges in the past, now covered by rising sea levels. A third view was that different biotas might have been produced by a special creation at each location! But this seemed hardly plausible to Darwin and, of course, did not explain the relatedness seen between species on different islands (for instance the finches discussed in Chapter 1).

When discussing fossil evidence for evolution earlier in this chapter, a series of observations were listed that led to a strong evidence base. This process is repeated and presents the argument for biogeography as a major indicator of evolutionary change:

1. The pattern of distribution of plants and animals cannot be explained by environmental factors alone: their *history* must be invoked.
2. Comparison of geographically distant but similar environments makes it probable that each species developed separately in the environment to which it was most highly adapted.

3. All other things being equal, the resemblance between any two floras or faunas is inversely related to the width and/or effectiveness of the barrier between them.
4. Geographical regions can be arranged as a hierarchical classification (regions within regions) based on classification of the different organisms that inhabit them, and that regional classification can be corroborated by geological events.

The French botanist Augustine de Candolle was one of the first to attempt to put biogeography on a scientific footing. In 1820 he pointed out the distinction between what he called 'stations' and 'habitations' of plants. Thus, the station of a plant is the immediate type of environment in which it flourishes – sundew in acid bogs, water crowfoot in ponds and streams, mahogany in tropical rain forests, marram grass in coastal sand dunes, and so on. But habitations require some other sort of explanation – why does poison ivy occur in all sorts of environments in temperate North America but not in Europe, or magnolia trees in south-eastern USA and Central America, as well as in south-east Asia, but not at similar latitudes in between? Or for that matter, why do some plants, such as the plantain occur in suitable habitats anywhere in the world?

De Candolle then divided the world into first 20, then 40 regions of endemism, i.e. major regions to which part of their flora was exclusively confined. He was followed by zoologists defining land regions. In 1858 Philip Sclater (a prominent lawyer and zoologist) suggested six land areas, based principally on birds, and this pattern was later adopted by Alfred Russel Wallace in his (1876) *Geographical Distribution of Animals*. In most cases there is an obvious barrier between these zoogeographical regions. The Atlantic Ocean separates the two New-World regions from the Palaearctic and African regions, which are separated by the Sahara and the deserts of the northern Arabian Peninsula. The Oriental region is outlined in the north by the Himalayas. The separation though of the Oriental and Australian regions, with very different mammals and birds, was a mystery to Wallace and others and has only been explained in the mid-twentieth century with the theory of plate tectonics.

But why should faunal regions be evidence of past history and thus for evolution? Perhaps there are important differences between the forests of South America and Africa, with jaguars and New-World monkeys designed to fit the former and leopards and Old-World monkeys the latter? The history of Australia gives the lie to this precept. Humans have introduced a whole species of placental mammals – mice, rabbits, pigs, buffalo and even camels – into the island continent, and they have flourished often at the expense of the native marsupials. As Darwin puts it in the *Origin of Species*:

No country can be named in which all the native inhabitants are now so perfectly adapted to each other and to the physical conditions under which they live, that none of them could anyhow be improved; for in all countries the natives have been so far conquered by naturalised productions, that they have allowed foreigners to take possession of the land.

The fact that the distribution of animals and plants demands a historical explanation is emphasised by the comparison of the faunas of islands with the nearest mainland. The Galapagos Islands off the west coast of South America and the Cape Verde islands off the west coast of Africa are very similar. Both archipelagos are tropical

volcanic groups and have never been connected to the mainland. They have a similar climate. Both lack amphibians and naturally occurring mammals, which cannot easily disperse over oceans. But in each case the fauna is obviously derived from that of the nearest continent. The Cape Verdes have a bird fauna, notably with several species of kingfisher, derived from that of West Africa, while that of the Galapagos (including Darwin's finches) is derived from that of South America, as are other elements of the fauna such as the land and marine iguana lizards.

This leads us to another comparison. We can compare the biota of distant oceanic islands, with reference to the nearest continental mainland (as with the Galapagos and the Cape Verdes) and close continental islands such as the British Isles. The British fauna is principally an impoverished version of that of continental Europe; unique mammals are merely endemic subspecies while in the Galapagos Darwin's finches are an endemic subfamily.

This comparison suggests another hierarchy. Britain and Western Europe could be compared to two geographical 'species' within the same 'genus': the Galapagos fauna is sufficiently different from that of South America to give the Galapagos 'genus' status (with the individual islands as 'species'?). On the world scale of land animals, the Sclater/Wallace regions would rank as the highest groups. In an essay published in1855 (three years before his joint presentation with Darwin of the theory of natural selection) Wallace said:

Large groups, such as classes and orders, are generally spread over the whole earth, while smaller ones, such as families and genera, are frequently confined to one portion, often to a very limited district.

He then goes on to claim that the degree of difference between the fauna on either side of a natural barrier is proportional to the effectiveness of that barrier and to its age.

Wallace was obviously reaching for the idea of a biogeographical classification, but such a classification could only be realistically undertaken with two ingredients that only became available late in the twentieth century. These were the theory of plate tectonics and the rigorous method of classification known as cladistics. **Plate tectonics**, originally known as 'continental drift', is the theory that the Earth's crust is divided into a number of rigid plates, including ocean floor and the emergent continents. Plates grow at the volcanic mid-ocean ridges and are destroyed in subduction zones as they slide under the continental masses of other plates. As a result, over geological time, the continents have moved relative to one another. Thus, in our area classification, adjoining continents have split apart dividing originally connected animal or plant distributions – a **vicariance event** (splitting of biota into discontinuous parts). Subsequent evidence of such an event is that many unrelated groups of organisms appear to have been divided into separate species at the same time by that event.

Observational and Experimental Evidence

Evolutionary adaptation is seen in the house sparrow (*Passer domesticus*). Native to Europe and the Middle East, this species has been introduced throughout the world.

From an initial breeding population in New York in 1852 the birds spread rapidly throughout North America undergoing evolutionary change in both size and colour. Northern populations are darker and larger than those in the southwest, while an adaptation to hot humid climates in the south has resulted in lower metabolism and greater insulation. This example of slow, small-scale evolutionary change is well documented by Johnston and Selander from the 1960s onwards, while the consequence of increasing size (increased wing loading) is countered by directional selection on wing area (Monahan, 2008).

There are several such examples of evolution-in-action, but examples of evolution can also be produced experimentally. Changes in the fruit fly (*Drosophila melanogaster*) have been induced through selective breeding and subjecting flies to adverse environments such as low oxygen conditions. The short generation time of bacteria has also been employed to grow on substrates or to 'swarm' much faster than normal. Long-running experimental evolutionary experiments include Garland's (1998) selection of mice for running ability (65 generations), Rose's (1984) selection of multiple fruit fly traits indicating fitness (over 200 populations demonstrating evolutionary radiation) and the longest running of these (1988 to the present day), Lenski's *Escherichia coIi* experiment. From 1988 Richard Lenski has been tracking bacterial changes in 12 initially identical bacterial populations. In one investigation bacteria were encouraged to grow on a citrate substrate rather than glucose. Eventually a spontaneous citrate metabolising mutation (cit+) arose after around 31 000 generations (see Michigan state University website for an overview http://myxo.css.msu.edu/ecoli/overview.html).

3 Genetic Variation within Populations

One of the most arresting aspects of the living world is its diversity. No two individuals of a sexually reproducing population are the same; neither are two populations of the same species, two different species or any two of the higher taxa. The biological diversity of individuals within a species is the subject of this chapter.

Historically, the description of individual variation has been of interest to naturalists and farmers for centuries. A study of the *origins* of individual variation however is a recent phenomenon, contingent on our knowledge of inheritance and heredity.

Inheritance and Variation

Ladybirds, or ladybugs, are an amazingly variable group of insects. Although they all possess a similar body plan comprising domed hemispherical bodies, short legs and bright colours, the colour and pattern variation within species is nothing short of astounding. In Britain the 2-spot ladybird, *Adalia bipunctata*, has both black and red ground colour (black is especially common in the North aiding heat absorption) together with spot patterns merging to form bands, blotches, rectangles and discrete blobs. In Japan and much of the Far East, the Asiatic lady beetle, *Harmonia axyridis*, has at least 25 variants with colour and patterning changing as the animal's geographical distribution changes from East to West. Similarly, a look at any family photograph will reveal marked similarities and differences between close and extended family members. Physical factors such as hair colour, height and even relatively insignificant features such as whether or not the ear lobe is attached all contribute to a natural variation within the group. Even identical or monozygotic twins show differences in body structure through the effects of the environment or because of subtle changes during development.

So how is this variation brought about? Perhaps the simplest explanation is that the two sets of traits (mothers and fathers) are somehow mixed and blended together like paints in a tin? **Blending inheritance** is a theory (never formally submitted scientifically) that the offspring of two individuals will be an 'intermediate' or a mixture of the two parents. A tall male and a small female, for instance, will give rise to progeny intermediate in height. In the absence of any alternative, the 'blending' theory was a commonly held belief in the eighteenth and nineteenth centuries and was accepted by Charles Darwin – although he was acutely aware of its shortcomings. Because

logically blending inheritance will ultimately *remove* variation – the offspring in future generations becoming more and more uniform, more similar, more 'blended'? This is not what we see in nature - variation does not aggregate around the mean; variants are conserved.

From his studies on domesticated animals Darwin knew that variation was heritable, but he was unable to suggest a suitable mechanism.

The answer to this conundrum came six years after the publication of *Origin of Species* in a little-read paper published by Gregor Mendel, presented to his local natural history society in 1865. His **particulate theory of inheritance** postulated discrete characters or factors that are segregated during the formation of sex cells and recombined in the fertilised egg. We now recognise these factors as **alleles**. But it was only in 1900 when two biologists, the Dutch botanist Hugo De Vries and the German botanist Carl Correns, obtained hybridisation results similar to those of Gregor Mendel that Mendel's work (and what we now refer to as **Mendelian inheritance**) became acknowledged within the scientific community. William Bateson (an English biologist working at Cambridge University) translated Mendel's original paper into English (Bateson, 1902) and thereafter began to popularise his work.

When observing variation, it is noticeable that the majority of physical characteristics show what is termed **continuous variation**, which is a smooth *gradient* of the character trait from a very large value to a small value along a continuous scale. The beak size of Galapagos finches demonstrates this as does other measurable characteristics of animals such as height, weight and colour intensity. This is the type of distribution most of us (and certainly the naturalists in the nineteenth century) are familiar with. Mendel however had the good fortune to look at plant characters that varied discontinuously, that is in separate categories. The pea flower was either purple *or* white, the seeds wrinkled *or* round, the pod inflated *or* constricted. Appearance of discontinuous or discrete forms (**discontinuous or categorical variation**) can also be seen in humans (evidence of albinism or in blood groups) where the character within the population is seen in two or more distinct forms.

Discontinuous and continuous variation are examples of genetic variation that can best be described both in terms of phenotype and genotype. This type of *variation within populations* is further considered later in this chapter.

The **phenotype** is the outward or physical appearance of the organism. Collectively, populations of animals and plants may be represented as frequency distributions (see Figure 3.1). Notably, a continuously varying character is often graphed as a bell-shaped distribution with intermediate phenotypes more common than extreme ones. In contrast a discontinuously varying (or discrete) character appears as discrete blocks within a bar chart.

The origins of the two distribution types are dependent upon the **genotype** (the genetic make-up) of the organism. For instance, in the Galapagos finch, *G. fortis*, we know that parents with larger beaks produce offspring with larger than average beaks (and vice versa). We also know that there is a precise relationship between the probabilities of a child having a particular blood group and the blood group of its parents.

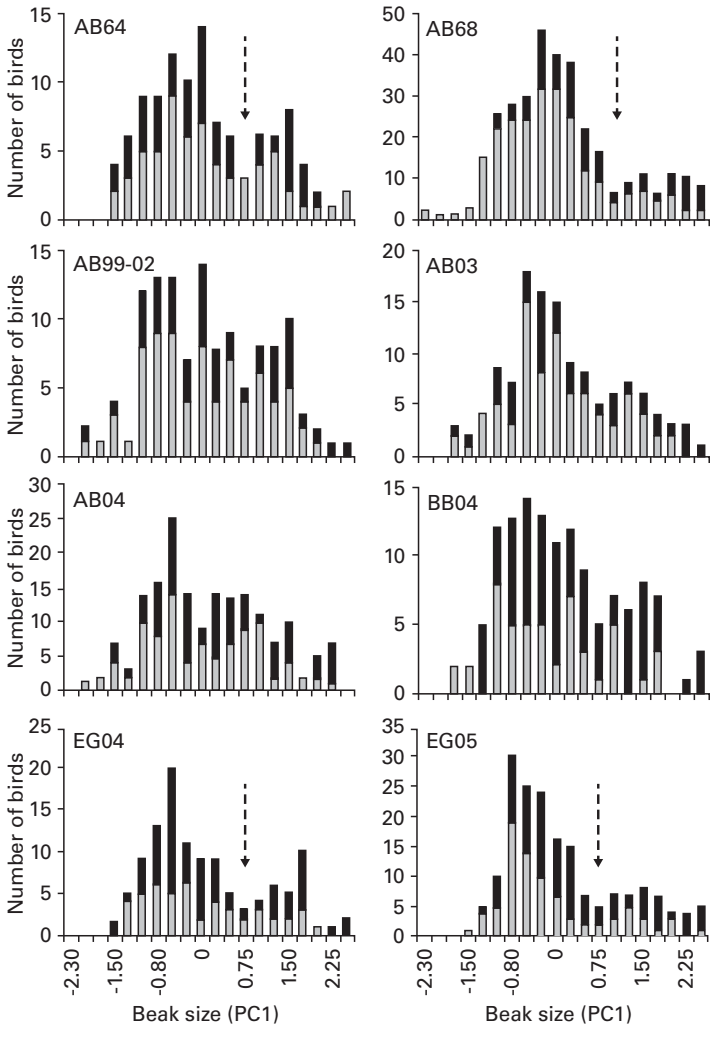


Figure 3.1 Frequency histograms showing variation in beak size of *G. fortis* (black bars represent mature males and arrows discontinuity between large and small beaks). Reproduced from Hendry et al. (2006) with permission.

If a character is determined by only a single allele, then the progeny within a population will conform to only a few discrete types. In Mendel's pea flowers, for example, pure breeding Tall plants (the dominant character) crossed with pure breeding dwarf plants (the recessive) will produce a first (F1) generation of only Tall pea plants (the heterozygote, 'Tt'). Thereafter crosses between these (F1) Tall plants will produce both Tall and dwarf offspring in the following (F2) generation in a ratio of 3:1 – see Figure 3.2. Similar results are seen with other traits in the pea plant such as purple and white flowers, round and wrinkled seeds.

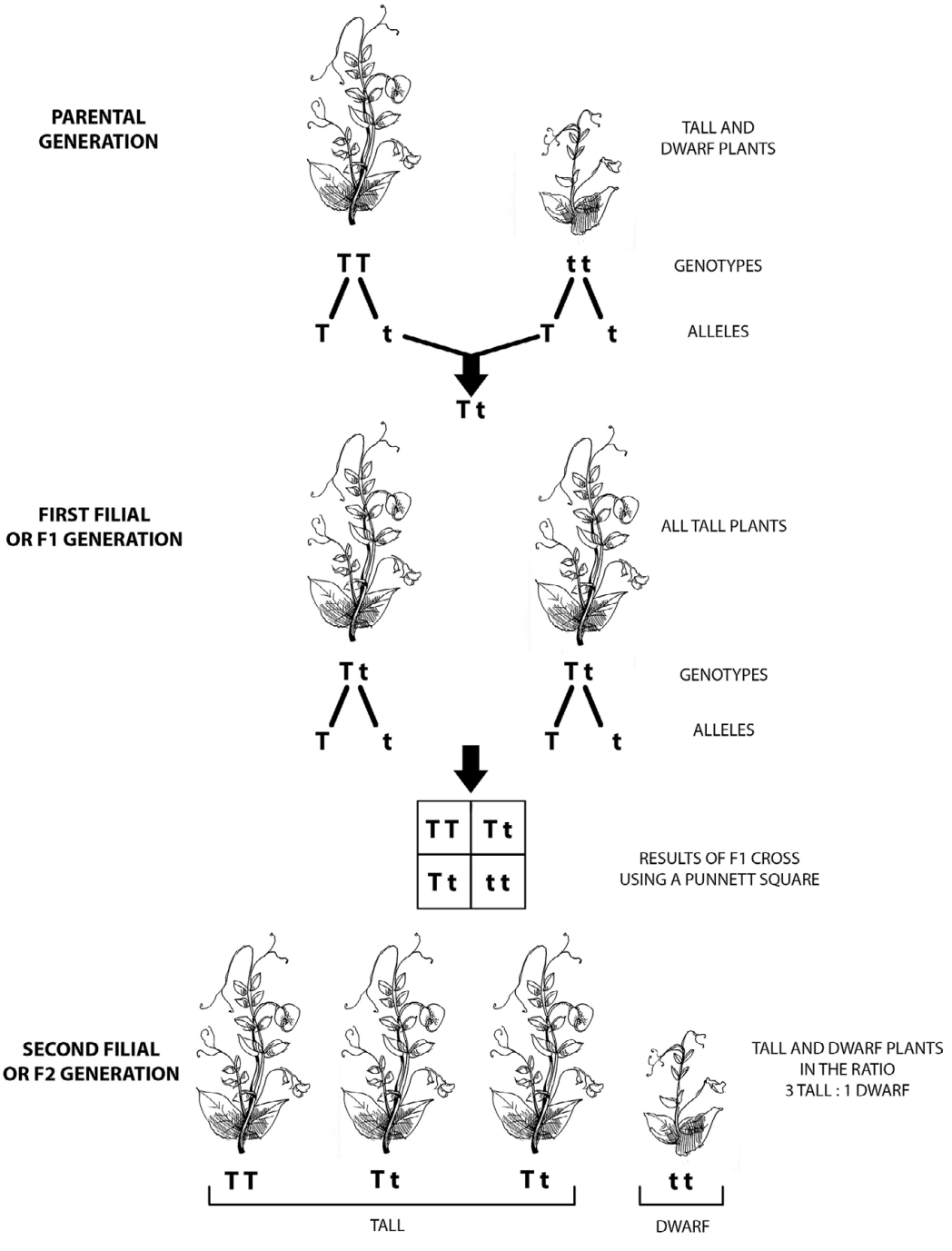


Figure 3.2 Diagrammatic representation of Mendel's early crosses using pea plants.

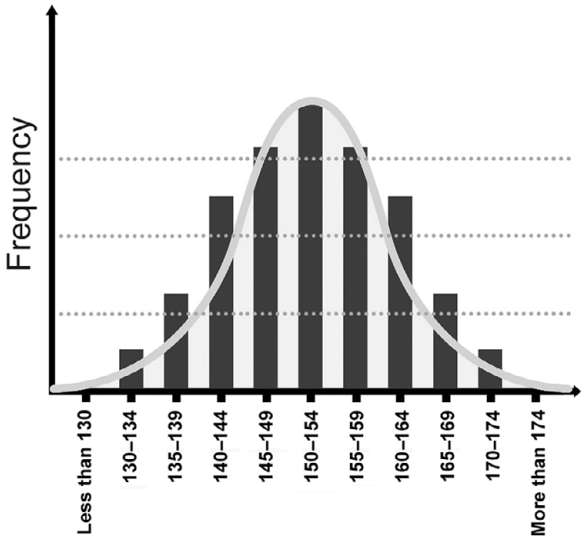


Figure 3.3 Continuous variation in human height (in metres). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

Similar Mendelian genetics can be used to observe future F3 and F4 generations. Also, the monohybrid (single gene or single allele pair) cross illustrated in Figure 3.2 could be expanded to explore dihybrid (two genes) or trihybrid (three genes) crosses.

But in characters such as human height, finch beak size or crop yield the observed variation could not be produced by a few alleles at selected chromosome loci. By increasing the number of alleles and the number of loci the frequency distribution becomes ever more continuous (Figure 3.3). Continuous variation is polygenic, that is controlled by many gene loci. Indeed, Mendel himself had noted (in his original 1865 paper) that multifactorial inheritance can generate a continuous frequency distribution, a point confirmed in genetics labs at the beginning of the twentieth century.

Two biological phenomena have been alluded to above – **variation** (referring to differences *within* a species) and **diversity** (applied to differences *between* species).

Origins of variation can be either genetic or environmental, but for any change to be heritable, a genetic influence is required. Short-term changes over the lifetime of an individual are termed **ontogeny**, whereas longer term changes, taking place over millions of years giving rise to distinct populations and even new species, are termed **phylogeny**. This distinction between the growth of the individual (ontogeny) and its ancestry (phylogeny) has been debated from the time of Aristotle onwards. Both these phenomena lead to changes within the individual genome, but over the longer time frame further genetic change may lead to an alteration of the entire gene pool.

Genetic variation within a species is the 'clay of evolution', it is the substrate on which biological selection operates. As such it forms an important research focus for evolutionary biologists. This chapter deals with questions such as the origins of variation, the extent of genetic variation and patterns of inheritance (transmission of variation).

Early Ideas Regarding the Continuity of Life

Strange hybrids of animals and human beings were a characteristic feature of ancient, and indeed more recent, mythologies. Reproduction was seen to be the dominant life force and by the nineteenth century over 300 theories of procreation had already been published. The Greek philosopher Aristotle was perhaps the first great scientist/observer of the natural world. He produced many written works with around one quarter of those surviving relating to the Life Sciences.

Three types of reproduction were known to Aristotle: sexual reproduction (in the 'higher' animals including some insects), regeneration (common in marine animals) and spontaneous generation (as seen in 'vermin', fleas, mosquitoes, maggots and the like). His main contribution to the subject of reproduction though was the concept of potentiality, the notion that an embryo is not complete and preformed but somehow acquires its potential during development. Male and female contributions are also specified. The female provides the basic matter or substance of the egg, the male provides the 'form' or the pattern in the seminal fluid – hence the idea that the role of the male in reproduction is somehow more significant than that of the female – an idea that persisted well into the nineteenth century (refuted only when Mendel demonstrated the equal contribution of the sexes).

During the eighteenth century, contrary to the idea of potentiality, the theory of preformation was proposed. The theory of **preformation** supposed that an embryo arose complete in every detail (as an organism in miniature). The male was said to implant a preformed 'homunculus' within the body of the female. This theory was not dependent on what was seen but what was *believed* to exist. Following the results of further embryo studies however, a later theory of pangenesis supplanted the theory of preformation. The homunculus theory fell into disrepute and the doctrine of **pangenesis** was put forward to explain heritable changes. The assumption here was that somehow invisible particles or 'gemmules' were transferred (in the blood) from all the organs of the body to the sex cells. Thereafter the fertilised egg cell (zygote) redistributed the particles to the developing embryo and eventually to the adult form. The pangenesis theory has long-lasting consequences, for instance, the notion of a blood line (still common in animal breeding circles) and terms such as 'blue blood' or 'blood relatives', which continue in everyday speech.

Biological Inheritance and the Work of Gregor Mendel

Charles Darwin knew nothing of modern genetics. Yet a knowledge of variation was central to, and a prerequisite of, his theory of evolution by natural selection. The first two chapters of his major work *Origin of Species* (1859) illustrate this. Chapter one is called 'Variation under domestication' and Chapter two 'Variation under nature'. He published 19 books in all, drawing material from his personal observations of many kinds of animal and plant. He studied barnacles, living and fossil, orchids and

primulas. Darwin studied variation to explain diversity, but the (genetic) nature of variation was unknown to him.

Between 1856 and 1863, Gregor Mendel, monk and latterly abbot of the monastery of St Thomas, Brunn, cultivated more than 33 000 plants and carried out dozens of experiments on the inheritance of different biological traits in the garden pea, *Pisum sativum*. He examined seven different physical traits or characteristics:

- seed shape (round or wrinkled)
- seed (cotyledon) colour (yellow or green)
- flower colour (purple or white)
- pod colour (green or yellow)
- pod shape (full or constricted)
- pod & flower positioning (axial or terminal pods and flowers)
- stem length (tall [6 feet] or dwarf [1 foot])

Mendel's aim was to investigate inheritance of these characteristics and to look for mathematical regularities. Problems with blending (a theory of inheritance where offspring appeared intermediate in appearance to their parents) had been known for many years. If all offspring were some sort of parental blend, then after only a few generations much variation within the population would be lost and individuals would all tend towards an 'average' appearance. Common sense told Mendel, Darwin and others that this was not so. Individual animals and plants retained their distinctive characteristics despite evidence to the contrary from human beings (in skin tone, for example, many children are in fact a blend of their parents' skin colour).

The sensible approach therefore was to cross pure strains of his plants and observe the hybrids formed. No doubt Mendel must have considered breeding animals or other plant types, but pea plants suited him well. They were small, easy to cultivate and had many clearly defined, heritable differences; varieties of pea were collected and sold by gardeners and seedsmen. In addition, pollination was easily controlled, and the plant had a short growing time. Earlier studies had indicated to Mendel that the pea plant usually reproduced by self-fertilisation, but outcrossing could be achieved by simply removing the stamens (together with developing pollen grains) from the plant before the pollen was shed. The carpels (female parts of the flower) could then be pollinated by brushing with mature pollen grains taken from another plant.

Upon analysis of these and many other results, Mendel derived several important conclusions:

- He supported the view of particulate inheritance. The 'factor' determining inheritance was solid and relatively immutable, certainly not a result of blending.
- Factors could be hidden but not destroyed. If both factors are present in the same plant, only one is expressed – the one that appears in the organism is termed dominant, the one that is masked is the recessive factor.
- Factors occur in pairs and during gamete formation they are separated or segregated so that only one factor appears in the gamete.

- ❖ Factors segregate independently of one another. When considering several traits together, gametes produced may contain any random selection of (single) factors.
- ❖ Factors recombine in the zygote at fertilisation restoring the pair.

Mendel's work was read to the local natural History Society in Brunn in 1865 and was published in 1866. There it remained undiscovered for 34 years.

Mendel has, rightly, been called the founder of modern genetics. His methodical planning, mathematical analysis and quite outstanding insight has provided the platform on which all genetic analysis stands. Modern terminology has changed of course. Mendel's factors are now recognised as **alleles** – alternative forms of a gene. Allele pairs may either be homozygous (alike) or heterozygous (differing), and, as they separate and recombine, they form the genotype or genetic constitution of the organism. Only certain alleles are expressed, and these contribute to the organism's phenotype (its outward physical appearance).

In practice though many alleles are linked together on the same chromosome (several thousands of genes of course but only tens of chromosomes). In theory therefore, all alleles on that chromosome will be transmitted together as a set. In practice, alleles are separated due to crossing over (as chromatids break and recombine). The nearer alleles are to one another (the closer their loci) the less likely they are to segregate. These events introduce an important exception to Mendel's Second Law.

Mendel also considered *patterns* of inheritance. He went from considering inheritance of a single characteristic (a monohybrid cross) to looking at the transmission of two independent traits (a dihybrid cross). For example, plants with wrinkled, yellow seeds could be crossed with those of round green seeds. As our 'parents' here are double homozygotes (rrYY and RRyy, respectively) then the resultant F1 hybrid will be the (double heterozygote) RrYy. Further genetic crosses of the F1 hybrids yield the familiar 9:3:3:1 ratio found in the F2 generation.

To confirm independent segregation of alleles Mendel also undertook the arduous task of carrying out a trihybrid cross – the transmission of three independent traits. Theoretically a 27:9:9:9:3:3:3:1 ratio is expected (obtained by multiplying three independent 3:1 ratios). The excellent agreement of Mendel's observed and expected results finally confirmed his views on particulate inheritance, segregation and assortment. Perhaps not surprisingly, this final activity for Mendel required 'the most time and effort'.

With many thousands of genes and relatively few chromosomes (numbering somewhere between 10 and 50 in most animals and plants) many genes must occupy sites on the same individual chromosome. Therefore, patterns of inheritance should differ from the standard Mendelian ratios. And this indeed is the case.

If pure breeding purple/long-flowered pea plants are crossed with pure breeding red/round plants, the following (F1) generation should be all heterozygotes. However, in the early 1900s, William Bateson (inventor of the term 'genetics') and R. Punnett (of 'Punnett square' fame) found this not to be the case. In their F2 generation Bateson and Punnett noted the predominance of purple/long and red/round phenotypes – the original (F1) lines. They suggested perhaps some form of 'coupling' between these

genes. Genes located on the same chromosome and transmitted together are said to show complete **linkage**.

At the beginning of the twentieth century the chromosomal theory of inheritance was developed suggesting that Mendelian factors, the genes, were carried on chromosomes. Later work by Thomas Hunt Morgan on the fruit fly, *Drosophila*, confirmed this general conclusion – genes could indeed be coupled or linked during transport into the sex cells. Morgan's team began mapping chromosomes showing how genes for characteristics such as white eye, miniature wings and yellow body are arranged linearly on the chromosome occupying limited but specific regions or loci. A view anticipating by several decades later work showing genes to be regions of chromosomal DNA.

Mapping the Genome

Bateson and Punnett discovered that, on occasion, sweet pea plants failed to show independent assortment (during gamete formation the alleles segregate or separate independently of one another so that, theoretically, any member of the pair can appear in any gamete). Progeny did not follow the expected Mendelian ratio. Thomas Hunt Morgan noticed similar deviations when looking at inheritance patterns in *Drosophila*. The conclusion was that some form of physical 'coupling' existed between alleles; that different traits may be located on the same pair of **homologous chromosomes**. Morgan also suggested that when homologous chromosomes come together during meiosis, chromosomes may exchange genetic material thus providing (recombinant) **cross-over** products. Under the microscope chromatid interactions are seen (Figure 3.4) with chiasmata (the point at which paired homologous chromosomes remain in contact) visible.

Further quantitative studies allowed a cross-over value to be determined:

$$\text{crossover Value} = \frac{\text{No.recombinants}}{\text{Total no.offspring}} \times 100\%$$

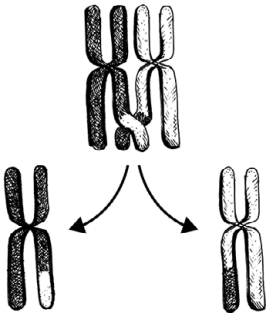


Figure 3.4 Crossing over in *Zea mays.*

Morgan discovered that the proportion of recombinant progeny varied considerably. He surmised that differences in cross-over values reflected actual distances separating genes on a chromosome (recombinants are more probable the greater the distance apart). Morgan's student, Alfred Sturtevant, enhanced the model linking proportion of recombinants to gene loci. The per cent recombinant value was then used to determine linkage maps.

It was decided that one genetic map unit (mu) was to be the distance between genes for which 1% of the products of meiosis were recombinant.

$$\begin{aligned} 1\text{mu} &= \text{RF (recombinant frequency) of } 1\%(0.01) \\ 1\text{mu} &= 1 \text{ cM (centimorgan)} \end{aligned}$$

A standard approach used in linkage analysis is the Three Point Test Cross (triple heterozygote to a triple recessive). Strange cross-over inconsistencies together with cytological evidence demonstrate the existence of double cross overs. And cross overs in one region may well affect the probability of cross over in an adjacent region, a phenomenon known as **interference**. Genetic interference can be quantified by calculating a coefficient of coincidence:

$$\textit{Coefficient of coincidence} = \frac{\textit{observable frequency of double recombinants}}{\textit{expected frequency of double recombinants}}$$

$$\textit{Interference} = 1 - \textit{coefficient of coincidence}$$

(if there are no double recombinants, then coefficient of coincidence = 0).

In summary, crossing over:

- ✓ takes place in prophase 1 of meiosis
- ✓ where chromosomes shorten & fatten
- ✓ chromosomes associate in homologous pairs forming bivalents
- ✓ each chromosome is made up of two chromatids
- ✓ chromatids wrap around each other
- ✓ chromatids repel but are joined at certain points (called chiasmata)
- ✓ chromatids break and recombine with other (non-sister) chromatids

Genomics is that branch of biology that attempts to understand the molecular organisation of the entire genome (that is, the information content and the gene products that the genome encodes). (Genome = entire complement of genetic material in a chromosome set.)

Genomics can be divided into two basic areas of study:

1. **structural genomics** characterising the physical nature of the genome

   and

2. **functional genomics** looking at the range of transcripts produced by a given organism (its transcriptome) and the set of encoded proteins (its proteome).

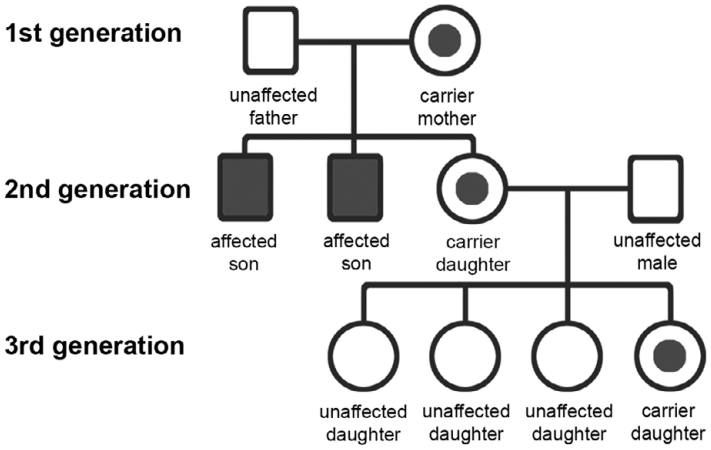


Figure 3.5 Transmission of an X-linked genetic disorder (Duchenne muscular dystrophy). Duchenne muscular dystrophy (DMD) is characterised by a wasting and degeneration of muscle tissue due to the lack of the protein dystrophin. (Incidentally, dystrophin is coded by one of the longest human genes, 2.4-Mb in length). This is a sex-linked condition with the mutation appearing on the X chromosome. As a consequence, this condition is usually found in males (no corresponding allele to counteract its effects on the male's Y chromosome).

The major aim of structural genomic analysis is the elucidation of the entire DNA sequence of a given species. Comparative genomics on the other hand compares the genomic sequences of different species with a view to understanding the course of evolution. It transpires that within species there is considerable synteny (conserved gene location within large blocks of the genome).

In contrast to the detailed experimental work carried out by Mendel, the study of human genetics has been largely observational. Patterns of inheritance are generally derived by inference. The basic tool of the human geneticist had been that of pedigree analysis. Family pedigrees are presented, in diagrammatic form, in such a way as to make clear the transmission of characteristics (often genetic defects) between parents and offspring (see Figure 3.5). However modern advances in human gene sequencing are revolutionising human and medical sciences.

To explore **whole genome sequencing**, tentative discussions took place in 1985 at the University of California, Santa Cruz, regarding the possibility of constructing a complete genome sequence for humans. Hitherto, DNA sequencing techniques had been developed in the mid-1970s by workers such as Ray Wu at Cornell, Fred Sanger at the MRC Centre, Cambridge and by Walter Gilbert and Alan Maxam at Harvard.

Early work centred on specific regions of DNA, often specific genes, using restriction enzymes (discovered in the late 1960s) to 'cut' the DNA in a specific way. The selected DNA pieces were then incorporated into a vector (often a bacterial plasmid), which was introduced into a host cell (again bacterial) and cloned on a

suitable medium. In this way an appropriate quantity of the desired gene was obtained. A labelled probe (generally a single-stranded piece of complementary RNA or DNA) was then used to identify the DNA region under consideration. Then, using the polymerase chain reaction (PCR) process, DNA was heated to separate its two strands (the chromatids), and 'free' nucleotide bases (A, C, G, T) were used to re-form the original DNA. In this way, a physical mapping and ordering of DNA fragments had been completed.

The move from manual sequencing methods (as employed initially by Sanger and his colleagues) to automated sequencing in the 1990s allowed molecular biologists the luxury of attempting to sequence an entire genome.

In the early stages of whole genome analysis, a technique called shotgun sequencing allowed relatively small bacterial genomes to be sequenced. This approach (very briefly) involved:

- Shearing DNA into random pieces
- For each piece reads (approximately 500 bp) were identified from each end
- A computer program assembles the multiple, overlapping ends or reads into a contiguous sequence (or contig)
- Contigs are placed together to elucidate the entire genome

This strategy was used to sequence the genome of the bacterium *Haemophilus influenzae* in 1995. The first eukaryotic genome (unicellular yeast cell, *Saccharomyces cerevisiae*) was sequenced the following year and the first multicellular organism (the nematode worm, *Caenorhabditis elegans*) in 1998. Of the other model organisms, the fruit fly genome (*D. melanogaster*) was sequenced in 2000.

The Human Genome Project was launched in 1990 in the United States through funding from the National Institutes of Health and Department of Energy. Its goal was to map 90% of the millions of base pairs in human DNA and to identify all human genes from both a structural and functional point of view (the DNA of telomeres and centromeres was omitted from the project). The consortium was joined in 1993 by scientists in the United Kingdom at the newly opened Sanger Centre (funded by the MRC and Wellcome Trust). An international collaboration then followed with researchers using variations of the shotgun approach to identify the make-up of specific DNA sequences. An initial draft of the genome was published in the year 2000 and was finally completed in 2003. Interestingly competition from a privately funded company, Celera Genomics, producing a rival sequence, accelerated the end stages of the project.

To summarise the main findings: the human genome was found to be smaller than expected with just over 20 000 genes uncovered; there were more repeated DNA sections than previously thought; and fewer than 7% of the protein families were vertebrate specific. Nearly half of the genes discovered had unknown function.

Origins and Maintenance of Variation

Each organism has a unique genome derived from the parental segregation of alleles at meiosis together with a random combination of alleles at conception. A population

therefore consists of a collection of unique genomes providing a **gene pool** with an inherent and measurable variability. Variation can be caused by internal or external events during the development of the organism.

External, environmental factors can affect individual development. For instance, pine trees growing at the edge of a plantation produce needles that are smaller and thinner than those, more protected, trees at the centre, and human skin subjected to sunlight will begin to darken over time. Such externally induced effects are generally reversible and non-heritable. Individual variation can also be the result of internal, genetic factors. Genetic variation can arise through:

1. gamete formation at meiosis (for example, crossing over)
2. during recombination of homologous chromosomes at fertilisation
3. through mutation (alteration of the DNA strand)

Also, phenotypic variation can occur during development as genes interact both with one another and their chemical environment.

But to return to our three potential origins of genetic variation:

1. During metaphase 1 and metaphase 2 of meiosis (meiosis remember is a double division) chromosome pairs (bivalents) align themselves randomly across the equator of the cell attached to the spindle. The distribution of the chromosomes within each pair is random. The independent assortment and segregation of both chromatids (meiosis 1) and chromosomes (meiosis 2) will result in unique allele combinations within the gametes. Another feature resulting in genetic re-assortment is the phenomenon of cross overs (see Figure 3.4).
2. Sexual reproduction also introduces an element of chance-mixing into chromosome combinations. Only one of two chromosomes from each parent will find its way into the gamete. If mating is random, then any one of many chromosome combinations (hence allele combinations) can occur in the zygote. This form of gene reshuffling forms a permanent impression on the genome of the zygote and is therefore heritable. No new forms are created, but this type of genetic variation gives rise to the continuous variation seen in features such as body mass, petal number, beak size of birds, etc.
3. Ultimately though, the origin of all evolutionary change is rooted in the creation of new forms and of new alleles – that is the production of **mutations**.

Mutation

A mutation is any alteration in the DNA of an organism. This may encompass either the *structure* of DNA (that is the nucleotide sequence) or the *amount* of DNA. For a mutation to be heritable it must occur in the sex cells or gametes rather than the somatic or body tissue (for only mutations in the germ line are heritable). There are several kinds of mutation, each with their own characteristics. These can for simplicity's sake be referred to as **gene (or point) mutations** and **chromosome mutations**, the former affecting a single nucleotide base, the latter changing the appearance of entire chromosomes.

In 1937 Dubine, a Russian biologist, discovered that up to 2% of fruit fly populations contained spontaneous mutations. This important observation was generally overlooked until about 20 years later as most biologists at the time viewed mutations as accidents and of no real significance. Work by Harris, Lewontin, Hubby, Stone and others in the 1960s established beyond doubt that mutation is a regular phenomenon, present in all species empowering variation and evolution.

Point mutations come about through DNA replication and involve either gain (addition/substitution) or loss (deletion) of nucleotides. Substitutions are the commonest form of nucleotide change occurring at a rate of around one substitution every thousand million generations. In one example, a single point mutation in the β amino acid chain in human haemoglobin alters the haemoglobin molecule leading to the condition known as sickle-cell anaemia. A simple substitution of uracil for adenine in the nucleotide alters the triplet code from GAA to GUA. The amino acid valine is produced instead of glutamic acid. Therefore, an abnormal polypeptide chain forms leading to abnormally long haemoglobin fibres which, at times of low oxygen concentration, results in the 'sickle' shape of the owner's red blood cells.

The speed or rate of mutation varies dramatically according to the location, sex and type of base of the nucleotide. For example, mitochondrial DNA often mutates faster than nuclear DNA, while the DNA of the AIDS virus mutates faster than either of those. In mammals, mutations are six times more likely in sperm cells than in egg cells, and in 1977 the French biologist Lucotte suggested that mutation rate varied with the complexity of the organism. Thus, eukaryotes will have higher mutation rates than prokaryotes, vertebrates will have higher rates than invertebrates and 'lower' vertebrates' higher rates than the 'higher' vertebrates and so on. Evidence for this point of view though is not very convincing. By and large, bacteria have lower rates of mutation than the Metazoa, and there is evidence that mammals have higher mutation rates than other animals. But the different ways of scoring mutation (based on morphological/physiological effects, mutation rate per gamete or mutation rate per genome) combined with factors that can elevate mutation rate (physical factors such as UV radiation, ionising radiation or chemicals together with transposable elements and 'mutator genes') all conspire to produce a confused picture.

The DNA strand is not simply a string of triplets coding for specific amino acids. Up to 90% of its length can be made up of non-coding DNA. The internal structure of the gene is also remarkably complex consisting as it does of **exons** (nucleotide sequences forming amino acids), **introns** (sequences transcribed but not translated into amino acids) and **flanking regions** (important in regulating gene expression, see Figure 3.6). The probability of mutation appears to vary as to where genes are found in this complex structure. Regions of high guanine–cytosine content (called **isochores**) can be mapped onto the chromosome yielding specific gene assemblages. Any gene moving from one isochore to another will experience a shift in the rate and direction of mutation. A further class of highly variable and mutable DNA sequences are the **variable number tandem repeats** (VNTRs), a region used for genetic fingerprinting. VNTRs comprise highly repetitive regions of DNA within the genome. These sequences, sometimes called minisatellites, are small (usually 15- to 60-bp long),

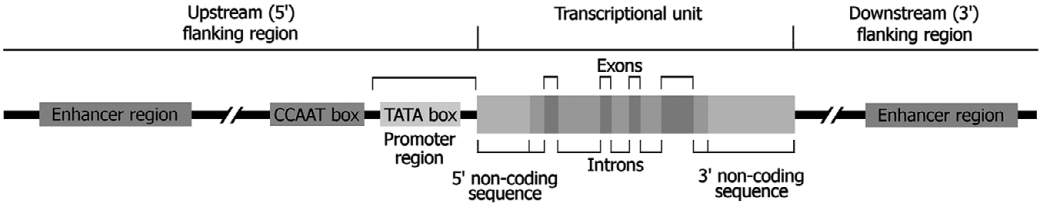


Figure 3.6 Detail of the protein-coding unit within a eukaryotic chromosome.
(A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

non-coding and suitable for use as genetic markers. VNTRs are however highly mutable with mutation rates of up to 15%. Naturally a common core is highly conserved, which will allow this material to be used as a genetic profile of the individual.

The process of protein manufacture within cells can be conveniently divided into two stages:

- TRANSCRIPTION: the copying or transcribing of the genetic code onto the (messenger) RNA molecule. This copy will pass out of the nucleus into the cytoplasm where it attaches to a ribosome. Studies of viral DNA infecting mammals revealed that viral DNA transcripts had little correspondence to the original DNA. The transcript was generally shorter in length with pieces removed. The RNA transcript therefore is processed in the nucleus before releasing different proteins.

  The transcriptional unit consists of those elements expressed in the formation of amino acids (exons) and intervening introns (not expressed). Flanking regions contain both 'promoters' needed for RNA polymerase recognition and 'enhancers' that control the amount and time of transcription.
- TRANSLATION: the implementation or translation of the genetic code into a polypeptide molecule. Messenger RNA makes its way into the cytoplasm through the nuclear pores to ribosomes where chemicals, called initiation factors, help combine the ribosome subunits and assist in the attachment of mRNA.

In 1927 Muller, an American geneticist, looked at the effect of induced mutation on fruit flies. Chromosome abnormalities can be caused by a wide array of physical and chemical disturbances as well as errors during meiosis such as non-disjunction (or separation) of chromosomes. Muller observed that rates of induced mutation were some 150x greater than control lines (with spontaneous, natural mutation). Chromosomes break naturally, but the frequency of this increases with ionising radiation, ultraviolet light and chemical agents such as mustard gas and acridine orange. The introduction of a virus into DNA may also have the effect of triggering mutation.

Chromosomal mutations such as alteration in chromosome number or chromosome structure are responsible for a wide range of important human conditions. Common structural mutations include:

- deletion (loss of a chromosome fragment during cell division),
- duplication (attachment of an extra segment on a sister chromatid),
- inversion (upside-down re-attachment of a chromosome fragment) and
- translocation (fragment joins a non-homologous chromosome).

Conditions caused by chromosome deletion include the mental retardation and small skull of 'cri du chat' victims, while translocation of fragments are implicated in several cancers including chronic myelogenous leukaemia. Translocation of a chromosome 21 fragment can produce Down syndrome. The evolutionary significance of structural mutations is to reduce the likelihood of cross overs during meiosis and increase the number of 'normal' gametes. Thereby the alteration (often an inversion) is conserved, the linked genes on the inversion (or altered component) being known as a supergene.

Changes in chromosome number can occur spontaneously or can be induced to produce organisms for research or for the table! Many of our plant (and some of our animal) foods are variants resulting from this type of change. The number of chromosomes in a basic set is called the monoploid number ($\times$). Organisms with successive multiples of the monoploid number are called euploid. Euploid organisms that have more than two chromosome sets are called polyploid. Polyploid individuals are referred to (respectively) as triploid ($3\times$), tetraploid ($4\times$), pentaploid ($5\times$), hexaploid ($6\times$) and so on. We have already come across the haploid condition (n) seen in gametes. In most animals and plants, the haploid number and the monoploid number are identical ($n = \times$). But in a few cases, for example modern wheat, haploid and monoploid numbers are different. Modern, agricultural wheat has 42 chromosomes. It is hexaploid so $\times = 42/6 = 7$; its gamete however has 21 chromosomes and therefore $n = 21$. Polyploidy is common in the Plant Kingdom and an important feature in plant evolution. It is less common in animals, being seen in fish, amphibia and one mammal (a rodent, *Typanoctomys barrerae*).

Within the set of polyploids we must distinguish between **autopolyploids** where chromosome sets come from the same species and **allopolyploids** where hybridisation allows the combination of chromosome sets from different (but closely related) species. In general, polyploid plants are often larger and have larger organs (e.g. larger fruits in strawberries) than their diploid relatives. Polyploid animals also occur but are much less common. The *Salmonidae* family of fishes (including salmon and trout) have twice as much DNA than related fish, while triploid oysters are more palatable than diploid forms. Human polyploidy is very rare and never results in viable offspring.

Aneuploidy is the third example of (polyploid) chromosome mutation. The normal chromosome set is usually altered through abnormal separation of chromosomes (non-disjunction) during either mitosis or meiosis. As a result, the diploid ($2n$) condition either has additional chromosomes (e.g. Down syndrome, $2n + 1$) or a reduction in chromosome number (e.g. Turner syndrome, $2n - 1$). These conditions are of especial importance to human health.

Mutations can be induced by certain physical and chemical agents called **mutagens**. The high incidence of scrotal cancer in chimney sweeps was noted as

early as 1775 – we now link the polyaromatic hydrocarbons in soot to this form of cell mutation. In the 1920s the mutagenic effects of X-Rays and Ultraviolet radiation was also demonstrated on fruit flies, providing discernible phenotypic (bodily malformation) and genotypic (chromosome) differences. But of greater evolutionary significance are the spontaneous mutations produced during DNA replication and repair. Mutation rates vary between organisms, between chromosomes and between loci, but with chromosomal mutation rates of 10^{-4} to 10^{-3} per gamete per generation and point mutations of around 10^{-5} to 10^{-6} per generation, the impact of this phenomenon on population change will be significant.

Genes and chromosomes can mutate in either body (somatic) or reproductive (germinal) tissue and the biological significance of the mutation rests on whether the alteration affects only a small part of the body (a mutant sector) or whether the mutation affects the germ line and is passed on from generation to generation. It is in the study of population genetics where germinal mutations are of much greater significance. The action of mutation is to produce novel alleles, but to effect evolutionary change these alleles must persist within the population.

What Sorts of Genes Are Needed by Living Things?

As we saw earlier in the chapter the science of **genomics** attempts to describe both the structure and function of **genomes** – that is the entire complement of genetic material within an organism. Moreover, DNA sequencing and genome analysis combined with the mathematical and investigative tools of **bioinformatics** have led to an explosion of genome sequencing projects including that of the human mitochondrion, reported in 1981, brewer's yeast (*Saccharomyces cerevisiae*) in 1992, the first free-living organism (*Haemophilus influenza*) in 1995 and, most famously, the Human Genome Project finalised in April 2003. The **Human Genome Project** was an international and collaborative research exercise whose early results were published in *Nature* in 2001. The group recognised the existence of around 21 000 genes on 46 human chromosomes as an amazing blueprint for the establishment and development of every human being! The whole genome sequencing of the human genome has led inexorably to advances in health care in the emerging field of genetic counselling, predictive and preventative medicine. However, human genome sequencing also carries the attendant problems of social and ethical issues. As the technology advances and sequencing costs are reduced, then this area of study will increasingly be used in genetic scanning and manipulation of human and other genomes. As of 2011 there were nearly 3000 microbial (the majority were viruses) and 36 eukaryotic (half of which were fungi) whole genome sequences available.

A complete genome sequencing has been carried out in several organisms including the nematode worm, *Caenorhabditis*, and the yeast, *Saccharomyces*. Results indicate that there is a division of labour between these genes with functional sets necessary for the correct functioning of the organism. The term **proteome** refers to the collection of protein-coding genes within an organism's genome. In yeasts and

nematode worms genes can be classified into functional categories. These include (in order of size – largest first):

- cell metabolism
- nucleic acid metabolism
- protein folding and degradation
- transport and secretion
- signal transduction
- ribosomal proteins
- cytoskeleton

Living cells therefore seem to have a list of 'core functions' that need to be carried out. Over and above this, the remainder of the proteome results in species-specific and individual differences.

A similar set of 'core functions' is seen in flowering plants, e.g. *Arabidopsis thaliania*, where it too has had its genome sequenced.

- 22% of genes are involved in metabolism
- 15% in transcription
- 13% in defence
- 10% in secondary metabolism
- 8% in signal transduction
- 6% in growth
- 6% in energy liberation
- 5% in protein destination
- 3% in protein synthesis
- 2% in extracellular transport
- 2% in intracellular transport

Comparative genomics can provide a useful tool for the evolutionary biologist. Genome sequences have demonstrated both the unity of life (there is enough similarity to suggest that all life forms had a common origin) and the differences. For instance, it has shed light on what we mean by a species. Formerly hybridisation of DNA was the criterion for similarity (most bacterial DNA will hybridise provided the similarity in nucleotide sequence is >80%). But following the work of Carl Woese (1928–2012) bacterial species were defined by the variation of their (16S) ribosomal RNA (rRNA). Differences of around 2.5–3% are now considered to represent different species. And based on 16S rRNA analyses, Woese divided life on Earth not into five or six kingdoms as had been suggested previously, but into three domains. These were the Bacteria, Archaea and Eukarya.

As species diverge, so do their DNA sequences. Pauling and Zuckerandl suggested that if such divergence occurred at a constant rate it would provide a **molecular clock** allowing scientists to date the splitting of distinct lineages and thereby providing a timeline for biological evolution.

Some of the most interesting aspects of genomes are in the dynamics of gene expression patterns, the so-called functional genomics. But genomes also differ in

structure. Similarities and differences in genome sequences (structural genomics) can take the following forms:

1. differences at the level of individual bases
2. differences at the gene level
3. differences in larger scale blocks
4. differences in entire genomes

Duplication of genetic elements has been an important driver of evolution. Estimates vary, but the incidence of duplication is significant; in *Arabidopsis thaliana* for instance the genome contains more than 60% duplications. The evolution of human globins provide a good example of **gene duplication**. Genes for haemoglobin α and β chains are found on chromosomes 16 and 11, while other loci accommodate genes for myoglobin, neuroglobin and cytoglobin. Closely linked genes such as the α and β haemoglobins suggest a more recent divergence. Conversely less closely clustered genes diverged earlier. It appears neuroglobin split from the ancestral globin forms about a billion years ago with myoglobin having diverged around 500 million years ago and the α and β haemoglobin chains around 450 million years ago. Whole genome duplication has occurred several times in animals, plants and microbial forms. Expression of Hox genes determines bilateral symmetry and posterior/anterior axes with many metazoan animals. Hox genes reveal the duplications that have occurred during vertebrate evolutionary history. *Amphioxus* has one HoX cluster, humans possess four clusters and zebrafish seven Hox clusters. This has been interpreted as a series of large-scale duplications, 1 ➔ 2 ➔ 4 ➔ 8 (with zebrafish having lost a duplication, 8 ➔ 7).

Genotypic and Phenotypic Variation

The phenotype of an organism describes its morphological, chemical or behavioural attributes and is produced by the action of genes in combination with the environment. Three qualities of a gene impact on the phenotype:

- **penetrance**: the degree to which the condition controlled by the gene is manifest
- **pleiotropy**: a single gene having multiple effects
- **epistasis**: where a gene alters the expression of a second, independent gene

Gene expression is the molecular process by which genetic information in the chromosomes is converted into protein molecules that determine the characteristics of the cell. Genes consist not simply of protein-coding units arranged linearly like beads on a chain, but are much more complex. In prokaryotes the nucleotide sequence matches the amino acid sequence in the polypeptide produced, an attribute known as **colinearity**. In eukaryotes the correspondence between DNA and the polypeptide chain is less precise. Gene expression is modified by the action of factors such as suppressors and modifiers. It is possible to measure gene expression by determining the penetrance or expressivity of that gene within the phenotype. These two terms,

penetrance and expressivity, are slightly different. Gene penetrance is defined as the percentage (or amount) of that particular characteristic present in the underlying genotype found in the phenotype: in other words what fraction of genes present in the cell are actually expressed. Expressivity refers to the degree to which genes are expressed (a pigment gene, for example, may not be expressed fully in the phenotype).

When considering phenotype, it must also be remembered that genes interact. They interact with one another and they interact with their immediate environment. Gene interaction includes aspects of inheritance such as incomplete dominance, codominance, lethal genes, suppressors and duplicate genes (all of which can be studied in basic genetics textbooks). The interaction of genes with their physical–chemical environment has also been well studied using 'temperature shock' in fruit flies, light availability in plants and sex determination in crocodiles.

Two generalisations are apparent: one is that a single gene can have multiple effects (pleiotropy) and the second is that a characteristic in the phenotype may derive from more than one gene. The latter phenomenon is perhaps easier to explain when considering, say, a biochemical pathway with several components each controlled by a single gene, but what about the converse? How are pleiotropic effects produced?

In humans, sickle-cell anaemia has a multitude of symptoms caused by a simple base substitution. These include skin ulcers, heart failure, physical weakness and kidney failure. In Marfan syndrome mutation of a single gene causes near sightedness, malformation of the sternum and a weakened aorta. Similarly, dog and cat breeders have known for many years that breeding for one characteristic often brings with it a range of unwanted features, for example white fur/blue-eyed cats often have problems with associated deafness. Genes producing apparently unrelated effects are known as **pleiotropic genes**. There are two models of gene–environment interaction.

- The first model postulates general genetic rules that are then qualified by more specific statements from the environment. So, for example, when constructing a model aeroplane, basic rules provide instructions to make a wing, fuselage, etc. Thereafter, specific statements regarding adornments and decoration determine the type of aircraft.
- The second model is more deterministic in that the genes supply a detailed plan or blueprint, the environment serving only to modify slightly the overall pattern.

In golden retriever dogs coat colour alleles are affected by nearby colour deposition alleles. The dominant form of the deposition allele promotes colour formation in the fur, the recessive form masks colour production. Therefore, genotypically a dog may be black or brown in colour, but if the double recessive form of the deposition allele occurs, then no colour is deposited, and the familiar golden retriever is the result. In the situation described, the expression of one gene is affected by a different gene at a different locus. This genetic condition is known as **epistasis** and accounts for much of the genetic interaction during development.

For many years, biologists have noted the loose coupling of genotype and phenotype. As we have described earlier in this chapter, the correspondence or colinearity between genes and gene expression is very variable particularly in

eukaryotes. Organisms may look similar (phenotypically) but differ significantly in genotype; the **convergent evolution** (similar structures though different evolutionary trajectories) of both animals and plants provides many examples of this. Alternatively, organisms may differ in phenotype but have very similar genotypes. Examples here include the many polymorphic forms of animal and plant together with those species, like Amphibia and metamorphic insects, that change their body form during their lifetime. The two main reasons for this loose coupling of genotype and phenotype are:

- that much of the DNA is never transcribed so that genetic and environmental changes will have little effect on phenotype;
- regulatory genes (e.g. Hox genes) can dramatically alter developmental pathways and therefore eventual phenotype with relatively little genotypic modification.

It has been stated before that the genome is the 'clay of evolution', the basis upon which a natural variation arises both in individuals and populations. Selection of course acts on individuals. But it is within the *population* that the macro changes occur and ultimately new forms arise.

Genes in Populations

The marriage of Darwinism and Mendelism in the mid-twentieth century gave rise to the **modern synthesis**. Within this framework, individual biological disciplines such as palaeontology, taxonomy, biogeography, evolutionary theory and population genetics combine to emphasise the role of natural selection in evolution. A central tenet of the modern synthesis was that selection acts on the individual – *but it is the population that evolves, not the individuals themselves*. The essence of any evolutionary change therefore is an alteration in population gene frequency.

The population is a basic unit of biology. It is not a static feature but a constantly changing entity shaped by its surroundings, both biotic and abiotic. A population of organisms can change both *quantitatively* (for example, numbers of individuals or population density) and *qualitatively* (as the characteristics of its constituent members change).

A population is a group of organisms of the same species occupying the same habitat at the same time.

Populations can differ; for instance, a northern population of butterflies, such as the northern brown argus butterfly, *Aricia artaxerxes*, in the United Kingdom, contrasts with its southern counterpart by the presence or absence of a white spot on the upper wing. Similarly, plants such as the early purple orchid and rock rose show distinct northern and southern 'races' with zones of hybridisation in between. We also know that populations in the past can differ from populations we see today. Population biology looks at both *geographical* and *temporal* variation. **Demography** is a study of processes that determine population change. Individuals are born and they die; groups migrate into and out of populations. Thus, the growth potential of populations under

different environmental conditions is one measure of their evolutionary success. Although the term 'demography' is often restricted to human populations and human statistical analysis, the topic can also explore the statistics of sex and age to assess the mortality and natality rates of any biological population (this has been termed biodemography).

Both Charles Darwin and his younger half-cousin Francis Galton noted that within animal and plant populations individuals 'overreproduced', that is, produced more individuals than is necessary to replace themselves. Populations increase in several ways, but population growth is generally geometric rather than arithmetic. In other words, growth accelerates due to the participation of all individuals (geometric) rather than the simple addition of numbers (arithmetic). But no population of organisms can continue to grow indefinitely. A variety of environmental factors (collectively labelled **environmental resistance**) will determine the eventual size of the group. Some of these external factors are density independent such as fire and flood; the effect on the genotypes of individuals is almost random. But others such as predation, food availability, etc. are density dependent and, as such, will selectively alter the eventual genetic make-up (the gene pool) of a population. This of course is a cornerstone of natural selection.

Of course, a key element in population growth is reproductive capacity. A useful concept in this respect is that of a **panmictic population**, where the probability of mating is almost equally probable between any two individuals. Contrast this with a more structured population, say human social or geographical subgroups where mating is restricted by distance or social convention. A panmictic unit is one in which individuals are sufficiently close to allow the possibility of random mating with any other individual within that unit.

Variation within Populations

The goal of population genetics is to understand the genetic composition of a population (its gene pool) and to describe the forces that impact on both individuals and the group as a whole.

Until the middle of the twentieth century it was widely believed that genetic variation was limited in scope. Despite an impressive knowledge of human variability, the consensus was that animal and plant species were, by and large, genetically uniform. It was the work of population ecologists such as E. B. Ford (1901–1988) and his coworkers that brought the complexities of genetic variation to our attention. In the British Isles there has been a long tradition of natural history, resulting in the work of eminent naturalists such as John Ray, Gilbert White and Charles Darwin being placed in national and regional collections. And although animal and plant species have a generally uniform appearance, the existence of races, varieties, subspecies or 'sports' has been well documented. Intraspecific diversity has been recorded in a wide variety of animals and plants, for example in the banded snails *Cepaea nemoralis* and *C. hortensis* (see Figure 3.7). Several genes control the shell

Figure 3.7 Polymorphism in the banded snail. A composite image of polymorphism in the white-lipped banded land snail. Photo credit, Ian Alexander (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

appearance – genes for the ground colour, presence or absence of bands, spreading of the band pigment and colour of the aperture lips (black lips as in *C. nemoralis* and white lips as in *C. hortensis*). The 'colour' genes are multi-allelic and very often on the same chromosome. All in all, these snails have a complex genetic make-up. The (phenotypic) variation in colouring and banding patterns is generally referred to as a polymorphism with the appearance of morphs dependent upon the immediate environment, some colours and patterns providing camouflage others influencing albedo values (reflectance of light). But an interesting aspect of recent research (Silvertown et al., 2011) is that 'the relation of colour and banding patterns of banded snails has indeed changed and that this has taken place at an astonishing speed'. Further details regarding banding in *Cepaea* are found in Chapter 4.

Regarding global geographical variation of animal populations, we can safely say that the morphology, physiology and behaviour of these organisms appears well suited to those environments. A series of 'ecological rules' have been suggested to describe the distribution of different types or morphs:

- Bergman's Rule – related forms are larger in colder regions and smaller in warmer regions
- Allen's Rule – body extensions such as ears, tails and beaks tend to be smaller in colder regions

- Glober's Rule – dark body pigmentation is more highly developed in warm, humid regions

These generalisations (they are not strictly biological rules) can be useful when considering evolved, adaptive traits.

A difficulty when discussing ecological variation lies in determining how much of the variation is genetic and how much is environmental (or perhaps the result of an *interaction* between the environment and development of the organism). Sorting out environmental effects (such as food, light, moisture, etc.) on the organism and weighing up the contribution of its genes requires sophisticated techniques. Fortunately, there are mathematical techniques (sometimes simply referred to as quantitative genetics) that allow us to test for **heritability** - that is how much of the phenotypic variation is caused by genetic differences. The assumption is generally that the phenotype (P) is the result of both genetic effects (G) and environmental effects (E). This assumption, of course, ignores the complex interplay between genes and environment. If phenotypic variation (Var P) = genetic variation (Var G) + environmental variation (Var E), then it should be possible to carry out controlled experiments to estimate the part played by each component. For example, genetic variation can be reduced to almost zero by using genetically identical organisms (e.g. cuttings taken from the same plant or the use of genetically inbred animals). When different environmental conditions are applied, the heritability (H^2) of the condition can be measured:

$$H^2 = \frac{\text{Var (G)}}{\text{Var (P)}}$$

So, when measuring the variation within a population (the total phenotypic variance) we consider two factors, the variance between the genotypes and the environmental variance. Genetic variance is determined:

1. through crossing experiments (producing homozygous lines from which heterozygotes are formed/then measuring the phenotypic variance within each heterozygote genotype); and
2. by considering genetic similarities between relatives (their genetic correlation).

The remainder constitutes the environmental variance.

If heritability represents the proportion of phenotypic variance attributable to genetic causes, then the 'environmentability' of a trait is its analogue – the amount attributable to environmental variation. Both heritability and 'environmentability' show important attributes:

- ❖ They are population concepts, not referring to any individual.
- ❖ They depend upon the environments that animals find themselves in (if the environments are much the same, then phenotypic differences will be mainly due to genes – heritability will be high).

- ❖ The concepts are abstract – they refer only to proportions and tell us nothing about the genes themselves.

Heritability often arises of course when discussing the nature/nurture question. It can be described as: the amount heredity contributes to an individual trait. However, this is not quite accurate, a better definition might be: 'heritability is the *proportion* of the total variation between individuals in each population due to genetic variation'; this number can range from 0 (no genetic contribution) to 1 (all differences on a trait reflect genetic variation). Following on from this definition:

- ❖ The number does not apply to individuals – only to variations within a population.
- ❖ This value is not fixed; differences among groups (in the range of genetic variation and environmental variation) will result in different estimates of heritability.

From more than one thousand heritability estimates the average heritabilities were calculated. Heritability of physiological parameters such as oxygen consumption and resistance to heat stress averaged around 0.33 (33%), while structural features such as wing length and body size averaged around 0.46 (46%). These values are relatively high when compared with the heritability of traits connected with reproductive success (e.g. H^2 values for fecundity, viability and survivorship average around 26%). These characteristics are so important that any genetic variability has been eliminated by natural selection. Advantageous alleles have been consolidated by repeated selection thereby causing the heritability to decrease. Table 3.1 shows percentage estimates of heritability for typical farm animals. Once again heritability is seen to be decreased in those traits linked to fitness and reproductive success.

Table 3.1 Percentage estimates of heritability in UK livestock (various sources)

Livestock	Character observed	% Heritability (H^2)
Friesian cattle	White spotting	95
	Butterfat content	60
	Milk yield	30
	Conception rate	1
Pigs	Back fat	55
	Body length	50
	Weight at 180 days	30
	Litter size	15
White leghorn poultry	Egg weight	60
	Egg production	30
	Body weight	20
	Viability	10

Estimates of heritability apply only to the population under study in that environment.

The presence of variants in a population is termed **polymorphism** (many 'morphs' or forms) – that is two or more forms that are genetically distinct but still form part of the same species group.

Within the phenotype, variation is observed at several levels:

- morphological differences
- physiological differences
- chromosomal differences
- biochemical differences
- molecular/immunological differences
- behavioural differences

And within the genome, variation can be described either as a DNA sequence polymorphism (that is the inherent variation in base sequences) or as a variation in allele frequencies (an allele being an alternative form of a gene). **Population genetics** deals with genotypic variation but, by definition, only phenotypic variation can be observed.

Variation between Populations

Having already mentioned the banded snail earlier, there are two further classic stories of polymorphism within animal and plant populations.

In the case of the peppered moth, *Biston betularia*, the black form or morph predominates in the industrial Merseyside area whereas the peppered form predominates in the more rural areas of North Wales. This occurrence is associated with a phenomenon known as **industrial melanism** and is controlled by very few genes. Several butterflies and moths are known to produce black or melanic forms. Bernard Kettlewell in the mid-1950s suggested that the proportions of dark and peppered forms observed was due to selective predation by birds. To test this hypothesis he pinned different moth variants to tree trunks and observed the responses of birds. Sure enough, the dark forms survived better on the soot-blackened (industrial) tree trunks and the peppered forms showed increased survivorship on the speckled, lichen-covered trunks in more rural areas. One criticism of this work was that it was an artificial situation; moths normally rest (higher) elsewhere in the trees. But mark–release–recapture investigations provided equivalent results.

Cyanogenesis (production of cyanide) is a phenomenon found in around 50 orders of flowering plants. Like most secondary plant compounds (phenols and mustard oils for example) these chemicals are defensive in nature. In the flowering plant bird's foot trefoil (*Lotus corniculatus*), cyanogenic specimens are found mainly in woods and fields inland whereas the acyanogenic form is found nearer the coast. Cyanogenesis is controlled by two genes, one that controls production of a harmless sugar-cyanide compound and the other the production of an enzyme to release hydrogen cyanide

once the leaf is damaged. Natural populations are polymorphic for both genes but, once again, selective predation (this time by slugs) secures the survival of the cyanogenic forms in inland areas and acyanogenic forms in coastal zones. Slugs eating the (cyanogenic) trefoil leaf damage the cells, release the enzyme and are deterred from eating further. Now presumably the production of cyanide in the cyanogenic forms has an energy cost, so why is this condition predominant in inland areas but not near the coast? The answer lies in the distribution of the slugs. As any gardener will tell you, slugs do not like salt. And so, plants near the sea will not be predated by slugs, while those inland will almost certainly be attacked. Therefore, within a polymorphic population there will be differential survival (and therefore differential reproductive fitness) between those populations on the coast and those inland.

In both these cases we are *not* looking at a conscious decision of individuals – it is a gradual shift in the character of the population. As the population begins to change (for example during the rise of the melanic form of *B. betularia* in the late nineteenth century), we are looking at a **transitional polymorphism**. Once the populations have become established, such as those in *L. corniculatus*, then we describe this stable genotypic frequency as a **balanced polymorphism**.

Julian Huxley (1887–1975), grandson of 'Darwin's bulldog' T. H. Huxley, coined the term **cline** to describe a continuous change in a phenotypic trait along a geographical axis. Clines may exhibit a gradual or graded change such as the increase in body size of many North American mammals and birds with increasing latitude; alternatively, change may be sudden, abrupt and discrete such as genetically distinct populations of house mice in Madeira or the different sized populations of dog whelks on the Welsh coast. Clines reflect an environmental gradient and can be explained using an adaptationist model. The larger size of North American mammals and birds could be ascribed to a reduced surface area/volume ratio and increased heat conservation. Dog whelk populations in Wales seem to be responding both to the physical forces of wave action (smaller animals on exposed shores) and to predation pressure (thicker shells on sheltered shores with more predators).

John Endler (1947–present) described four ways in which a cline might form:

1. random genetic drift creating a difference in allele frequencies within isolated populations;
2. continuous environmental gradients such as temperature, altitude or humidity gradients;
3. spatially discontinuous changes in environment (e.g. island and mountain top populations) and
4. establishment of contact between genetically distinct populations.

To this list might also be added changing predation pressures and human intervention.

Clines demonstrate that strong localised selection pressures can produce local adaptations irrespective of gene flow, but how does genetic change in populations arise?

Population Genetics

In 1908 Messrs Hardy and Weinberg independently described mathematical rules by which genotype frequencies behave in the absence of selection. The genetic puzzle up until this point was to describe how genetic variation was maintained in a population. Many alleles are deleterious and should, perhaps, be removed from the population – yet we often see a remarkable genetic constancy. At the turn of the twentieth century, it was argued that dominant alleles should be more common in the population – in the ratio three to one in fact. The existence of dominant alleles at relatively low frequencies suggested that Mendelian dominants and recessives were not segregating properly.

But Godfrey Hardy in England and Wilhelm Weinberg in Germany (a third, independent discovery was also made by the Russian geneticist, Chetverikov) disproved this supposition by demonstrating that allele frequencies are not dependent upon dominance or 'recessiveness' but remain essentially unchanged from generation to generation. The Hardy–Weinberg principle states that:

'in a sexually reproducing population the frequency of both dominant and recessive alleles will remain constant provided that certain conditions are met.'

The conservation of gene (and genotype) frequencies is one of the most important concepts in population biology and responsible for our further understanding of human diseases (carrier individuals) and selective breeding programmes (heterozygote advantage).

The Hardy–Weinberg principle can be restated as a formula. If we imagine two alleles (A) and (a) at a single locus and a population of individuals mating at random, then the expected allele frequencies and genotype frequencies can be calculated using simple algebra.

If we say the frequency of the dominant allele (A) = p and the frequency of the recessive allele (a) = q, then the following two formulae represent the Hardy–Weinberg equations:

$$p + q = 1.0 \text{ (to describe allele frequencies)}$$
$$p2 + 2pq + q2 = 1.0 \text{ (describing genotype frequencies)}$$

The **gene pool** represents the sum of all genes in the reproductive cells of a population. It can be regarded as a genetic reservoir from which samples are taken at random to create the next generation. We have seen that given certain conditions, the frequency of alleles and the frequency of genotypes in the gene pool remain constant. What are these 'certain conditions' and how might they cause deviation from the Hardy–Weinberg equilibrium?

Certain assumptions must be made if we wish to hold to the Hardy–Weinberg equilibrium:

- mating has to be random and

- there must be no
  - *selection* of alleles either positive or negative
  - *migration* of alleles into or out of the population
  - *mutation* creating new alleles
  - *genetic subdivision* of the population
  - *linkage disequilibrium* disrupting the predicted occurrences of linked genes

Deviations from the Hardy–Weinberg equilibrium often occur when there is non-random mating. For instance, it can transpire that individuals mate with others closely related to themselves (inbreeding). As a rule, inbreeding reduces heterozygosity in the population increasing the proportion of homozygous individuals. And, as many of the deleterious genes are recessive, an increase in homozygosity will increase the frequency of the homozygous recessives thereby increasing the probability of disadvantageous conditions in the population. Population variation is reduced; systematic inbreeding between close relatives will eventually lead to complete homozygosity. A second form of non-random mating occurs when individuals choose a mate not based on genetic relationship but because of their resemblance and mating preferences (**assortative mating**). Bias towards choosing a mate like one's self is termed positive assortative mating; mating with unlike partners is called negative assortative mating. Human mate choice is often put down to positive assortative mating!

4 Natural Selection and Adaptive Change

In chapter 3 of *Origin of Species*, Charles Darwin muses on the reproductive rate of elephants:

> The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till 90 years old (something of an overestimate of its longevity), bringing forth three pairs of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants descended from the first pair.

Darwin was of course making the point that no animal species, or that of any other organism, ever achieves its full reproductive potential. This is vividly the case with organisms that produce significantly more potential offspring per generation; for instance, cod who lay more than a million eggs over their lifetime or the vast clouds of fungal spores. There is an enormous overproduction of offspring and yet the population numbers of most established species are roughly stable from one generation to the next.

One frequent limiting factor on population growth is that of natural resources. Both Darwin and Alfred Russel Wallace acknowledged the influence of the Rev. Thomas Malthus in inspiring their respective theories of natural selection as the principal evolutionary mechanism. Malthus's *An Essay on the Principle of Population* was first published in 1789 and considerably revised in 1803. It was this second edition that both Darwin and Wallace read. Briefly and brutally Malthus' principle was that any attempt to ameliorate the lot of the (human) lower orders was doomed to failure because they would reproduce to the limit, beyond the available food supply – the poor would always be with us. The only hope was to encourage restraint in reproduction.

Malthus's insight was, of course, not necessarily true of humanity, but both Darwin and Wallace saw it as a spur in the development of their theory. In summary, all organisms are capable of exponential population growth, but this is never achieved. Typically, populations of organisms in the wild are stable or fluctuate in numbers well below their reproductive potential. Some go extinct, others may expand rapidly into a new environment, but stability is the norm. Only a small proportion of potential or actual organisms survive to reproduce.

Both Darwin and Wallace acknowledge their debt to Malthus (and may have also been inspired along similar lines by Adam Smith's (1776*) An Inquiry into the Nature*

and Causes of the Wealth of Nations). But Darwin also records the inspiration of Archdeacon William Paley's (1802) *Natural Theology; or Evidences of the Existence and Attributes of the Deity Collected from the Appearances of Nature*, which was probably read by Darwin while he was still an undergraduate.

Paley's ideas set up a challenge to anyone attempting a natural explanation of evolutionary change. His thesis is that organisms (particularly humans and other animals) are machine-like, and that their anatomy and physiology are evidences of deliberate design without evolution and thus proof of the existence of a designing God. Darwin saw it as his greatest challenge to explain the *origin of adaptation* by natural processes. We have already seen the first stage of his argument leading to the inference that only a very small proportion of organisms in any generation survive to reproduce. The second stage concerns the nature of natural populations. There is variation between individuals in almost all populations; the exception would be a population of identical clones reared under identical conditions! Some of that within-population variation is heritable; a fact known to Darwin and Wallace from agricultural breeding as well as other examples seen in nature. This was further amply documented by genetic studies later in the twentieth century. Of that heritable variation it can also be demonstrated that at least some of it represents a difference in '**fitness**', meaning the potential to survive and reproduce in a particular environment.

Charles Darwin demonstrated that in any population of organisms constrained by natural resources the fittest individuals will survive differentially and thus pass on the heritable traits that confer increased fitness to the next generation. Over time those traits will increase in frequency in the population (given a constant environment). Any new and fitter feature must therefore appear in the population before it can be tested by natural selection. Wallace's view was that heritable variation in populations was 'random' with respect to the direction of natural selection, which he saw as the cause of all adaptive change with one startling exception - the evolution of the human mind could not be explained by natural processes.

Possible rivals to randomness include two factors proposed by Jean de Monet, Chevalier de Lamarck (1744–1829):

- The first of these, thought by many to be the entirety of Lamarck's theory, is the 'inheritance of acquired characters'. This hypothesis attempted to explain the origin of adaptive features in an organism and its descendants. An animal, it suggests, develops a new characteristic because of its own striving in response to the environment. The lengthening of the neck in the giraffe to reach higher in browsing trees is the school textbook example. Thereafter, the acquired character becomes a hereditary one, so that the giraffe's offspring, when mature, will have the long neck of their parent, even if there is no further effort on their part. This principle was then extended by Lamarck to include the origins of new organs arising from the animals' environmental needs, and the 'use and disuse of parts' resulting in their enlargement or reduction, respectively.
- But all these facets of 'the inheritance of acquired characters', which even Darwin was open-minded about, are not the core of Lamarck's theory. Lamarck's core idea,

later termed 'orthogenesis' was the notion that in all organisms there was an innate drive to evolve from one generation to the next. Lamarck believed, as did many other naturalists into the nineteenth century and beyond, that all organisms (especially animals) could be arranged in a linear series, the *scala naturae* (ladder of nature) from most primitive at the bottom to the most advanced (inevitably *Homo sapiens*) at the top. **Orthogenesis** is the theory that creatures are programmed to ascend this 'ladder' and evolve along some predetermined track over the generations. It was very popular, particularly among palaeontologists, at the end of the nineteenth century (although Lamarck himself conceded later that there must be at least two animal scalae).

Notice that both 'acquired characters' and orthogenesis are theories that postulate an innate component in the determination of evolutionary direction. In the first, the animal itself can be thought of as contributing a directional component to the evolution of its descendants; in the second, direction is entirely innate. In the early years of the twentieth century another type of innate evolutionary force was suggested by pioneer geneticists, notably Hugo de Vries, H. L Johannsen and William Bateson. Evolutionary change, including the origin of new species, occurred by '**saltation**', a sudden radical 'mutation' (from the Latin *saltare* to leap about) between one generation and the next. Natural selection, if it acted at all, merely tidied up lethal mutants.

It was the singular triumph of the '**Modern or Synthetic Theory**' with its development of population genetics that reconciled Darwinism and Mendelian genetics.

Natural and Artificial Selection

Organisms reproduce prolifically; often more than the capacity of the environment to sustain them. Under these conditions, of increasing population size, there will naturally appear a competition for resources such as potential mates, food and shelter. Which organisms survive and reproduce and which ones die of starvation or fail to reproduce is not random; a range of factors will contribute to their reproductive success. The process by which these factors govern survivorship is known as **selection**.

An environment is said to select *for* those factors (and those individuals) favourable to success and to select *against* other factors that are less favourable. The language unfortunately implies a choice – of which there is none. Selection in this sense is a consequence of an interaction between living things and their environment. The survivors of this process are now thought of as being more closely adapted to their environment, that is, they can survive more readily. For selection to occur four conditions are necessary:

- The units describing the trait (to be selected) must be variable.
- This trait must vary within the parent population.
- There needs to be an association between the trait and the organism's reproductive success.
- The trait must be heritable for selection to be effective.

Although 'survivors' of the selection process are better adapted, simple natural selection is a dynamic, active process. Genes that produce better adaptations become more frequent over time. A simple example will explain. The beach deer mouse, *Peromyscus polionotus*, lives in the Southeast of the United States in grass-covered sand dunes or scrub areas nearby. They have variable colouration: those living in darker soil burrows are coloured predominantly brown, and those in lighter, sandy areas are predominantly white. A good example of adaptation to their environment perhaps; but what of the mechanism, how did this situation arise? In this instance one can quite readily envisage a natural selection by predation. Lighter mice on darker soils are more apparent to a predator than the same mice on lighter sandy soils. This hypothesis was put to the test by Donald Kaufman at Kansas State University who introduced a hungry predator (an owl) into outdoor cages with equal numbers of light and dark mice. Perhaps unsurprisingly, the white mice on light soil survived better than the dark ones (and vice versa). The superficial explanation for the differential survival is, of course, improved camouflage providing a selective advantage. However, to gain a deeper understanding of the process we need to examine the genetic composition of the beech deer mice population. For several variants of the coat colour allele exist. And the shift in allele frequency (from light to dark or from dark to light depending upon environment) is dependent upon specific allele forms or **allelomorphs** being removed from the population – in this case by a hungry owl!

To generate an adaptation to the environment the following are required:

- a genetic *variability* within the population;
- the ability to pass on the specific variation to the next generation (heritability);
- a developmental *link between genotype and phenotype*;
- the capability to *'translate' adaptive genes* into new offspring.

By contrast, **artificial selection** is the deliberate selection of organisms by humans for their benefit. The term artificial however is something of a misnomer. The selection is real, but the agency is not the unthinking natural environment but the purposive hand of human beings.

The term, of course, is most closely associated with animal and plant breeding – the systematic reproduction of favoured types. The hope is that through selective breeding the next generation will contain more of the desirable characteristic. Thereafter if selected individuals are also mated then a greater and greater frequency of that characteristic (be it milk yield, thick fur, quantity of seeds, palatability of fruit) will be found in subsequent generations.

Selective breeding is evidenced through an exploration of stock records at Smithfield market London (increase in carcass weight of cattle or the fleece weight of sheep over the past 200 years) or global crop yields for rice and wheat. Similarly, cat and dog breeders, pigeon fanciers (breeders) and rose growers all tell of deliberate mating of organisms with desirable characteristics causing replication of those characteristics in the offspring; indeed, some new ones! Artificial selection is also seen in the fruit and vegetables in our kitchen. A range of edible brassicas have been produced from the

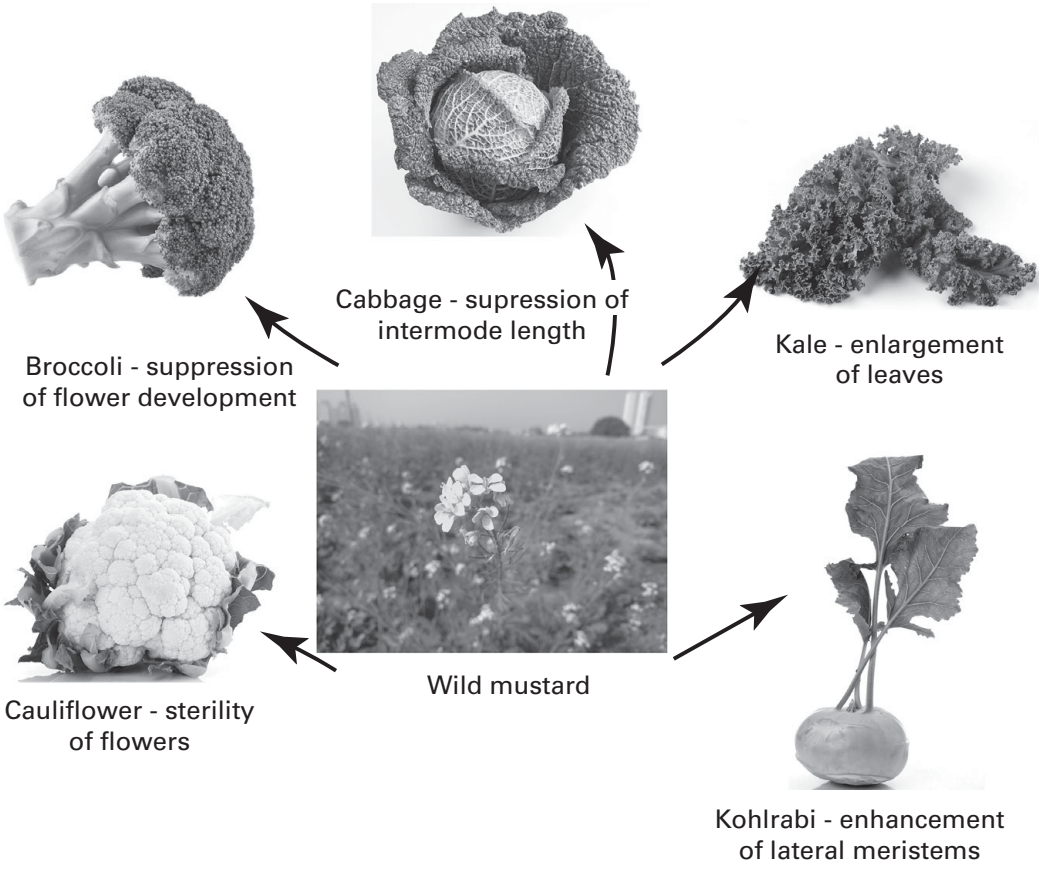


Figure 4.1 Popular cultivated vegetables derived from wild mustard. Credit Creativ Studio Heinemann / Getty Images (cauliflower); Avadhesh Maurya / iStock / Getty Images Plus (mustard flower); Creativ Studio Heinemann / Getty Images (kohlrabi); Joff Lee / The Image Bank / Getty Images (kale); Axel Göhns / EyeEm / Getty Images (cabbage); Patricia Soon Mei Yung / EyeEm / Getty Images (broccoli).

rather uninspiring wild mustard (Figure 4.1), an aggressive weed only edible in small amounts in the young stages.

Fish farming, or aquaculture, is a centuries old source of food production with European and Asian fishponds providing a plentiful and reliable source of nourishment and raw materials. But with acute land shortages the only way to increase production from fish farms is to increase yield. Fish yield can be increased either by altering the environment (antibiotics, food, temperature and water quality) or by manipulating the genome of the fish – that is growing genetically improved animals. If both approaches are employed, yields can improve dramatically.

There are several breeding programmes that can be used to improve fish stocks genetically. Traditional approaches include selective breeding and cross-breeding, while more recent approaches include the production of sex-reversed brood stock and chromosomal manipulation.

- Traditional selective breeding programmes select only the most promising fish (size, colour, egg mass, etc.) from a fish population from which to breed. The resulting offspring will then embody many of these favourable traits.
- Cross-breeding however attempts to find mating combinations from *different* fish populations; such offspring should then exhibit **hybrid vigour**. Cross-breeding programmes are a tried and tested technique, but results are unpredictable unless the combinations have been evaluated beforehand.
- Sex-reversed programmes use the fact that one sex may be more valuable than another. And so, the sex of a population or brood may be reversed through the use of male and female sex hormones (oestrogens and androgens). For instance, female sturgeon are more valuable than males because they produce the caviar (eggs), while male tilapia are more useful because they grow twice as fast. One of the major goals in tilapia farming is to prevent reproduction, and this is best accomplished through generating a monosex male population.
- Chromosomal manipulation is a recent technique that produces sterile fish. This is done to induce sterility in species that mature before they reach market size or to comply with legal restrictions that apply to growing exotic species (whose culture otherwise might be illegal). For example, grass carp culture is only legal in much of the USA if the aquaculturist raised sterile individuals (generally triploids). The most common form of chromosomal manipulation (producing triploid individuals) is to treat the newly fertilised eggs with heat or pressure in order to 'shock' them into preventing the second polar body nucleus from leaving the egg. In this way the zygote will contain a haploid sperm nucleus, a haploid egg nucleus and a haploid second polar body. Thus, producing a triploid, and therefore sterile, zygote.

In order to characterise the theory of natural selection, we are now able to provide a simple description of this process:

In the competitive struggle for existence **better adapted individuals increase in frequency in a population with time**, this differential increase we call natural selection.

Many authors cite something like this, backed up by statements regarding the overproduction of individuals within a population and differences in heritable adaptedness among individuals. Put simply, we can re-state the principles of natural selection as follows:

1. There is a natural ***overproduction*** of offspring by parents (commonly two parents produce many more offspring in their lifetime).
2. ***Genetic variability*** is found in all sexually reproducing organisms.
3. Genetic variability may be translated into ***physical variability*** (in morphology, physiology or behaviour).
4. The environment will normally favour one variant over another (we say the organism is better ***adapted***).
5. The more favoured type will thrive while the less favoured type will be disadvantaged (we say the more favoured type has a ***selective advantage***).

6. By virtue of its more favourable circumstances the organism with the advantage will generally live longer (increased survivorship) and produce more offspring (a greater ***fecundity***). The better adapted organism has increased *fitness*.
7. Genetic variability is ***heritable*** (hence parents can pass these favourable characteristics on to their offspring).
8. And, over time, the population will ***change*** as the better adapted forms make up a greater and greater percentage of the population.

In the summation thus far, adaptive evolutionary change has resulted from the action of natural selection. This formulation though then leads to two further problems:

- While all adaptive evolutionary change may result from natural selection; natural selection does not always result in evolutionary change.
- If there is also a non-adaptive evolutionary change, such that two or more hereditary variants do not differ from one another in degree of adaptedness (i.e. fitness), then evolutionary change from one to the other cannot be a result of natural selection.

In the later editions of *Origin of Species* Charles Darwin borrows Herbert Spencer's expression 'survival of the fittest' to describe animals and plants that appeared to be best adapted to their environment. However, C. H. Waddington in 1960 suggested that the phrase 'survival of the fittest' might be tautological (repeating a meaning that has already been conveyed). And if we equate fitness with survivorship, then that is indeed true – we have 'survival of the survivors'! However, in modern usage the term 'fitness' is a portmanteau word implying a general reproductive fitness including several components (fecundity, viability, survivorship, etc.) and, at best, we can call this a partial tautology.

Selection in Populations

In an unchanging environment natural selection should theoretically result in a supremely adapted population of individuals. However, fluctuations in the surroundings will often produce a shift in the *direction* of selection while influx of new individuals might introduce new traits and therefore alter existing selection pressures. In such examples populations will be *sorted* according to new conditions and, after several generations, new population parameters can be described. Within a population natural selection can affect the frequency of a heritable trait in three or four different ways (Figure 4.2):

1. The type of selection that results in direct evolutionary change in a population over time is known as **directional selection**. This is most easily envisaged if one imagines selection acting on some continuous variable, like adult body size (which will probably be due to the additive effect of some gene loci). In directional selection one extreme phenotype is the fittest.
2. In the case of a normalising selection some intermediate size is optimal ('selection for ordinariness') – over time the extremes of the range will be reduced in frequency. Some authors use the term 'stabilising selection' for this mode.

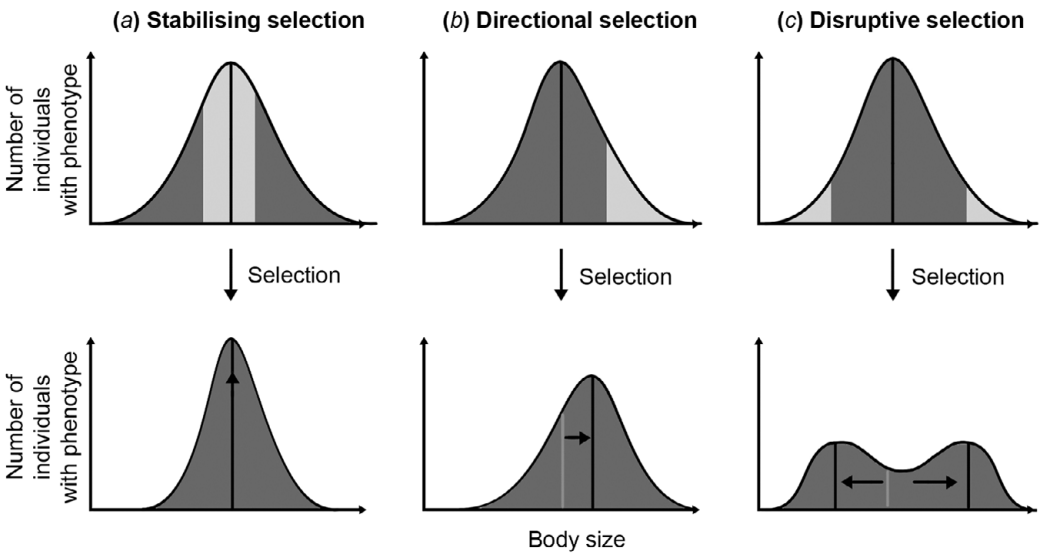


Figure 4.2 Diagrammatic representation of (a) stabilising, (b) directional and (c) disruptive selection.

3. Here, the use of the term **stabilising selection** is reserved for describing selection that maintains the status quo, rather than resulting in elimination of the extremes.
4. The fourth mode is **disruptive selection**: two or more phenotypes are fitter than the intermediates between them, so the population becomes polymorphic. In the simplest case for body size, the largest and the smallest phenotypes are favoured.

Polymorphism

Organisms vary genetically and phenotypically both within and between populations. They can exist in many forms; a feature we call **polymorphism**. The variation includes both quantitative (continuous) and discrete (discontinuous) characters; (incidentally, geneticists generally use the term **character** for a heritable feature, flower colour, etc., that varies between individuals in a population; each variant for that character, red or white flowers for example, is referred to as a **trait**).

The investigation of polymorphism (presumed to have originated by disruptive selection) was regarded as particularly important in the development of the Synthetic Theory from the 1930s onwards. Before that time, laboratory geneticists had a picture of the nature of the genome as consisting of a series of mainly homozygous (identical) loci each with a pair of the 'best' alleles – the 'wildtype'. A few loci, probably heterozygous, were occupied by 'mutant' alleles that were almost uniformly less fit

than their respective wildtype (unless active directional selection was in play). These mutant alleles manifested themselves as the obvious abnormalities on which transmission genetics was principally founded.

Notably this was the case with *Drosophila*, but nobody, at least in Western Europe or North America, had studied the nature of the *Drosophila* genome in wild populations. From the mid-1930s onwards, such studies were undertaken in California by Theodosius Dobzhansky (1900–1975), a Russian émigré whose most notable work, with a series of colleagues, was undertaken in the laboratory and the field on the species *D. pseudoobscura*. Dobzhansky discovered not only that the populations were polymorphic at many gene loci, but also that there was extensive chromosome polymorphism as well.

It was a fortunate circumstance that several species of *Drosophila* had been used in early research, because in that genus it was subsequently discovered that in the salivary gland there were 'giant chromosomes' consisting of hundreds of copies of each single chromosome bound together and extended along their length. Each polytene or giant chromosome has a characteristic pattern of bands like a bar code, allowing each gene locus to be assigned a position relative to nearby stripes. Chromosome polymorphism is due to 'mistakes' at cell division, so that lengths of chromosome are inverted within the chromosome, or bits of chromatid separate in association with the 'wrong' partner chromatid. Dobzhansky found that these abnormal chromosomes were retained in wild populations not as abnormal freaks but at a high frequency, often in the heterozygous (or more correctly heterokaryotype) condition. When an abnormal chromosome is paired with a normal one, they go through all sorts of contortions in an' attempt' to pair corresponding loci. The resulting bizarre shapes can easily be seen in the giant chromosomes.

Dobzhansky was also able to show from observations in the field and the laboratory that the differences between these polymorphic **karyotypes** were of adaptive significance. A karyotype is a diagram or photograph showing the organised sequence of chromosomes within a cell.

One example here will suffice. In *D. pseudoobscura* there are several karyotypes of the third chromosome. Two are known as Standard (ST) and Chiricahua (CH). In the wild the relative frequencies of these two vary in systematic fashion throughout that period of the year when the flies are active. In the laboratory the two karyotypes were left to interbreed freely for several generations. It was found that at any given temperature the ratio between the two stabilised to a constant value, whatever the initial frequencies were. At 25°C these were about 70% ST and 30% CH; however, at 15°C they were equal at 50%. In the wild at first ST occurs at more than twice the rate of CH but declines from the beginning of June when the temperatures of high summer begin. Then ST increases rapidly, as better heat adapted, until the end of the season. The increase of CH from March to the beginning of June was suggested as being due to its advantage in sparser populations before the summer build-up in numbers. This alteration in frequency could be compared with selection on beak size and shape in the Darwin's finch *G. fortis* described in Chapter 1. Both are examples of stabilising selection in the sense that we use the term: the maintenance of a range of frequencies,

in the case of *Drosophila* a stable but seasonal polymorphism; in the case of *Geospiza*, the range of a continuous variable dictated by a less predictable external cause.

During the same period in the middle of the twentieth century that Dobzhansky and his colleagues were investigating the hidden polymorphisms of *Drosophila*, E. B. Ford and a few associates and colleagues were studying visible polymorphisms as part of the research programme that Ford himself described as 'Ecological Genetics' (the title of his text on the subject in 1964). Ford's definition of genetic polymorphism is as follows:

> Genetic polymorphism is the occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation.

Ford goes on to say '. . . Evidently it [the definition] excludes geographical races, as well as continuous variation controlled by polygenes, and falling within a curve of normal distribution, as with human height. It excludes also the suggestion of rare recessives, or heterozygous conditions eliminated by selection and maintained only by mutation pressure'. Differences between one generation and the next, as between spring and summer forms of some butterflies, are also excluded.

It is obvious, a priori, that two kinds of genetic polymorphism could exist. If in a population some hereditary trait, in the simplest case due to a single gene, is replacing its 'normal' allele because of selection, then until the new allele has gone to fixation, both will be present in the population 'in such proportions that the rarest of them cannot be maintained merely by recurrent mutation'. This is a transitional polymorphism due to directional selection. **Stable polymorphism** is exemplified by Dobzhansky's work on *Drosophila.*

Another highly variable polymorphic species is the common weed of wasteland, the dandelion, *Taraxacum officinale* complex. Dandelion is a globally widespread and exceptionally variable plant. There are more than 2000 subspecies of *Taraxacum* with 90% of them polyploid (chromosome number ranges from 16 to 48 with ploidy levels rising to hexaploid). Although exhibiting quite wide-ranging plasticity in body form, the plant is still considered a single species (though an aggregate group for practical purposes) and debate is still on-going as to whether the observed variation is due to phenotypic plasticity or genetic differentiation arising from multiple introductions across Europe and the Americas. It is apparently of recent speciation along with other apomictically (asexually) reproducing plants such as bramble (*Rubus*) and rose (*Rosa*). In *T. officinale*, virtually every floret produces a seed which is genetically identical to the mother so that mother–daughter lines form 'seed clones' (Richards, 1996) hence retaining the stable polymorphism.

As mentioned in the previous chapter, several cases of polymorphism were investigated by the Oxford school of Ford and his associates (seeking adaptive explanations of visible polymorphism). A notable case was that of shell colour and banding pattern in the snail *Cepaea nemoralis* (and in its sister-species *C. hortensis)*. For most of the twentieth century this has been the subject of investigation, and the investigation continues.

Cepaea is an outcrossing hermaphrodite, so that after mating both partners produce eggs. The offspring can have shells of various background colours, inherited as an allelic series, and bracketed as *brown* (the dominant form), *pink* and *yellow* (with pale yellow as the recessive). This genetic locus is closely linked to a locus that determines whether bands occur on the shell. Without the recessive bands being present no banding can occur. Also, closely linked to these two loci is one that may or may not give rise to the presence of bands. Unlinked loci then determine the number of bands. These snails normally have a maximum of five, usually brownish-black bands that spiral down the shell from the apex to the lip of the aperture. A 5-banded specimen is recorded as 12345, if only band 3 is present (mid-banded), 00300, absence of bands 1 and 2 as 00345, and so on (totally unbanded = 0000). Spread bands refer to those that are wider than non-spread; 4 and 5 particularly can be so wide that they run into one another. Other loci control band colour, with rare variants, and body colour. Most populations are polymorphic for some of the possible variants. From the 1950s onward Cain and Sheppard and others studied *Cepaea* from a selection point of view.

At first it was concluded that colour and banding pattern together acted as camouflage. Populations (relatively static and occupying a small area: <30-m radius) had a majority of pink and brown shells against a brown background of leaf litter, but of yellow (greenish with the dark body inside) on herbage or grass. Banded shells were in the majority on variegated backgrounds, such as hedgerows and rough meadows, while unbanded were favoured in uniform environments, cropped or grazed turf. One of the principal predators was the song thrush, particularly in the early spring when other more favoured foods were not available. The thrush has the useful habit of picking up its snail prey and breaking open the shell on a stone. Such 'thrush anvils' are seen surrounded by broken shells and the morph ratios can be compared with those in the local living population. These studies were conducted over a very wide area (ca. 30 sq. miles) near Oxford. However, when the attention was directed to the chalk Marlborough Downs, some 30 miles southwest of Oxford, the pattern of polymorphism was found to be radically different. Here, large areas were found to have many separate populations with the same feature. Thus, in one area of several square kilometres there were no 5-banded shells at all, irrespective of background. Part of that area had an enormous excess of brown shells, another part an excess of yellows. Then mapping showed an abrupt change to other polymorphic ratios with no apparent change in ecological conditions. This phenomenon was termed **area effects** by Cain and Curry. Subsequently, area effects have been recorded all over Britain and Western Europe. Recently Davison and Clarke have investigated area effect polymorphisms using mitochondrial DNA and microsatellite DNA to elucidate the history of the Marlborough snails; mDNA showed no significant correlations, but microsatellites did correlate with 'areas' suggesting long separate histories of one or another, possibly because of expansion from Ice Age refuges.

But the problems of *Cepaea* do not end there. Polymorphisms may be controlled by factors other than predation and history. Background temperature is also important. Animals with dark shells, whether due to background colour or spread bands, absorb

more heat and are thus less tolerant of high temperature. This applies locally and over a wide area. The ratio of yellow shells is higher in southern Europe. Many other selective agents have been suggested. This illustrates a general principle. In laboratory experiments an attempt is made to eliminate, or at least control, all variables except one, but in the wild this is impossible.

Heterozygote Advantage

One factor frequently cited as maintaining polymorphisms is **heterozygote advantage** (sometimes referred to as 'over dominance'). This has often been suggested in *Cepaea* but is very difficult to establish as heterozygotes are not easily recognised. The classic case is that of sickle-cell anaemia (AS). In many tropical human populations, notably in West Africa, a severe form of anaemia, such that the victims seldom survive to reproduce, is relatively common. The frequency of the sickle-cell trait, characterised by the shrivelling of the red blood cells into a sickle shape (Figure 4.3), is not diminished despite the expected elimination of the trait by selection. The reason is that the heterozygote produces sickling only under conditions of low oxygen pressure. However, it also confers resistance or even immunity to *Plasmodium falciparum*, a parasite that causes a virulent and often fatal form of malaria. Thus, in malarial regions extending as far eastwards as India the recessive 'sickling' allele (S) is maintained in the population. The phenomenon is known to be due to a single amino acid substitution at the β haemoglobin locus, but as always, there are complications. There is a third allele (C) at the same locus in some West African populations that also confers some immunity to malaria: in the normal human condition fetal haemoglobin is replaced by normal (AA) haemoglobin, but in sickle-cell victims (AS) some fetal haemoglobin is retained as fetal haemoglobin is less affected by the sickle cell

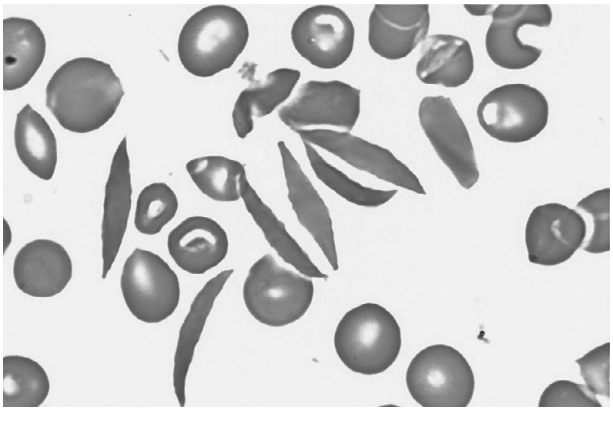


Figure 4.3 Sickling of red blood cells. Photo credit, Kristine Krafts

mutation. Fetal haemoglobin has been shown to moderate the (sickling) condition by providing both a higher affinity for oxygen and preventing premature destruction of red blood cells.

It used to be thought that heterozygote advantage was the principal cause of balanced polymorphism, but examples from the wild are difficult to find. There is, however, one meticulously researched laboratory case that is worth noting. It concerns the *ebony* locus of *D. melanogaster*, which produces a fly that is almost uniformly black. Homozygous male ebony flies are partially blind and as a result are at a disadvantage in courtship behaviour, but this disadvantage has been shown to disappear for courtship in the dark. The heterozygous males, on the other hand, are at an advantage compared to homozygous normal males because hyperactivity in the heterozygotes enhances mating success as it results in a higher intensity of courtship song (produced by wing vibration).

In the case of the ebony locus, the reasons for heterozygote advantage are manifest: wildtype males are at a disadvantage because of less vigorous courtship song; homozygous ebony males are at a disadvantage due to blindness. But another feature makes this case convincing. Kyriacou, Burnet and Connolly, who investigated it, did many generations of outcrossing into different *Drosophila* stocks to break any linkage to any adjacent genes, which otherwise might have been truly responsible for the effect.

Directional Selection and Local Adaptation

The classic case of directional selection is that of the night-flying peppered moth *Biston betularia.* The simplified (and textbook!) version of the story is that there are two forms of the moths apparently controlled by two alleles at the same locus. The 'wildtype' (*typica*) has white wings and body speckled with a pattern of dark brown spots. The other form (*carbonaria*) is uniform, dark brown or nearly black: *carbonaria* is genetically dominant to *typica*. Until the end of the nineteenth century, typica was the principal or only morph found in British rural populations. The first melanic (*carbonaria*) specimen was recorded in Manchester in 1848 and by the mid-1860s was the commoner form in that city. By the 1880s it was found quite commonly throughout Britain. In 1895 it comprised 98% of the Manchester population and in the twentieth century *carbonaria* was the characteristic form in industrial cities, although most or all populations retained *typica* at a low frequency, in addition to an intermediate form (or series of genotypes) known collectively as *insularia*. Most rural populations remained largely or exclusively *typica*. The phenomenon was later dubbed 'industrial mechanism'. A similar polymorphism was known in other moth species, and in the first half of the twentieth century several explanations were proposed, by E. B. Ford and others.

The generally accepted solution was demonstrated by Ford's Oxford colleague H. B. D. Kettlewell in the 1950s. In 1953 after preliminary aviary experiments with captive birds as predators, Bernard Kettlewell (1907–1979) experimented in the

Christopher Cadbury Bird Reserve on the outskirts of Birmingham. His hypothesis was that *carbonaria* was favoured in polluted industrial neighbourhoods by camouflage against soot-blackened trees devoid of lichens, on whose trunks they were said to rest during the day; whereas in rural areas with pale lichen-covered tree trunks *typica* was favoured by natural selection. He released nearly 600 moths in the Cadbury Reserve, of which 447 were *carbonaria*, 137 *typica* and 46 *insularia*. Each moth was marked on its underside for identification and placed in a conspicuous position on a tree trunk. The survivors were then recaptured after dark at a light trap as a measure of survivorship: 27.5% of *carbonaria* were recaptured, 13.13% *typica* and 17.39% *insularia*. The differences were strongly significant – *carbonaria* was at a selective advantage in Birmingham.

A mirror-image experiment was conducted in 1955 in the unpolluted woodland of Dean End, Dorset. Here the percentage recaptured were 4.67% *carbonaria*, 13.74% *typica* and 0% *insularia*. In Birmingham robins and a hedge sparrows (dunnock) had been seen taking moths, so in 1955 Kettlewell invited Niko Tinbergen to take cine-films of the predation. He then produced footage of fly catchers, nuthatches, yellow hammers, robins and thrushes taking moths. In a return to the Cadbury Reserve, also in 1955, Tinbergen filmed redstarts eating *B. betularia*. Kettlewell also employed a large team of amateur helpers to map the frequencies of *typica* vs. *carbonaria* from sites all over Britain. The correlation with pollution was reinforced, but there were some anomalies, notably a high frequency of *carbonaria* in rural East Anglia. This was matched by high frequencies of the melanic form of the American subspecies in rural New England.

Subsequently, as with *Cepaea*, a number of complications and objections to Kettlewell's work and the appealing simple story have arisen. Firstly, the moths do not usually rest on tree trunks during the day, but under the base of branches in shadow, or among leaves. Secondly, the pale *typica* form reflects ultraviolet light (visible to birds) strongly which foliose lichen does not, so that *typica* would be easily seen against this background. To test Kettlewell's results, large numbers of moths were put out at the Cadbury Reserve and at Dene End. At the Birmingham site significant results were confined to the first-day recaptures; thereafter recapture rates of the two morphs were not significantly different.

It was predicted that with the passing of clean air acts after the Second World War, pollution and with it the frequency of *carbonaria* would decrease, and indeed it did. However, in *B.betularia* populations in Michigan, it seems that the decrease in frequency of the melanic form is more likely due to an increase in SO_2 and airborne particulates rather than camouflage. The investigation continues . . .!

Selection does not necessarily operate the same way in all populations. The magnitude and even the direction of selection can differ depending upon prevailing conditions. If selection acts in a different direction to a conspecific population, then we say **divergent selection** is operating. Divergent selection is important:

- ❖ in promoting local adaptations and
- ❖ in setting up ecological barriers to gene exchange.

In discussing polymorphic ratios in *Cepaea* earlier in the chapter, it was noted that **area effects** may prove significant with the local environment producing additional selection pressures. Divergent selection is also seen in plants growing in areas with different soil chemistry such as the presence of heavy metals. As populations diverge from their conspecifics, a degree of genetic isolation may emerge possibly leading to speciation. Therefore, divergent selection is important. As we have seen, it may arise because of differences in the *abiotic* environment; but another factor promoting divergent selection is where populations differ in their interactions with other species (parasites, predators, competitors) – that is due to *biotic* factors. Experimental studies consistently demonstrate that local adaptation in natural populations is widespread providing those adapted individuals with a 'fitness advantage'.

Sexual Selection

Cases occur where an organism is subject to opposing selection pressures. In the case of the guppy (*Poecilia reticulata*), a popular aquarium fish, a different type of selection has been demonstrated in captivity and in the wild by John Endler. Guppies are native to mountain streams of Venezuela and adjoining islands. The streams are very clear and flow over gravel bottoms with often many coloured stones. The males are highly variable in external colour, being ornamented with spots of various sizes and colours, notably blue and green (structural colours), red, yellow and black (pigments). Endler's observations and experiments concerned the conspicuousness of the male fish on the backgrounds of gravel of different size and with and without predators. He set up 10 ponds in a greenhouse with multi-coloured gravel in two grades and introduced 180 fish per pond. After about 6 months, when the populations had stabilised, he introduced two species of predator, a cichlid, seen as dangerous because it ate guppies of all sizes, and a fish that ate only baby guppies, against the two gravel backgrounds. Two ponds then remained as controls, with no predators. After a period of months censuses of the populations were taken on two occasions. In the control and 'mild' predator ponds the number of spots in male guppies decreased significantly. In the field in Trinidad Endler introduced fish from a site where they lived with the cichlid and other predators to one which had the 'mild' predators but no others. After 15 generations, the male guppies resembled a population, in which both guppies and 'mild' predators coexisted, in brightness and variety of spot patterns. Thus, the stock that had lived with the cichlid, when isolated from it, became more conspicuous (this also related to greater contrast between spot and gravel particle size). The explanation given was that, in the absence of predators, *female choice* resulted in greater mating potential for the most conspicuous males. This is an example of **sexual selection**.

Observation of animal and plant reproduction suggests that there is a form of natural selection, called **sexual selection**, which can produce significant differences in the morphology, physiology and behaviour of male and female organisms. The existence of two distinct morphological forms (we call sexual dimorphism) can be incredibly striking in animals. The male peacock is larger and more brightly coloured

than the peahen, the red deer stag is equipped with enormous antlers and in humans, the male is generally more powerful (and aggressive?) than the female. Both Darwin and Wallace (who had lived with primitive natives) speculated that natural selection alone could not have produced these differences. So, what causes these differences? The answer is sexual selection.

In a traditional sense, sexual selection consists of two processes:

- Intrasexual (within the same sex) competition for mates; generally, competition between males for females
- Intersexual (between sexes) choice of mates

In other words, there is a competition for mates (a scarce resource) with the more 'attractive' males for instance being preferred by females. The advantage, of course, is increased fitness or increased reproductive success for both the male and female participants. The question then arises – what characteristics of a male is attractive to the female? In simple terms the female is attracted to physical traits that she can observe in the male that would suggest he would make a good sexual partner. Body size is important; larger males are generally healthier and stronger, but bright colours, conspicuous displays and exhibition of nestbuilding ability (in the Bower bird say or three-spined stickleback) all indicate a preferred male partner. If such a trait is selected for (by female choice), then competition between males will ensue.

Sexual selection is at first sight maladaptive; large size, bright colours and ritual displays may encourage predators! And certainly, before Darwin, naturalists could not explain the phenomenon. But selection through mate choice provides a satisfactory, if basic, explanation. Several questions remain however; how do genes for male 'attractiveness' and female 'choosiness' evolve in tandem, how did sexual selection originate and what limits the males from being even more 'showy'? These questions will be answered later in the chapter.

The term was first used by Charles Darwin in the *Descent of Man, and Selection in Relation to Sex* (1871). He realised that although natural selection could explain differences *between* species it was difficult to explain differences between the sexes *within* a species. Darwin proposed a secondary mechanism operating alongside natural selection involving a physical adaptation in males together with an aesthetic or strong preference in females. This could, of course, be the other way around, but female choice is by far the commoner situation. Examples of this sexual selection include superior body size and antlers, used in competing deer, which constitute an enormous metabolic drain on the individual stag. In several animals with internal fertilisation, such as some *Drosophila* species and some snakes, the male deposits a 'copulatory plug' to prevent further insemination by other males. In butterflies the male inseminates the female with a spermatophore, a package of sperm, and a plug (or sphragis) is attached to a stalk on the spermatophore. In the enormous birdwing butterflies of Southeast Asia and Australia the sphragis is a conspicuous and apparently permanent structure in mated females. Notoriously, other animals, particularly male lions taking over a pride, kill the cubs of previous matings that might compete with their own subsequent offspring (incidentally bringing the females into oestrus again).

An even more subtle way in which males compete is that of **sperm competition**. Paternity is of such crucial importance to males that they will go to great lengths to ensure that only their sperm fertilise the female eggs. For instance, in the damselfly *Calopteryx maculata*, the male will physically scoop out any rival's sperm before inseminating the female himself, while male European house sparrows will mate repeatedly (between 30 and 40 times per day) as the female begins to lay her eggs. Sex and reproduction are different processes and should not be confused. Reproduction simply means the production of new offspring while sex involves gamete production and fertilisation; in simple terms, reproduction increases the number of individuals while sex changes the nature of the progeny.

If we wish to explore sexual selection in the laboratory, then unicellular organisms provide a simple and convenient model. Cell lineages of simple single-celled organisms can be cultured for several thousand generations. In the early twentieth century ciliates were cultured in the laboratory. These reproduce by binary fission (asexual) and, as usual, each became extinct after a few hundred generations in the lab. However, those cultures derived from sexual propagation (conjugation) were significantly longer lived, perhaps due to the production of a new somatic cytoplasm. Sex therefore appeared to have an 'invigorating' effect on cell lines. Other experiments have also confirmed that in populations of cells (for example, *Chlamydomonas* and several yeasts) sexual populations evolve more rapidly under stressful conditions – presumably by the addition of advantageous mutations and the removal of deleterious ones. Sexual mating systems evolved early in the history of life on Earth and appear to confer several advantages to living organisms.

So, to return to the earlier question, how does preference for an exaggerated male trait evolve in concert with female preference? The answer was suggested by Fisher in the 1930s. He suggested that when female preference begins (for any reason) then it becomes almost self-fulfilling in that the female preference for favourable genes will cause those genes to spread within the population. Thereafter any mutation that increases the favoured effect, such as orange spots in guppies or the red underbelly of sticklebacks, will be selected for by the action of female choice. Fisher argued that this process of sexual selection will increasingly exaggerate the favoured effect until the female preference is ultimately balanced by the opposing selection pressure of male predation. Overly large antlers in deer or excessively bright colouration in birds will become disadvantageous if maintained for too long a time (hence breeding colours) or makes flight difficult.

The argument then is that females will choose males based on their genetic quality, and two ideas have been put forward to suggest a possible mechanism for this type of selection:

- Males will indicate their genetic suitability by displaying 'costly' signals to the female – *look at me I am a superior male because I can survive without a parasite burden and I have survived despite all this ornamentation*. This is sometimes referred to as **Zahavi's handicap hypothesis**.
- Females inherit sensory capabilities from their ancestors which bias their current choice of mates (**the sensory bias hypothesis**). Male tungara frogs in Central

America emit a second mating call (a risky business as the first one would do perfectly well) to make the frog more attractive. When exploring the neurophysiology of the female frog, the frequency range of this secondary call appears to match the bias of the female ear for low-frequency components.

Genetic Drift and the Adaptive Landscape

Genetic drift is a change in population allele frequency that cannot be ascribed to any of the selection processes. For instance, with enzyme morphs (known as allozymes) evolution can occur without natural selection. Due to the 'invisibility' of allozyme differences for selection, another type of evolution unmediated by selection is theoretically possible. It is known as 'genetic drift' and was proposed by one of the founding fathers of population genetics, Sewell Wright. This concept of genetic drift was part of Wright's **shifting balance theory**.

Wright's picture of evolution within species was of individual species consisting of large numbers of small populations or **demes** (local populations sharing the same gene pool). Varying amounts of gene flow, as migration or outbreeding, occurs between demes. The expected results of natural selection in a large population are always in terms of probability. But in small populations sampling error becomes significant. Just imagine if one tosses a coin a thousand times, the result will be close to 50:50 heads to tails, but if one tosses it only 10 times, then the chances of getting a result far different from 5:5 are very high. Thus, in a deme there are chances of the retention of slightly disadvantageous genes, against the pull of selection. These *sampling effects* constitute genetic drift.

The Unit of Selection

Most biologists who accept the theory of natural selection, from Darwin and Wallace to the present-day, agree that selection acts on individual organisms. But other suggestions have been put forward.

For instance, the publication of Richard Dawkins' book *The Selfish Gene* in 1976 led to the popularisation of the 'gene-centric' view of evolution. Dawkins described 'replicators' (the genes) which were housed within protective 'vehicles' (the bodies of animals and plants). And it is towards the gene, Dawkins argued, where we must focus on the action of natural selection and the process of evolution. The body, he points out, is expendable – only the gene persists, and therefore evolution proceeds in a manner that will maximise transmission of an individual's genes into the next generation. Arguments are provided in favour of this idea in the form of explaining otherwise 'difficult' social behaviours like altruism. How could altruism evolve in which the individual sacrifices their own breeding potential to assist others? The answer, he says, lies in that this strategy ultimately results in the individual promoting *more* of their genes into the next generation; often through helping close relatives (with which they share a large proportion of their genes).

In the 1960s and 1970s many biologists had begun looking at the social behaviour of animals from an evolutionary point of view. And in 1975 E. O. Wilson's book *Sociobiology* proposed that complex social behaviours of animals such as cooperation and altruism, although adaptive, could not simply be explained by selection acting on individuals. Rather, Wilson argued, adaptations occurred within groups and were selected according to the survival or extinction of these groups. Therefore, it is groups that are the units of selection. The *Selfish Gene* was written at the height of the individual versus group selectionist debate and Dawkins' achievement was to synthesise earlier ideas around kin selection and to formulate a new evolutionary perspective with which to explore social behaviours.

Kin selection is a variant of natural selection that enables all sorts of cooperative and altruistic behaviour to be explained – from termite architecture that can reach astonishing sizes to the cooperative behaviour of naked mole rats in tunnelling through hard earth to young Florida scrub jays helping their parents to rear new young. This principle (called inclusive fitness) is evoked as a way of calculating how a gene for a behaviour, say altruism, might spread considering the degree of family relatedness of the participants

Looking again at group selection, others, including Darwin, had suggested that natural selection might act, not just on individuals, but on whole populations, the whole population being the 'target' of selection. Selection at higher levels was even suggested (species selection?). In 1962, V. C. Wynne- Edwards (1906–1997) threw down the gauntlet as far as competition between populations was concerned in his book *Animal Dispersion in Relation to Social Behaviour*, with a proposal of **group selection**. If a population of animals occupied a limited area with limited resources, it would be advantageous to that population if its numbers could be adjusted in a given generation so that the resources were not exhausted, resulting in extinction. Such a population would be at an advantage compared to other populations without this characteristic. Wynne-Edwards imagined a population of birds in which there was (literally) a 'peck order' and territorial male birds could signal to one another by song or otherwise that the number of potential territories was less than the number of potential territory holders. Low-ranking males would then fail to breed but the population would survive. In some way the sacrificial behaviour was supposed to be programmed in the gene pool of the whole group. Unfortunately, as we now know, such an arrangement would be unstable. Any individual bird which had a genotype that 'cheated' the system would outbreed all its neighbours, whatever the fate of the population.

Thus, three units of selection have been proposed (Figure 4.4):

- selection at the level of the ***Individual***
- selection at the level of the ***Group***
- selection at the level of the ***Gene***

Richard Dawkins's views on the selfish gene have been criticised on several levels:

- *The language used* – this book was deliberately written for a more popular audience hence the widespread use of metaphor (a 'selfish' gene?). Dawkins

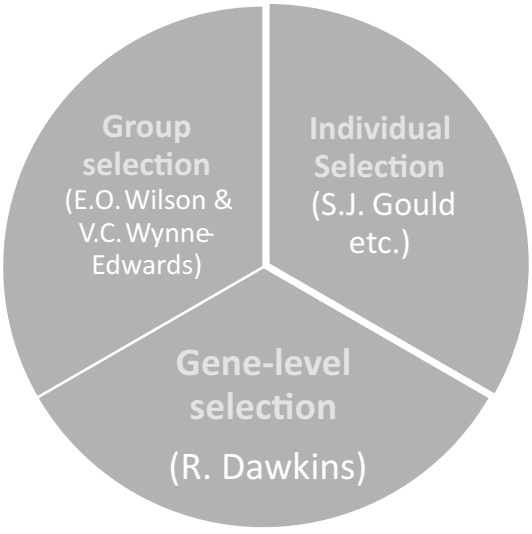


Figure 4.4 Proposed units of selection.

avoided complex scientific terminology and mathematical formulae but did tend to anthropomorphise his subjects (e.g. the vehicles carrying their replicators).

- The rather **deterministic and reductionist approach** was critised, not recognising, for example, that genes are not independent entities but act as groups interacting with each other and their environment.
- Dawkins had **redefined the gene** not as a 'nucleotide sequence coding for a protein' but as any portion of a chromosome lasting long enough to serve as a unit of natural selection'. This ignores of course genetic variation and change processes affecting chromosomes.
- The notion that genes are the **sole unit of natural selection** has been seriously questioned. In a critique of this view, Stephen J. Gould argued that the situation was much more complex with chance factors, species extinction and the physical environment all being additional determinants of evolutionary change.
- Finally, and perhaps most seriously, *The Selfish Gene* was criticised for its apparent ***political and moral stand*** that selfishness was somehow a natural behaviour to justify free-market economies or that it provided a scientific explanation for human greed and self-interest.

But 'the proof of the pudding', as they say, 'is in the eating'. And more than 30 years since its publication, *The Selfish Gene* continues to sell in 27 countries and has introduced the gene as an important component in evolutionary biology. Secondary ideas such as the 'extended phenotype' (genes expressed as behaviours and physical constructions as well as biochemical components) and 'memes' (the cultural transmission of information) are important additions to the evolutionary canon.

5 Evolution and Development

Early animal morphologists (students of body form and structure) welcomed evolutionary theory as a way of explaining the relatedness of internal body structures to those of other animals. Later, embryologists, such as Karl Ernst von Baer (1792–1876), were busy overturning old ideas of **preformation** (the concept that the animal was somehow 'preformed' within the sex cells) into a more sophisticated concept of **epigenesis** in which the developing embryo was influenced by a range of local factors. The development of the individual (its **ontogeny**) was viewed as complementary to its evolutionary development or **phylogeny**. Some individuals though (such as Ernst Haeckel) thought that ontogeny even mirrored phylogeny. One consequence of nineteenth-century biology therefore was that the cell was regarded as fundamental to biology. **Cell theory** promoted the later discoveries regarding heredity and *transmission of information* both from parents to offspring and from the gene to the developing organism. The link therefore between life history trajectories and evolutionary trajectories was already being forged in the late nineteenth century; but it was towards the end of the twentieth century that developmental and evolutionary biologists began to collude and see the merit in their respective disciplines.

The 'Synthetic Theory' of evolution was established in the late 1930s and early 1940s and was applauded by scientists as a successful reconciliation of Mendelian genetics and Darwinian natural selection. But if a full account of evolutionary processes was the aim, then something was missing. Natural selection acts on individual phenotypes – on characters that result from the developmental interaction of numerous genes with one another and with the environment. But in both experimental genetics and in population genetics it is the individual gene that is the focus of attention. What was missing in the Synthetic Theory was any account of gene action in the *developing organism*, and thus the evolution of development. This gap in evolutionary theory was largely ignored at the time of the synthesis, but two evolutionary scientists are notable for drawing attention to it: Schmalhausen in Russia in the 1940s and C. H. Waddington in Great Britain a little later.

Evolutionary Developmental Biology (Evo-Devo)

An evolutionary perspective can be applied to the study of developmental biology; the conservation of developmental mechanisms (such as the widespread use of the **Hox**

gene complex among distantly related organisms) is a testament to this characteristic. Comparative embryology shows us that more general or 'basic' characters appear earlier in embryonic development than the more specialised ones. For instance, in the phylum Chordata the notochord (a general feature) is found in the early embryo while paired appendages (limbs) appear later. This developmental generalisation mirrors evolution; the notochord is found in all Chordate groups while paired appendages are found in vertebrates but no other chordates. Also, an examination of vertebrate embryos reveals a remarkable similarity of form indicating that *they have descended from a common ancestor* and so form part of a **monophyletic** group (common ancestor plus all its descendants). Embryos of chicken, fish, rabbits and humans all look remarkably similar (see Figure 5.1); but a common misconception is that the gill slits that one sees (more accurately branchial arches and clefts) are remnants from an earlier, adult fish-like ancestor somehow preserved in the modern-day vertebrate. A more reasonable explanation is that the branchial arches were present in an early ancestor of the vertebrates and that these embryonic structures acquired new functions during evolution – in fish they became the gill bars and gills while in land tetrapods they became modified forming the jaws (and interestingly the bones of the inner ear!).

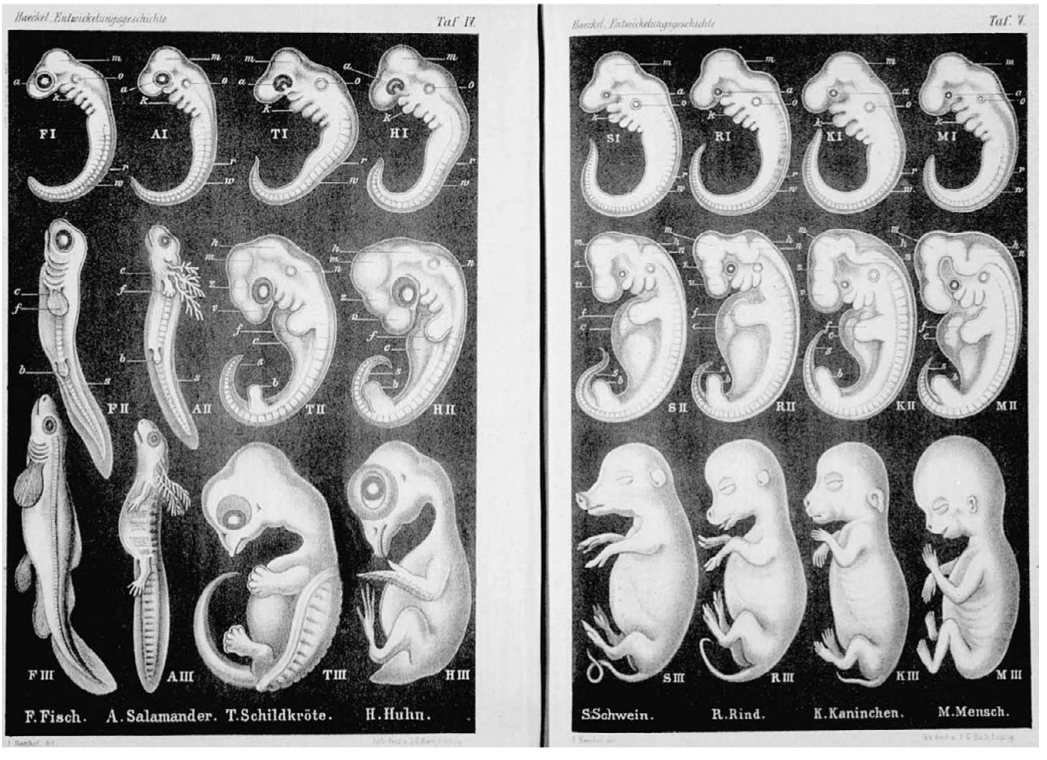


Figure 5.1 Vertebrate embryo comparisons. Early anatomists noted the similarities in appearance between the early embryos of vertebrates. Branchial gill arches are visible which develop into different adult structures (Fish, Salamander, Tortoise, Chicken, Pig, Cow, Rabbit, Human).

Common examples of where a study of development sheds light on evolution include:

- The development of limbs from fins
  The bone patterns of the limbs and limb girdles are highly conserved. Tetrapod limbs probably evolved from the lobe-finned fish in the Devonian period.
- Diversification of the pentadactyl (five-fingered) limb
  The pattern of single bone of the upper limb, double bones of the forelimbs and five digits is seen both in embryonic development and in adult vertebrate limbs. Changes in the proportion and fusion of bones have resulted in the diversity of limb types (particularly in mammals) we see today.
- Positional identity and vertebrate/arthropod body plans
  There are around 35 animal phyla each with its own particular body plan. Hox genes specify the identity of specific regions along the anterior–posterior axis and, as these genes are both universal and regulatory (that is control the expression of other regulatory genes), they are instrumental in determining the overall structure of an animal's body.
- The evolution of vertebrate and insect wings
  Despite obvious differences within these two structurally dissimilar body parts, there is notable similarity both in their genetic expression and molecular signalling. A fringe-type gene is found in the boundary (dorsoventral) layer in both chick and fruit fly wing buds.

The intellectual union of 'evolution' and 'developmental biology' is termed **evolutionary developmental biology** or simply contracted to 'evo-devo'. From a study of genetically linked morphologies (such as the eyes and wings of vertebrates and invertebrates) ancient gene complexes have been identified that perform crucial roles in controlling the formation of body parts. This so-called evo-devo gene toolkit is undoubtedly ancestral and has evolved to provide the body plans of present-day animal phyla.

The Epigenetic Landscape

Epigenetics is an area of study that examines changes in gene expression not attributable to the hereditary material; in other words, a natural occurrence caused by factors (other than the genotype) affecting the phenotype. Such epigenetic factors include lifestyle in humans or DNA methylation in plants and other organisms. In its strict sense any epigenetic change needs to be heritable.

A pioneer in the union of evolutionary and developmental biology was Conrad Hal Waddington (1905–1975), professor of animal genetics at the University of Edinburgh. One of Waddington's most fruitful ideas for a theory of development was that of canalisation. During its development an individual organism results from a complex of interactions of its genes and the products of those genes. There is a series of feedback mechanisms in the developing embryo that restores the normal course of

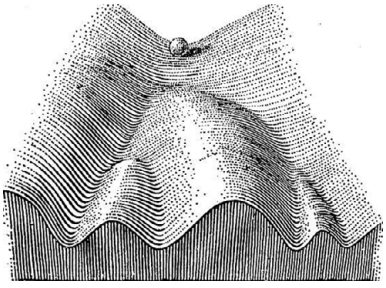


Figure 5.2 A visual representation of canalisation, a process modelling the developmental pathways cells can take during differentiation. Disturbances to the movement of the ball will affect choices made and the eventual developmental pathway of the organism. From *The Strategy of Genes* (Waddington, 1957) with permission from Taylor & Francis.

development if it is upset, either by a mutant gene, or by some external factor. Waddington envisaged this normal course of development by the pictorial metaphor of the **epigenetic landscape**, a series of diverging hills and valleys in an overall slope that represented the course of development. The embryo was represented by a ball rolling down the slope, its course constrained by the hills and valleys. Major mutations resulted in a change of landscape so that the ball was deflected from one valley to another as it rolled downhill (Figure 5.2). The form of the epigenetic landscape was maintained by the interaction of all the genes in the genome. In a self-regulating system, such as a home central-heating arrangement, a constant temperature is maintained by the thermostat acting as a homeostatic device, switching the source of heat off if the system gets too hot, and on again if the system gets too cold. Canalisation, like homeostasis, is a negative feedback device, but its results are not static – the embryo is developing in a dynamic fashion, it is not stationary. So, for homeostasis in development, Waddington substituted the term **homeorhesis** – constraint during development.

The concepts of canalisation, homeorhesis and the epigenetic landscape provide a useful mental picture of the course of development. But they also provide a framework for understanding the evolution of development. Evolution is any change in the epigenetic landscape. But it was not until the discoveries of developmental genetics that empirical evidence could be fitted into Waddington's picture.

Homeosis

In the latter part of the nineteenth century, there was a passion among naturalists for the collection of butterflies and moths. Naturalists devoted to this occupation (lepidopterists) often collected enormous numbers of specimens from the same species, and variants from the normal were highly prized. Among the rarest were specimens that showed elements of the forewing pattern on the hind wing. William Bateson in 1894 described a similar phenomenon in other animals – insects with a leg where an

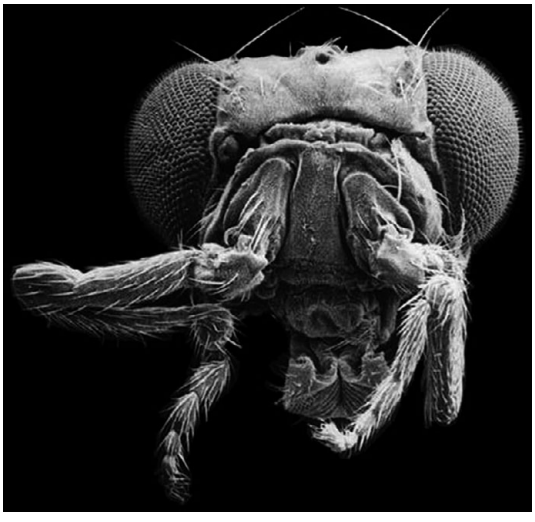


Figure 5.3 Antennapedia in *Drosophila.* Photo courtesy of Tony Mahowald.

antenna should be or maybe vertebrae with features from another part of the vertebral column – and termed the specimens homeotic. **Homeosis** describes the replacement of one animal part with that of another elsewhere in the body; a homeotic gene is a regulatory gene controlling the development of anatomical body structures.

In 1915, Calvin Bridges, working in Morgan's 'fly room' at Columbia University isolated a mutation in *Drosophila* in which the haltere on the third and last thoracic segment had some wing tissue. In normal dipteran flies, including *Drosophila*, the third segment wings seen in other insects are replaced by halteres, small gyroscopic balancing organs. In the mutant form, known as *bithorax*, the haltere was partially transformed into its serial homologue the wing. The action of *bithorax* together with other mutations can result in the complete transformation of halteres into wings, resulting in a four-winged fly – this of course is unusual in that flies belong to the Family Diptera, that is two-winged insects. A few years later other homeotic mutations were isolated, notably antennapedia in which a leg replaces an antenna on the head (legs and antennae are serial homologues). It should be realised that the mutant genes responsible may specify which appendage develops but other genes are responsible for the details of pattern. **Homeosis**, the transformation of one body organ into another, is a result of genetic mutation.

Hox Genes

Until recent developments in molecular genetics, homeotic mutations, like all other mutations, could only be studied by breeding and crossing whole animals. But molecular techniques, such as gene cloning and nucleic acid sequencing, now allow the study of the genes themselves. And a series of genes, known as **Hox genes** or

homeotic genes, are known to be critical in determining patterning in the anterior–posterior axis of animals. Hox genes have been observed controlling the individual nature of a series of *Drosophila* segments, both in the larva and in the adult fly. Without Hox genes, all the segments would be identical.

Thomas Hunt Morgan (1866–1945) was an early Nobel-Prize-winning geneticist who demonstrated that genes were indeed both physical and functional entities, located upon chromosomes. It was in Morgan's 'fly room' at Columbia University that the first *Drosophila* (white-eyed) mutant was discovered. Thereafter Calvin Bridges and later Theodosius Dobzhansky (1900–1975) worked on *Drosophila* mutations and the population genetics view of evolution. Incidentally, it was Dobzhansky who coined the phrase 'nothing in biology makes sense except in the light of evolution'.

Calvin Bridges' original *bithorax* mutation now reveals a complex of three homeobox genes. The *bithorax* genes control differentiation of posterior segments while the *antennapedia* gene complex, which we met earlier, controls the anterior region. Halteres formed from *bithorax* genes were only partially of wing tissue: the mutant gene must have been acting within cells rather than dictating 'wing' as a whole. Gene behaviour was therefore 'cell autonomous'; that is the cells themselves contained the active mutant genes. Techniques of gene cloning thereafter showed that there were eight Hox genes (two gene complexes) concerned with segment identity. The action of Hox genes is not, however, confined between segmental boundaries. Firstly, their region of influence is better defined by para-segments. At a more fundamental stage of differentiation, that of segmental boundaries, there is division into para-segments, each comprising the rear of one future segment and the front of one immediately behind. Secondly, there is often considerable overlap in the action of sequential Hox genes.

Hox genes show two intriguing features of significance. The first is ***colinearity***. There are eight Hox genes in *Drosophila*, all situated on the same chromosome and in the same order as the sequence of segments along the body that they influence; that is, they are colinear. The eight genes as we have seen are grouped into two widely separated complexes:

1. Antennapedia and
2. Bithorax.

Hox genes influence other (target) genes that control various aspects of development such as rates of cell division, cell differentiation and the orientation of mitotic spindles. They can also restrict the activities of other structural genes that define spatial patterns in the developing organism. The *bithorax* mutation transforms the anterior part of the third thoracic segment (where halteres normally appear) into the anterior part of the second thoracic segment (where the wings develop). The antennapedia mutation results in the transformation of antenna into legs.

The second feature of Hox genes is the ***homeobox***. It was discovered that single strand copies (produced by splitting the double helix of DNA, for example by heating) of one Hox gene would readily pair with a single strand of another different Hox gene. This was largely due to the presence in all Hox genes of a sequence of nucleotides of

180 base pairs which coded for a corresponding sequence of 60 amino acids. The gene sequence is known as the **homeobox** (abbreviated as 'Hox'); the amino-acid sequence is known as the **homeodomain**. It is characteristic of the homeodomain that it binds DNA so that the protein coded by the Hox gene is responsible for the nature of another gene 'downstream' of the Hox genes.

Homeotic selector genes (or just selector genes) are a group of major regulatory genes. The Hox genes are region-specific selectors. Selector genes control other genes thereby maintaining the species-specific pattern of gene expression during embryo development. *Drosophila* sector genes, the *bithorax* and *antennapedia* complexes, control segment identity and are therefore region-specific.

Hox genes are sometimes referred to as 'executive' genes acting on other developmental gene hierarchies. At the bottom of such hierarchies are genes that effect the formation of tissues and specific organs. Another category of selector gene is that of field-specific selectors. Field-specific selector genes act within specific areas to control the formation or patterning of an entire structure. Two examples here will suffice. The first is the eyeless gene (*ey*). It should be noted that most genes are first recognised by an abnormal mutant allele, so that in this case the normal or wild-type eyeless gene is responsible for the normal development of the eye – a somewhat confusing state of affairs! In the case of a fly that lacks the *ey* function, due to a mutation, or for other reasons, the insect survives to the adult stage but lacks eyes. It is known that the *ey* protein binds one of a downstream family of genes that each include a homeobox, so that the protein regulates the expression of other genes. An extraordinary feature of eyeless is that if cells in which the eye is due to develop are transplanted to part of the imaginal disc, they will develop as some other part of the body, such as the wing. Here this gene induces development of an ectopic eye with pigmentation and the characteristic ommatidia of the insect compound eye.

The second field-specific selector gene is *Distal-less* (*Dll*). Once again, the name is derived from a mutant that cancels the normal action of the gene. The *Distal-less* gene is the first genetic signal for limb (or more accurately appendage) formation. Like the *ey* gene, *Dll* codes for a protein that regulates the expression of other genes. When its expression is prevented, ectopic limbs can arise. The *Dll* gene is therefore reckoned to be an early 'limb generator' in the early Bilateria (that is early bilaterally symmetrical animals).

As well as its role in the development of appendages in animals, more recent *Distal-less* research (Plavicki et al., 2016) is supporting its ancestral role in neural development. In humans, members of the DLX gene family contain a homeobox that is related to that of *Distal-less* (*Dll*) gene in *Drosophila*. The DLX proteins found in humans seem to be essential in forebrain development (DLX2), while DLX3 is important in the functioning of the placenta.

The Body Axes and Segmentation

The *Drosophila* genes we have looked at so far, the Hox genes together with those 'downstream' homeobox-containing genes that are bound by them, are all regulatory

genes controlling further genes that eventually code for actual bodily structures. But there are also regulatory genes 'upstream' of these (upstream and downstream here refer to different ends of the DNA molecule – downstream is towards the 3′ carbon end and upstream towards the 5′ carbon end). Hox genes could not begin to act in the embryo and the developing adult fly unless the body segments were properly differentiated. Even prior to segmentation, the body must have definite anterior and posterior ends (the anteroposterior axis) as well as a defined top and bottom (the dorsoventral) axis. The genes determining these fundamental features form part of *Drosophila*'s **maternal-effect genes** (for instance the *bicoid* gene, which informs the larva which is the front end, and which is the rear end).

A *Drosophila* oocyte, or unfertilised egg, arises within a structure known as the follicle. The follicle is lined by small follicle cells, but also included are 15 nurse cells that, together with the oocyte, result from four rounds of cell division. The nurse cells communicate with the oocyte by cytoplasmic 'bridges' that allow various molecules to travel from one to the other. Maternal-effect genes code for proteins that will establish a concentration gradient across the embryo. In addition, mRNA transcripts (also found within the cytoplasm of the oocyte – hence the term 'maternal-effect') control the transcription of segmentation genes. In other words, before the egg cell is fertilised, an anterior/posterior axis has already been established.

As usual these genes are first recognised by mutants that inhibit normal gene activity. In the case of the *bicoid* mutant, if it is homozygous, the larva lacks mouthparts and mouth hooks and the mutation soon proves lethal. At the other extreme (literally) mutant *nanos* homozygotes lack posterior structures. Together normal *bicoid* and *nanos* (both maternal-effect genes) establish the anterior/posterior differentiation of the zygote. There is, however, another important feature of this action. Mutant *bicoid* not only lacks anterior structures, but also has some posterior structures developed at the anterior end. This immediately suggests a phenomenon known to classical experimental embryology long before the triumphs of developmental genetics. Proteins derived from *bicoid* and *nanos* mutants form gradients of concentration from, respectively, the anterior and posterior ends of the egg and then the developing embryo. These diffusing chemicals are **morphogens**, and the balance of concentration of both determines the major features distinguishing anterior and posterior along the body axis.

Segment polarity genes such as *engrailed* play a key role in delineating segment boundaries. This gene is expressed in the anterior region of each para segment and segment boundaries are maintained by chemical signalling between adjacent boundary cells. Other segment polarity genes such as *hedgehog* and *wingless* also contribute to the formation and maintenance of compartment boundaries.

So, there are three classes of gene involved in early *Drosophila* embryo development:

- Maternal-effect genes
- Segmentation genes
- Homeotic or Hox genes

And all are important in establishing the pattern of segmentation together with the anterior/posterior axis. The early *Drosophila* larva is recognised by a pattern of stripes or bands on the main trunk. As the embryo develops, these repeated units (or para-segments) have a temporary existence in that they affect gene expression.

Early development of the *Drosophila* embryo requires the translation of maternal RNA molecules found in the oocyte. They establish polarity even before fertilisation takes place. Early body patterns are then defined by segmentation genes. These include:

- Coordinate genes – determine principal anterior/posterior, dorsoventral axes
- Gap genes – establish regional specificity
- Pair-rule genes – determine the separation of the embryo into discrete segments
- Segment polarity genes – determine polarity within each segment of the embryo

And finally, Hox genes transform this basic pattern into a specific body plan demonstrating linear differentiation of segments.

The Dorsoventral Axis

Discussion of the control of the *Drosophila* dorsoventral axis has been briefly postponed because its description can be used as an introduction to evolutionary development genetics or evo-devo. It represents a vivid series of recent discoveries corroborating an ancient theory.

Étienne Geoffroy Saint-Hilaire (1772–1844) was a French naturalist who believed in the underlying unity of living things. His main scientific preoccupation was the discovery of homologies between major groups of animals, not necessarily as data for evolution (although he did accept that evolution had occurred relatively late in life) but as evidence of unity of plan throughout the animal kingdom. He was particularly anxious to find homologies between vertebrates and segmented animals, insects, crustaceans and the like. One of the principal stumbling blocks was the different orientation of vertebrates and invertebrates about the longitudinal axis that is the difference in the dorsoventral axis. Arthropods possess a ventral nerve cord and vertebrates a dorsal one. Geoffroy chose a lobster as his standard of comparison and to make his point (in 1822) drew it upside down. For the most conspicuous difference between a (bilateral) invertebrate and vertebrate is that the lobster has its central nerve cord ventrally, below and parallel to the gut, while the nerve cord of the vertebrate is dorsal, running through the chain of vertebrae and situated dorsal to the gut. Later comparative anatomists in the nineteenth and early twentieth centuries attempted to give the comparison an evolutionary twist (literally). They postulated that the divergence between invertebrates and vertebrates took place when the ancestor(s) of one group, usually taken to be the vertebrates as ‘higher’ animals, rolled over and developed a new mouth. Such speculation was ridiculed towards the end of this period and biologists occupied themselves with other problems. Now in the last decade developmental genetics has provided strong evidence that Geoffroy Saint-Hilaire was right!

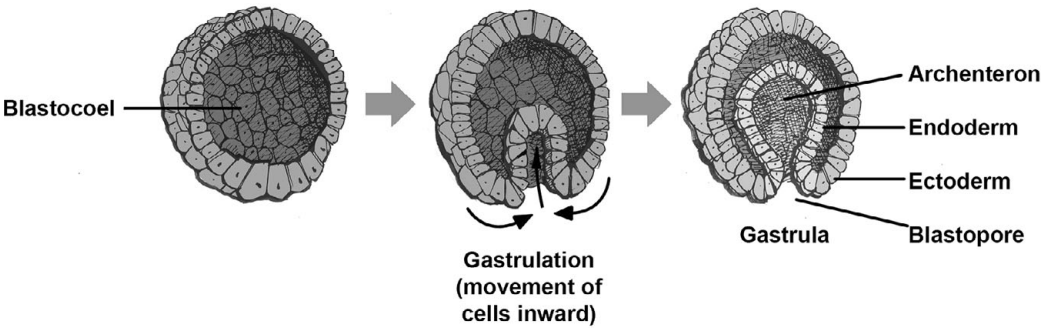


Figure 5.4 Gastrulation in the early animal embryo (a mesoderm will develop between the ectoderm and endoderm in most animals).
(A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

The animals whose development provided the data this time were *Drosophila* (with further evidence from polychaete annelids) and, for vertebrates, *Xenopus*, the clawed toad, a favourite experimental animal. To make the case perhaps we can look at the anatomy of the embryo in a little more detail. By the blastoderm stage, the original single fertilised egg (zygote) has divided into many cells forming a single-celled layer around a hollow sphere. The next major development stage is that of gastrulation (see Figure 5.4) when cells from the mid-ventral region fold inwards to produce a two (diploblastic) or maybe three (triploblastic) layered embryo. Within these germ layers, endoderm develops into the animal's gut and ectoderm into the epidermis and nervous system of the adult. Mesoderm develops into the muscles, circulatory system and sex organs in triploblasts (which includes most multicellular animals excluding the coelenterates and sponges).

The initiation of the dorsoventral distinction depends on a series of maternal-effect genes that result in the protein product of the *dorsal* gene (once again named for a mutant that inhibits its function). Thus, normal dorsal protein is a ventralising factor that diffuses upwards from the ventral midline. Dorsally another gene *decapentaplegic* (*dpp*) is expressed. The product diffuses ventrally but its effect is switched off where and when it meets the dorsal protein. Ventrally a third gene *snail* (*sna*) is also expressed, and its product appears to be involved in gastrulation. Lying between the regions on each side of the embryo is the region of expression of the gene *short gastrulation* (*sog*) which also produces a ventralising protein antagonising the activity of *decapentaplegic*. Short gastrulation protein is also involved in the development of the ventral nerve cord.

In *Xenopus* dorsoventral patterning is effected by a similar system, but the central nerve cord differentiates from specialised ectodermal cells occupying the dorsal midline. After gastrulation (inward folding of the hollow cell ball), the notochord, forerunner of the vertebral column, comes to underlie the neuro-ectoderm cells and induces them to roll up into the hollow nerve cord. This activity is prompted by the organiser, representing another concept from classical embryology. The organiser is a

region within the embryo responsible for coordinating major aspects of the body plan. Translocating this region into another embryo at the appropriate stage can induce a complete body axis (anterior-posterior, dorsoventral plus development of neural tissue from the ectoderm). It has more recently been discovered that a protein dubbed 'chordin' (*ch*) mimics the action of the organiser.

In *Drosophila*, the gene sog is expressed ventrally and is involved in the differentiation of the nerve cord. In *Xenopus*, the gene *chordin* is expressed dorsally and is involved in the differentiation of the nerve cord. The genes have similar functions, but their results are inverted with respect to each other. Furthermore, *sog* and *ch* are known to be closely similar in their respective nucleotide sequences. But most remarkable is the fact that they are functionally interchangeable. This has been tested by injection of the gene product, in the form of messenger RNA (mRNA), from one animal into the developing embryo of the other. If *sog* mRNA from *Drosophila* is injected into *Xenopus* embryos, it causes dorsal development: similarly, chordin mRNA from *Xenopus*, when injected into *Drosophila*, promotes ventralisation. As we saw above, the action of *sog* opposes that of *decapentaplegic*. In *Xenopus* the corresponding pair are *ch* and bone morphogenetic protein 4 (*Bmp-4*). Both *Bmp-4* and *Drosophila dpp* gene have similar sequences. The conclusion seems inescapable that the last common ancestor of *Drosophila* and *Xenopus*, some 600 million years ago or more, gave rise to two evolutionary lines: the first including bilateral invertebrates with a ventral nerve cord; the second including vertebrates with a dorsal nerve cord. So, at some stage in their phylogeny, one group must have rotated about its long axis relative to the other.

Functional Analogy

The actions of *short gastrulation/chordin* and *decapentaplegic/Bmp-4* constitute two pairs of analogous features between *Drosophila* and *Xenopus*. They display similar functions. There are other examples of such analogy among toolkit genes, notably two of field-specific selector genes noted above: *eyeless* and *Distal less*. The eyes of insects and vertebrates are very different in their mode of functioning. Adult insects have compound eyes, consisting of many units, or ommatidia, each of which is a receptor organ in its own right with an external lens and receptor cells. Vertebrates have unitary cup eyes with a single lens. But the selector genes in *Drosophila* and the mouse, *eyeless* and *Pax 6*, respectively, have each been shown to be active in the other organism, despite the very different nature of their respective eyes. Once again there is strong sequence similarity between the genes, and genes closely similar to *Pax 6* have been found to control eye development across the spectrum of animals with any sort of photo-receptor, suggesting a common evolutionary origin from the simple eye-spot to the complex eyes of insects, vertebrates (and cephalopods such as octopus and squid, which are very distant from insects and vertebrates on the evolutionary tree).

Similarly, homologues of the gene *Distal-less* are to be found in vertebrates and other animal phyla and play an important part in the development of limbs and other

appendages, for instance in the development of tube-feet in echinoderms. *Distal-less* has an important role to play in theories of the development and evolution of paired limbs in insects and crustaceans, a story developed below. However, we have just introduced the idea of homology among toolkit genes. The examples of correspondence between genes in widely different groups of animals cited above are all examples of **analogy**, similarity of function, but are the respective genes of a fly/vertebrate pair **homologous**? The question is a difficult one, to which the answer is, 'yes . . . but'!

In old-fashioned comparative anatomy, homology is judged by similarity of structure. When similarity of structure between genes became commonplace in the form of similarity of nucleotide sequence, molecular biologists started to talk about percentage homology, a concept alien to traditional comparative anatomy. There are further complications. A single gene in one animal may correspond to two or more in another. The latter pair are both homologues of their evolutionary history. When similar genes are recognised in two different animals as being derived from that of a common ancestor, those genes are known as **orthologous**. If two genes in the same animal are thought to have originated by gene duplication, those genes are described as **paralogous**; but what are we to call the relationship between either of the paralogous pair and the single gene in another animal from which they are presumed to be derived?

Nevertheless, the study of gene homology is one of the most important preoccupations of evolutionary developmental genetics, and it has been extensively studied particularly in the case of Hox genes. Another equally important subject is the study of the evolution of gene function.

The History of Hox Genes

Hox genes are clustered, control genes regulating the posterior/anterior axis of animals during early embryonic development. They control the development of the posterior/anterior axis, they are arranged along the chromosome in the same order as their sequence of expression and they produce a protein transcription factor.

The pioneering study of Hox genes was that of E. B. Lewis from the late 1940s onwards on what was then thought of as the *bithorax* locus of *Drosophila*, in which he discovered several mutations of homeotic effect. Later Lewis realised that he was dealing with a cluster of genes, each of localised action, and then that his *bithorax* mutations showed the phenomenon of colinearity. An important feature of this, not mentioned before, is the incorporation in each Hox cluster gene (in *antennapedia* and *bithorax*) of cis regulatory DNA in tandem with the coding bases and responsible for switching each gene on or off as required. Indeed, Lewis noted that in the *bithorax* complex 95% of the DNA was regulatory as contrasted with only 5% that is transcribed.

It has already been noted that the homeobox sequence in *Drosophila* is not confined to the *antennapedia* and *bithorax* complexes, the Hox genes of normal definition. But only in these do we find colinearity and the occurrence of homeotic mutation, the mutants taking on the characteristics of a shift in the nature of a segment

to that of an adjacent one. The homeobox itself was discovered more or less simultaneously in two laboratories in the early 1980s, both as a result of cloning the *antennapedia* gene for sequencing and discovering that it would hybridise with other genes from the genome, and that it coded for a DNA-binding protein.

As one might expect, the search was on for Hox genes in other animals. It was discovered that in mouse and *Xenopus* there was not just one cluster corresponding to *antennapedia* plus *bithorax* complexes, but four, each on a different chromosome. In animal history there had apparently been replication of the Hox sequence. The zebra fish, *Denio*, a favourite experimental genetic species, has seven. An unexpected discovery of the expression of the replicated vertebrate Hox genes was made in the mouse. The four clusters are known as Hox A, Hox B, Hox C and Hox D, while the individual numbers are numbered from the front, so that Hox A1, Hox B1 and Hox D1 are all homologues of the *Drosophila* labial Hox gene (common evolutionary history) and paralogues of one another (arise through duplication).

Hox genes have now been discovered in a wide variety of animals, but with the cluster replication confined to vertebrates as far as we know. One point of interest was whether they existed in apparently non-segmented animals. The tiny nematode worm *Caenorhabditis elegans* is a favourite experimental animal for developmental studies because the adult always has the same number of body cells (959) whose history can be followed individually. It has no apparent segments but has five Hox genes. Hox genes have now been discovered in many major animal groups (phyla), and the nature of those genes is valuable evidence of interrelationships among phyla. The lines of evidence are the sequence differences between homologous genes, the presence or absence of genes, and the cluster replication events as in vertebrates. It has always been difficult in the past to arrange the phyla on a family tree, but now the history of Hox genes corroborates other molecular evidence, notably that from the sequencing of ribosomal RNA, allowing the reconstruction of the phylogeny of the animal kingdom (Figure 5.5).

The Divergence of Body Plans

In looking at the history of Hox genes among animal groups it is now possible to reconstruct the history of those (and other) genes and to use that history to corroborate the pattern of evolution of the animal kingdom. But it is also possible to investigate the evolution of animal body plans by study of the action of the genes themselves. We will look at one such study.

Artemia, the brine shrimp, is a primitive crustacean not closely related to the true shrimps. It has a series of 11 trunk segments each with a pair of swimming legs, the whole apparently corresponding to the three-segment thorax of insects. In *Artemia* the head and jaws are situated in front of the thorax, which is succeeded by two genital segments, and a slender abdomen and terminal telson (Figure 5.6). We noted in talking about Hox genes that while in *Drosophila* each corresponds to a specific region, often one or more segments in linear order, the expression of each Hox gene

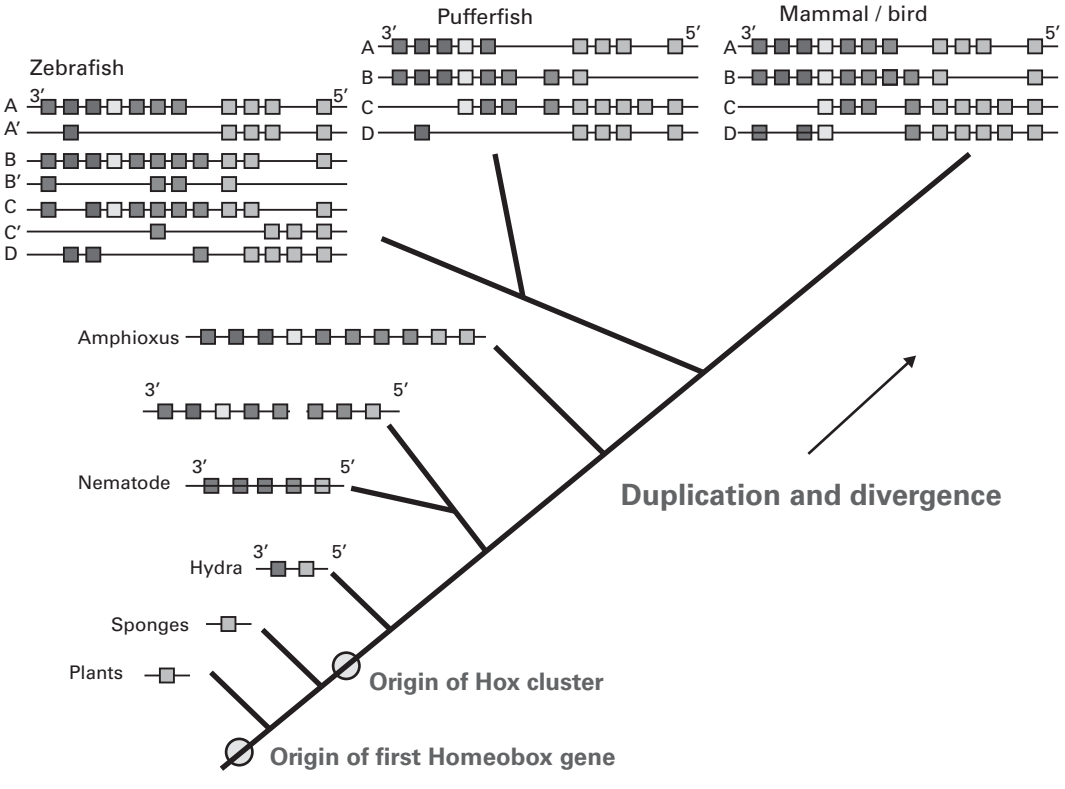


Figure 5.5 Evolution of Hox gene clusters, by processes of duplication and divergence, from an ancestor around one billion years ago. Reproduced from Lappin et al. (2006) courtesy of Ulster Med J. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

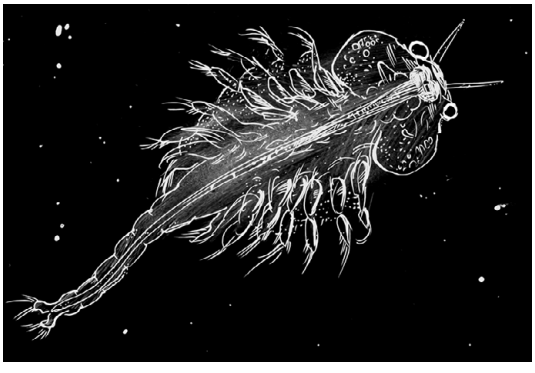


Figure 5.6 The brine shrimp (genus *Artemia*) an ancient crustacean having changed little since the Triassic period.

often overlaps with its successor. Averof and Akam (1995) discovered that in *Artemia* the domains of expression of *antennapedia*, *ultrabithorax* and *abdominal-A* genes coincide and extend the whole length of the 11 trunk segments, whereas *abdominal-B* is confined to the two genital segments.

There is little doubt that the three Hox genes *Antp*, *Ubx* and *abdA* are paralogues of one another, produced by gene replication in some ancestral form, and thus analogous to *HoxA*, *HoxB*, *HoxC* and *HoxD* clusters in vertebrates. In *Artemia*, the domains of the three Hox genes suggest that their functions have diverged little from the ancestral condition of a single gene.

What can these studies of genetic control of body plans tell us about the evolution and radiation of the Arthropoda? The ancestral arthropod is thought to possess segmented repeated, similar segments, each bearing unspecialised appendages or limbs, and studies have shown that changes in Hox genes correlate with major evolutionary events:

- For example, we believe that insects and crustaceans are derived from a common ancestor with a distinct head but undifferentiated trunk segments. The specialisation of the trunk into functionally distinct units, a thorax and abdomen, is thought to have evolved independently in these two groups. In insects, the differences between segments in the trunk are controlled by the *antennapedia*-like genes of the homeotic gene clusters. Using a PCR/inverse PCR strategy, Averof and Akam (1997) isolated six genes of the HOM/Hox family from the crustacean *Artemia franciscana*. Five of these are clearly identifiable as specific homologues of the insect homeotic genes *Dfd*, *Scr*, *Antp*, *Ubx* and *abdA*. We now think that all the homeotic genes that specify middle body regions in insects originated before the divergence of the insect and crustacean lineages, probably not later than the Cambrian (about 500 million years ago).
- A second example is observed during limb formation in arthropods. Here there appear to be three types of genetic control:
  - The *wingless* gene (*wg*) determines whether a limb is made
  - The *Distal-less* gene (*Dll*) extends the limb primordium and begins the growth of the limb
  - Hox genes then determine the type of limb produced with these homeotic genes specifying the fate of the appendage.

In *Artemia* the *Distal-less* gene also has a homeotic role in determining limb shape. Using antibodies to the *Distal-less* gene product, it has been shown how these genes regulate limb formation. *Distal-less* can be switched on and off and it is this temporal patterning, along with its location in the embryo, that determines the form of the appendage: single (uniramous), forked (biramous) or multi-lobate (phyllopodous).

Homeotic Genes and Control of Development in Higher Plants

Reproductive and developmental processes in plants differ significantly from those of animals. Plants undergo an alternation of generations – two distinct generational forms

with a diploid sporophyte (spore or seed producing) and haploid gametophyte (producing the sex cells or gametes). Animals, on the other hand, inhabit a body mainly comprising diploid somatic (body) cells with haploid gametes produced prior to reproduction. Within the embryo, germ cells in plants are produced at various locations and not just in gonadial tissue as in animals. A further difference is that in the higher plants, root and shoot **meristems** provide actively dividing tissue almost continuously. Animals do not have growth points or specific regions of actively dividing tissue; growth is continuous across all body parts.

'Higher' land plants are found in terrestrial environments from around 440 million years ago with four major radiation lineages:

- green algae
- bryophytes (mosses and liverworts)
- pteridophytes (ferns and horsetails)
- seed-bearing plants (the conifers and the flowering plants or angiosperms)

You will note that the kingdom Plantae has a disputed phylogeny and a difficult classification. Indeed, many of us regularly use both formal Latin or Greek nomenclature (Angiospermae, Pteridophyta) alongside the more vernacular (conifers, ferns, flowering plants).

Plant evolution can be seen to follow ecological and structural transitions analogous with those of animals:

- A transition from single-celled to multicellular as seen in the green algae with movement from single cells (*Chlamydomonas*) to colonial (*Volvox*) to true multicellular (the green seaweeds, e.g. Ulva)
- From aquatic to terrestrial modes of life (with development of a waterproof cuticle and stomata for gas exchange)
- From simple body forms relying on diffusion to larger vascular plants with specialised conducting vessels (xylem, phloem, tracheids)
- Greater protection of the embryo; from spores (in mosses and ferns) to seeds (in conifers and flowering plants) with their enhanced food reserves and elaborate dispersal mechanisms

The plasticity of plant development ('indeterminate' growth patterns) has offered unusual resilience and remarkable ability to adapt to varying environmental conditions.

The floral meristem produces in angiosperms (flowering plants) a distinct pattern of flower development consisting of four concentric whorls of leaf-like structures, the sepals and petals, and inner gamete-forming structures, the stamens (male parts) and carpels (female parts). Genetic analysis of *Arabidopsis thaliana* reveals important factors controlling flower development.

As with *Drosophila,* earlier studies of control of development began with exposing plants to mutagens and observing the consequences. Three main classes of floral mutation emerged:

Table 5.1 Mutation and floral development in *Arabidopsis*

Genotype	Phenotype	Whorls			
		1	**2**	**3**	**4**
Wildtype	Wildtype	Sepals	Petals	Stamens	Carpels
ap1/ap1	Class A	Carpels	Stamens	Stamens	Carpels
ap3/ap3	Class B	Sepals	Sepals	Carpels	Carpels
pi/pi	Class B	Sepals	Sepals	Carpels	Carpels
ag/ag	Class C	Sepals	Petals	Petals	Sepals

- Class A: lacks petals and sepals (replaced by duplicate sex organs, stamens and carpels)
- Class B: lacks petals and stamens (replaced by duplicate sepals and carpels)
- Class C: lacks stamens and carpels (replaced by duplicate petals and sepals)

Mutations lacking both sepals and petals are caused by the gene *apetala-1* (ap1). The phenotype lacking stamens and petals is due to a mutation in either the *apetala-3* (ap3) or *pistillata* (pi) gene. Those plants lacking stamens and carpels are formed through mutation of the *agamous* (ag) gene. All plants are homozygous for this recessive mutation (see Table 5.1).

The different floral phenotypes seen in these three classes of mutation are caused by transcription factors produced by one of the four genes. Transcription factors encoded by the *ap3*, *pi* and *ag* genes were found to have a common structure and belong to the MADS-box family of transcription factors (a conserved sequence motif comprising 58 amino acids) and are commonly found in plants. This (three classes) model of flower determination is generally referred to as the ABC Model.

There are several evolutionary implications to the ABC model of flower development. MADS genes do not form structural proteins in the flower; like Hox genes they indicate location and process (do this to whorl 2, etc.). Again, like Hox genes, they were 'requisitioned' later with a new purpose (in this case directing floral development). However, the similarities of developmental control systems in animals and plants is impressive. Multicellularity arose independently in animals and plants yet there is a striking convergence in these regulatory genes and their signalling mechanisms.

MADS-box genes have been found in nearly all eukaryotes studied. The genomes of animals (and fungi interestingly) contain only a small number (1–5) of these genes; flowering plants typically have around 100 MADS genes. The name 'MADS' is an acronym of the first letters of the original four organisms studied, and generally the gene comprises 160–180 base pairs with the encoded domain having a length of 50–60 amino acids. There is evidence that this MADS domain evolved from a topoisomerase which may be the ancestor of all

eukaryotes. MADS-box genes in both animals and plants have a wide variety of functions.

Evolutionary Developmental Repatterning

The evolution of life on Earth is characterised, paradoxically, by both a robustness and conservation of body form along with plasticity and change. The potential to produce different forms during development, from zygote to adult, requires explanation. Living systems appear to be fixed in terms of their genomes and their morphologies yet, within species groups, plastic at the same time. This appears to be an inherent characteristic of living things.

During the development of an organism several processes may contribute to evolutionary change:

- ❖ Differences in the timing of events
- ❖ Differences in the type of events
- ❖ Differences in the spatial location of these events
- ❖ Differences in the amount of activity

Therefore, differences in the timing, location or kind of DNA activity may determine the production of novel characteristics in the offspring. Wallace Arthur (2002) referred to this as 'developmental repatterning'. Such regulation or repatterning of development can produce significant changes. For instance, change in dorsoventral axis (see 'Homeotic Genes and Control of Development in Higher Plants') between vertebrates (deuterostomes) and selected invertebrates (protostomes). An inversion in the position of the nerve cord, caused by a change in gene expression, has resulted in profound morphological transformations.

Evolutionary developmental biology or evo-devo is a powerful and recent addition to the biological canon. It tells us that evolution can throw up novelties not simply by mutation and molecular changes during gamete formation but that changes in developmental processes in the embryo can also produce significant changes to the body plan in both animals and plants. Perhaps one of the greatest achievements of evo-devo is to help resolve the long-standing debate as to how the processes of small-scale, within-population changes (**microevolution**) can be reconciled with the broader, long-term changes between taxonomic groups (**macroevolution**). Mutation, selection, genetic drift and gene flow can explain the (microevolutionary) population changes, but we need to look to patterns of gene expression and recent evo-devo research to explain the broader changes in the history of life on Earth.

6 The Origins of Biodiversity

It is ironic that one subject barely covered in Darwin's *Origin of Species* is the origin of species. To Darwin there was a smooth continuum from varieties to species: he did not see speciation as an event. He did, however, pronounce a principle of divergence. The economy of nature would be more efficiently exploited if two groups of organisms diverged from one another in anatomy and behaviour so that each came to occupy a different ecological niche. This process would be promoted by natural selection (though for purposes of classification and evolutionary history, the concept of 'species' needs to be discussed further).

Charles Darwin pondered long and hard over the concept of species. In chapter 1 of *Origin of Species* (Variation under domestication) Darwin explored the various breeds of domestic animal including, one of his favourites, the pigeon – the diversity of which he found 'astonishing'. And, having 'kept every breed that I could purchase or obtain' plus obtaining 'skins from several quarters of the world', Darwin explored the variety of this collection of domestic bird types. Skeletal anatomy, size and shape of the eggs together with their plumage were carefully examined. He admitted that if he chose some of these breeds and presented them to an ornithologist as wild birds, they would certainly 'be ranked by him as well-defined species'. But Darwin (along with others) recognised that all the domestic pigeons he was observing were derived originally from the rock pigeon and had become 'modified' by the deliberate breeding attempts of humans. He argued for their status as breeds and not as distinct species because:

- Generic rock pigeon characteristics are held by all the different types ('agreeing generally in constitution, habits, voice, colouring and, in most parts, of their structure with the wild rock pigeon')
- The ability of the breed to revert to their 'aboriginal' form when intercrossed ('the well-known principle of reversion to ancestral characters')
- And 'lastly the hybrids or mongrels from between all the domestic breeds of pigeons are perfectly fertile'

Darwin therefore begins to characterise what it means to be a species; and in chapter 7 (On the races of Man) he points out that when determining whether allied forms should be ranked as species or varieties (races or breeds), then the following considerations should be considered:

- ❖ The quantifiable differences between them – are there a few or many points of difference?
- ❖ The physiological importance of these differences
- ❖ The constancy of character (for that is 'chiefly valued and sought for by naturalists')
- ❖ Along with degree of sterility when crossed, for that is 'generally considered as a decisive test of their specific distinctiveness' (though he did then go on to discuss the 'blending' of different forms from intercrossing)

Charles Darwin was particularly adept at describing concepts through individual cases. It may be of interest to know that today we still value this early work through a website dedicated to pigeons and their genomic diversity (http://darwinspigeons.com/).

Species Concepts

It was with the development of the Synthetic Theory that speciation was incorporated into the Darwinian fold, largely due to Dobzhansky and Mayr. Before the synthesis there was little agreement, either on the definition of a species, or on the 'species concept' on which it should be based. The discussion continues to the present day, but Mayr's influence marks a base line from which that discussion takes place. He insisted that a 'biological species concept' was essential, rather than what he described as a 'typological concept'. The biological species concept relies on the primacy of being able to interbreed. The earlier typological concept describes a species as a set of observable features that all members of that species set share.

Species concepts are a set of rules or distinctive features used to define a species. Argument and debate over what constitutes a species remains a problem for evolutionary biologists to this very day. Both the biological and typological views have been described as *pattern-oriented views*, that is specific characteristics, rules or patterns of appearance that can be used to define a species. So-called process-oriented views do not use set criteria to indicate membership of the 'species' group; rather, the process-oriented view uses some level of *divergence* (such as ecological divergence or evolutionary divergence) to separate different species. A summary overview of differing species concepts is given in Table 6.1.

So, to return to the earlier discussion, in the typological case a specimen is recognised as a member of a species solely on anatomical and other characteristics. From a practical point of view this is still the method by which specimens of organisms are named today. They are compared with a standard description or, better still, with **type specimens** in a museum. A type specimen is the original example of a species that serves as an example against which others are compared. But there are difficulties with a comparative approach. Linnaeus did not realise that the male and female mallard duck were the same species, naming the former *Anas boschas* and the female *Anas platyrhynchos*. At the other extreme, two or more species living at least partly in overlapping areas (i.e. **sympatric**) may be closely similar in appearance yet

Table 6.1 What is a species? Comparing the different species concepts

Species concept	Descriptor	Notes
Morphological species concept	Organisms classified based on their appearance	Often difficult to distinguish males from females or old from young
Biological species concept	A freely interbreeding population whose members produce viable offspring. This concept is based on breeding success	Based on a discrete mechanism but what about asexual forms or fossils!
Phylogenetic species concept	Considers the evolutionary relationships between organisms and their common ancestry. The species represents a terminal 'branch' of the evolutionary tree	Rather arbitrary division of lineages
Recognition species concept	Emphasises the development of different fertilisation systems; it is based on the 'recognition' (for mating purposes) of one species by another	Applies only to sexually reproducing organisms
Genetic species concept	Species are defined by the measure of genetic similarity and hence their 'relatedness'	Particularly useful for prokaryotes and closely related forms. Interpretation of 'genetic distance' can be subjective
Cladistic species concept	Uses the presence of shared or derived characters (synapomorphies) as its main criterion	Relative to a particular clade only
Ecological species concept	Employs the discrete adaptations of organisms to environmental niches. This acknowledges the role of the environment in shaping morphological and physiological development	Omits the variability of niche separation. Some species may be overlooked; there is also the difficulty of objectively defining a niche

not interbreed. A classic case here is that of two species of *Drosophila* studied by Dobzhansky and his colleagues in western North America. Originally these were described as *D. pseudoobscura* race A and *D. pseudoobscura* race B. Crosses between the two yielded fertile females and sterile males. It was also found that 'race A' had a more southerly distribution than 'race B', although their ranges overlapped broadly along the west coast. Subsequently, after intensive study several anatomical and behavioural differences were discovered, and the salivary gland giant chromosomes were found to be very different. 'Race A' retained the name *D. pseudoobscura*, while 'Race B' was renamed *D. persimilis.*

In the United Kingdom two common warblers, the willow warbler and the chiffchaff, are indistinguishable in the field except for their song, which is a good example of **reinforcement** (process by which natural selection increases reproductive isolation). However, the distinction between the two groups is that interbreeding does not take place between them. To make this point Mayr invoked his **biological species concept**, which involved 'population thinking'. Members of a species should not be

thought of as specimens with defining characteristics, but as members of several populations that could all potentially interbreed. The biological species concept is based on a mechanism – breeding success.

Mayr in his great book on the subject, *Animal Species and Evolution* (Mayr, 1963), distinguished two ways of looking at species for the working taxonomist:

- The 'non-dimensional concept' would be that used in distinguishing a number of similar sympatric species ('sibling species' as in the two *Drosophila* species). The emphasis would be on discovering significant differences between them, and, particularly, evidence of reproductive isolation.
- The 'multidimensional concept' looks at the world-wide range of populations which may or may not form a single species, to judge whether they might interbreed successfully.

The biological species concept, although attractive in many ways, contains within it three main practical problems:

- Firstly, it only applies to sexually reproducing populations. Thus, several of the fungi, the water flea *Daphnia* and that complex botanical group the dandelions (*Taraxacum* species) all show some form of asexual reproduction. In the dandelion *Taraxacum officinale* an asexual triploid form is seen. Do we therefore group these clones within the same species as their diploid relatives? Similarly, in *Daphnia,* hybridisation events occur giving rise to obligate asexual forms.
- The biological species concept is difficult with extinct species where the only evidence is their fossil remains.
- Finally, another problem is that of hybridisation. Isolating mechanisms, which tend to favour formation of new species, often break down with the result that fertile **hybrids** are formed. This is less common in animals but relatively common in plants.

To overcome the problems associated with reproductive isolation mechanisms authors such as Paterson, in the mid-1980s, suggested that a species is one that shares a common fertilisation system (courtship behaviour, genitalia structure, etc.). The **recognition species concept** emphasises the evolution of fertilisation systems and their similarity rather than the practical problems of successful interbreeding which may not be observable.

Another problem with the biological species concept is that it fails to recognise evolutionary lineage. Organisms may have demonstrated a continuity of reproductive success for millions of years before modification occurs. A phylogenetic perspective recognises derived ancestral characters that make up discrete species groups. And in this definition (often referred to as the phylogenetic species concept) the delineation between species is made based on clusters of organisms in which there is a common pattern of ancestry and descent. We call such a group **monophyletic** (a single phylogeny).

Another suggestion, particularly with plants in view, involves a 'cohesion concept' (Templeton, 1989) with 'cohesion mechanisms'. Some plant species have intrinsic populations where there is little or no interbreeding among them but may on the other hand interbreed with members of other populations that have no ecological continuity.

The essential criterion of the cohesion species concept is that of genetic 'exchangeability'.

So, what exactly is a species? Such a fundamental unit of biology has a rather fluid definition depending upon the perspective (morphological/reproductive/phylogenetic) one takes. A working definition though might look something like this:

A morphologically and genomically distinct population of organisms that can freely interbreed producing viable and fertile offspring.

A historical account of the 30 or so species concepts, the notion of species being derived from Aristotle's 'essences' along with the more practical aspects of defining a species, is given in Frank Zachos's book *Species Concepts in Biology* (Zachos, 2016).

Isolating Mechanisms

How do two closely related species not interbreed? The answer is that they are reproductively ***isolated*** with mechanisms having evolved to prevent such an occurrence. Barriers to successful reproduction are of two main types:

- **Physical**: geographical separation (mountains, rivers, deserts) preventing individuals in sexually reproducing populations from contacting one another. Species geographically separated are termed **allopatric**.
- **Biological**: of two types. Firstly, *premating isolation mechanisms* involving either an ecological barrier, a seasonal isolation or a behavioural (courtship) problem. Secondly, *postmating reproductive isolation*, either preventing the zygote from forming or rendering the newly formed zygote inviable. Where populations occupy the same geographical space, this is termed **sympatric**.

In 1937 Dobzhansky introduced the concept of '**isolating mechanisms**' keeping species apart. He distinguished two categories: **prezygotic mechanisms** and **postzygotic mechanisms**. These are defined in terms of zygote formation (the fusion of sperm and egg), or rather the failure thereof. In prezygotic mechanisms, no zygote is formed; in postzygotic mechanisms, a zygote is formed but the result fails: it is inviable, sterile or at a strong selective disadvantage.

Prezygotic barriers may be either physical or biological. The major causes are:

- Potential mates do not meet (physical separation)
- Potential mates meet but do not mate (behavioural isolation)
- Mating takes place, but without transfer of gametes (mechanical isolation)
- Gamete transfer occurs, but there is no zygote formation (gametic incompatibility)

The first category (not meeting) may be further subdivided into **temporal isolation** (temporal = time) and **habitat isolation**. In the case of temporal isolation, the two sympatric species will have different mating times. This can be different times of day, as is said to be the case between *D. pseudoobscura* and *D. persimilis*, or different times of year, as is the case with two species of gull, the herring gull (*Larus argentatus*) and the lesser black-backed gull (*Larus fuscus*). The herring gull has the

height of its egg-laying season in Britain in the last third of April, the lesser black-backed gull in mid-May. These two are sympatric in Britain and Scandinavia. Habitat isolation is illustrated by studies on two species of North American toads, *Bufo fowleri* and *B. americanus* occupying different ecological niches. *B. fowleri* mates and lays its eggs in ponds and large semi-permanent rain pools, while *B. americanus* uses shallow puddles and brook pools. Habitat isolation is even more manifest where the organism is sessile and thus fixed, or when, as in phytophagous (plant-feeding) insects, it breeds, feeds on and inhabits its unique food plant.

There are several examples of **behavioural isolation**, where sympatric species are kept apart by incompatibility in their mating behaviour. When Kettlewell was recapturing his samples of the peppered moth he used light traps, but also the technique of 'assaulting'. In this a female moth is presented in a gauze cage and males, attracted by her scent, flock around the cage. Thus, all his samples were of males only (incidentally they also visit light traps more readily). The males were attracted by the female's sex pheromone, a species-specific cocktail of organic chemicals to which they are incredibly sensitive. Other closely related species do not respond to this sexual signal, and so it acts as an effective reproductive isolating mechanism for the moth. Similarly, other sensory signals are species-specific, as with the male song of grasshoppers and crickets, or the bright and distinctive appearance of many male birds – here isolating barriers merge with sexual selection!

Speciation

So far it has been intimated that isolating mechanisms prevent interbreeding within populations. But the self-same mechanisms can also encourage populations develop independently. Speciation, the process by which organisms form new and distinct evolutionary lineages, is at the centre of modern evolutionary biology and as Francisco Ayala states, new species are formed '*as a result of gradual change prompted by natural selection*'. This process, though profound, is not so clear cut, however. Several 'intermediate' stages may be witnessed (different varieties and subspecies for instance) while the 'shading' of one species to the next is as imperceptible as night into day or winter into spring.

Ernst Mayr maintained that, at least in animals, **allopatric speciation** (occupying distinct non-overlapping geographical areas) is the predominant, or even only, mode for the origin of species. The scenario for allopatric speciation was sketched earlier in the book for two variants of Darwin's finches. The first was illustrated by the migration of a founding sample of a few individuals to a new environment, almost completely isolated from the parent stock (the dispersal of the ancestors from the South American mainland to the Galapagos). The second variant of allopatric speciation is illustrated by the division of the Galapagos finches into several species.

The first (migration) account illustrates another thesis of Mayr's: that the 'sample' of birds, because of its small size, had a gene pool that was impoverished with respect to the parent stock and atypical in the frequency of the alleles that were there. Thus, according to his theory, the founding population had a 'kick-start' with respect to

genetic isolation from the parent stock. This is known as the '**founder effect**'. The founder effect is an example of a **genetic drift** where relatively few individuals from a larger population colonise an isolated habitat. In such situations, previously rare alleles (in the parent population) may come to predominate or unusual allele combinations appear. In some human populations, for instance, diseases that are relatively rare in mainland Europe are very common in newly established colonies abroad. Examples here include a progressive blindness called retinitis pigmentosa found in Tristan da Cunha, a small group of islands mid-way between Africa and South America in the Atlantic Ocean. It was here in 1814 that 15 British colonists first founded their small settlement. Other examples include the inherited disorder of blood metabolism, porphyria variegata, found in the Dutch Afrikaans population of South Africa, and experimental populations of *Drosophila.* In *Drosophila* small populations and large populations were removed from a parent population in which there was a 50% frequency of a chromosome inversion. Over a period of five months, the frequency of the chromosomal aberration showed much greater variety in the small than in the large populations indicating that the gene frequencies of the 'founder' individuals were instrumental in determining that of the final population.

The second account of allopatric speciation is that of the speciation of the Galapagos. This is an example of '**adaptive radiation'**. The original ancestral stock, from which all of Darwin's finches were derived, are taken to have arrived on one (or more) of the Galapagos Islands. The population derived from them is thought to have then migrated to and colonised other islands. Each population would, over time, become adapted to specific features of its new island home. Occasionally, samples of adapted population would migrate to another island with its own finch population. If the two populations had become sufficiently distinct, **reinforcement** would occur – selection would emphasise the distinction in the ecology of the two so that speciation would be completed in sympatry. But, as we saw in the case of the finches, there are doubts about the proposed pattern – the islands are not especially distant from one another, so that the island allopatric phase is 'leaky'. Hybridisation between presumed different species can produce well-adapted offspring, and there is a hint of the possibility of **sympatric speciation** in the large cactus finch on the island of *Genovesa*. There are also other cases of adaptive radiation (notably that of cichlid fishes in Africa) where the allopatric origin of sibling species would seem to have been impossible and so sympatric speciation is the most likely cause.

Under most circumstances natural selection does not favour isolation – rather it is the other way around, isolation is a product of natural selection. Populations that have evolved separately may experience postzygotic barriers, leading to no offspring or offspring with a decreased fitness. In such a case it is advantageous to avoid mating at all; the evolution of prezygotic barriers is now a selective advantage. This is where **reinforcement** comes in. Reinforcement is a process in which selection favours isolation to decrease unfit hybrids. The isolation seen on the Galapagos and the different songs of willow warbler and chiffchaff (mentioned earlier) may well have arisen via this pathway.

If evolution is slow and gradual (which quite often it will be), then over time we can imagine it leading to two separate species with so many differences that (postzygotic) barriers are in place that prevent hybridisation. However, after the very first steps on this long road, these barriers will not be there yet. In the case of allopatric speciation this is not a problem: mating will not occur simply because the diverging populations will never meet. In the case of sympatric speciation though the crucial question is what keeps the populations apart in those early stages?

Ernst Mayr did not believe sympatric speciation could happen (at least initially he did not) but he never discounted that evidence might be forthcoming, stating that fresh water fish 'seem to have sympatric speciation'.

If the question is posed, 'does **sympatric speciation** actually occur?' (sympatric speciation is where a biological barrier exists within populations occupying the same geographical area), the answer is an unequivocal 'yes'! This is because of the phenomenon of speciation by polyploidy.

Speciation through Polyploidy

Polyploidy describes the multiplication of whole chromosome sets within cells and is a phenomenon common in plants but also occurring in some animal species such as earthworms and rotifers. In the production of normal gametes, reduction division (meiosis) occurs, resulting in half the number of chromosomes in each gamete, sperm or egg (haploid), than in normal body cells (diploid), respectively. In the case of polyploidy, a reduction division at meiosis fails in one of several ways, so that a pollen grain (or ovule) contains a double or diploid number of chromosomes. A doubling of chromosome 'sets' is the most common form of polyploidisation.

If a diploid pollen grain nucleus fertilises a normal haploid ovule (or vice versa), the resulting zygote has three sets of chromosomes (in triploid), signified by $3n$, where n is haploid and $2n$ is diploid. A triploid plant is usually sterile, because at meiosis, the cellular mechanism cannot cope with reduction division of the $3n$ number. Another possible dead-end result is when the normal pollen of one plant species fertilises the ovule of another different-but-related species. This will occur if the chromosomes of one plant are sufficiently different from those of the other that the process of crossing over between parts of the paired chromosomes cannot take place.

Nevertheless, speciation by hybridisation between species yielding a new form does occur. This is thought to be particularly important in the flowering plants where perhaps three-quarters of species have arisen through these (polyploidy) means. An example is the common cultivated tree, the London plane, *Platanus*. Its parent species are the oriental plane, *Platanus orientalis*, originally distributed in Asia Minor, and *Platanus occidentalis*, from the eastern United States. Even though the parent species are known to have been isolated from one another for more than 20 million years, their hybrid is vigorous and fully fertile. Full genetic isolation between the parent species has not yet occurred.

With hybrid pairing followed by polyploidy, however, chromosomal incompatibility between the parent species need not inhibit the production of a daughter species. The polyploidy results in a tetraploid. Then meiosis results in diploid gametes, each with a contribution from both parents.

Such a plant, originating from hybridisation of two species, followed by polyploidy, is called an **allopolyploid** (different polyploid). Pairing between diploid gametes of the same species yields an **autopolyploid** (a self-polyploid).

A much-studied example of allopolyploidy concerns the originally European species of goatsbeards, dandelion-like weeds. Three species have becomes widely distributed in the USA – *Tragopogon dubius*, *T. porrifolius* and *T. pratensis*. All three have a diploid number of 12 chromosomes. In 1950, two apparently new species of *Tragopogon* were described from the north-west USA, each with 24 chromosomes: one a tetraploid hybrid between *dubius* and *porrifolius*, the other between *dubius* and *pratensis*. The new species have ecological requirements intermediate between those of their parents, and studies of their genome confirm the identification. Furthermore, by investigating the chlorophyll-bearing chloroplasts, which like mitochondria are passed down only in the female line, it has been shown that in some populations the original parent of the hybrid was from the opposite species to that in other populations; thus, confirming the suspicion that the new hybrid species has arisen several times.

Another famous example is the evolution of wheat (*Triticum aestivus*), which combines rounds of hybridisation leading to sterile hybrids, followed by polyploidisation, which restores fertility.

Cases of speciation by autopolyploidy are probably less frequent than those of allopolyploidy, though many cases are known when several species in the same genus have a diploid number that form a series. Thus, in *Chrysanthemum* there are the numbers 18, 36, 54, 72 and 90, all multiples of 9. The cultivated potato (*Solanum tuberosum*) is thought to be an autotetraploid of a wild South American species.

All these cases of hybrid and polyploid origin are essentially examples of instant speciation, which produce new plants that are morphologically different (usually with larger somatic cells), but also differ in their ecology from their parent species. They do not, however, differ in the origin of new anatomical structures; so it is probable that the new instant species is not ‘placeable’ in a new genus, whatever the fate of its descendants. Nevertheless, botanists agree on very high estimates of the percentage of species with hybridisation in their history (perhaps up to 70% of all plant species) and that this process is both ancient and recurrent (see Adams and Wendel, 2006).

Parapatric Distribution, Speciation and Hybrid Zones

To form a new species, a variant (or variants) must arise in a population of interbreeding organisms. If features of the new variant are heritable and if its progeny are

geographically isolated from others of the same species, then it is easy to imagine divergent selection between the two groups with each (geographically separated population) evolving independently. This scenario (**allopatry**) is like that seen in Darwin's finches, earlier in this chapter. If populations are contiguous (touching) rather than totally separate (we call this a **parapatric distribution**), then one might imagine an area of contact, a hybrid zone, between two noticeably different populations. But populations can also exist in **sympatry** that is occupying the same geographical space and, as we have already seen, new species formation may be induced through plant polyploidy. Thus, a newly evolving species may have one of three distinct geographical relationships with its immediate ancestor: an allopatric, parapatric or sympatric one (Figure 6.1).

A pair of related species have an allopatric distribution if their ranges do not overlap. If the ranges do not overlap to any considerable degree, they are sympatric. But between these two extremes there are many examples of pairs of species with adjoining distributions and varying degrees of genetic isolation between them. Frequently the genetic barrier between them is so slight that they regularly interbreed and produce fertile offspring. But their distinctness and difference in distribution is retained and interbreeding is restricted to a **hybrid zone** where the two meet. Such distributions are parapatric.

An example of such a parapatric distribution is that of two types of crow in Western Europe. The junction between the two habitats runs through Denmark and from north to south to the Mediterranean coast, with the carrion crow (*Corvus corone*) to the west, and the hooded crow (*Corvus cornix*) to the east. In the British Isles the border runs through Scotland from the west to the east with the hooded crow to the north. Only the hooded crow occurs in Ireland (Figure 6.2). One possible explanation for the differentiation between the two is that originally there was a **cline**, a geographical gradient of characters correlated with environmental features across the range of the

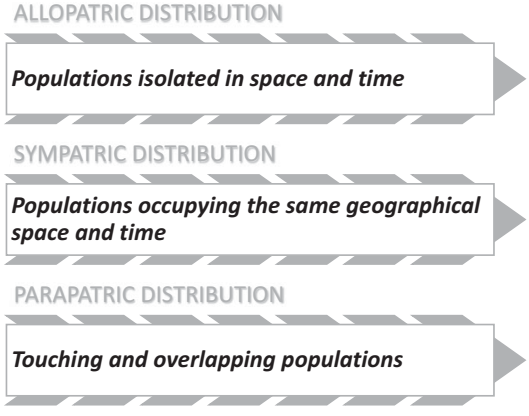


Figure 6.1 Distributions of plant and animal populations influencing species formation.

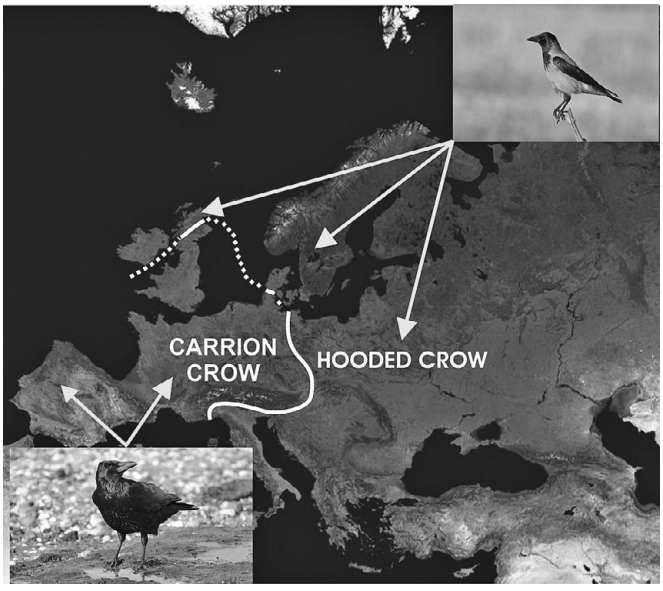


Figure 6.2 Distribution of both carrion crow and hooded crow in Europe. The two species are almost genetically identical (slightly different phenotypes) but can hybridise along the contact zone that separates them. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

single parent species, but the range of the cline narrowed to a hybrid zone, eventually resulting in parapatric speciation.

There has been an intensive study of hybrid zones in the hope of learning something of parapatric speciation. According to Endler's (1977) model, an ancestral species is distributed over a variable and heterogeneous area. Biological differences in different areas of the geographical range may therefore lead to the formation of a gradient of physical and genetic characteristics – an ecological cline. Further development of these differences can lead to two subpopulations with the cline now acting as a barrier to gene flow. Because of divergence, the cline becomes steeper until a very narrow hybrid zone is formed with highly differentiated subpopulations on either side.

It now seems more probable that parapatric distributions are to be explained by expansion of two or more original populations until they meet and interbreed along the hybrid zone. In some cases, if there is little reproductive isolation between the populations, there will be hybrids as well as the parent forms in the zone of overlap.

Another type of zone results from the junction occurring in a mosaic environment. An example of a 'mosaic hybrid zone' occurs along the eastern edge of the mountains in the USA from Connecticut to the South of Virginia. Of two species of cricket, *Gryllus firmus* to the east is adapted to an environment based on sandy soils, while to the west of the zone, *Gryllus pennsylvanius* is adapted to loamy soils. The zone region

has a mixture of both environments. There is some degree of genetic isolation between the two populations.

Two types of question arise from studies of parapatric distribution.

1. Did the differentiation either side of the hybrid zone arise in an originally continuous population?
2. Did present-day hybrid zones arise through secondary contact?

If the differentiation either side of the hybrid zone arose in an originally continuous population, then there are two possibilities:

(a) development from a cline that occurs in a series of steps, to one that has at least one large step in genetic, morphological or behavioural features;
(b) adaptation to some new features in the environment.

1. Plausible examples of (a) are difficult to find, but there exists a classic study as an example of (b). This concerns the adaptation of grass species to tolerate heavy metal pollution. The grass species *Agrostis tenuis* on mining spoil tips at a number of sites in Britain was the subject of study by A. D. Bradshaw in the late 1960s and early 1970s and by others more recently. Soil heaps from metal mining contain high levels of copper, zinc and lead and other poisonous metals, and are colonised by plants slowly if at all. But *Agrostis tenuis* and other grasses occur and flourish because they have evolved resistance. There is therefore a steep environmental boundary between the heap and the environment outside it resulting in a parapatric relationship between tolerant grasses on the spoil heap and non-tolerant grasses outside. There is still some gene flow between the two types because of wind-pollen, but strong natural selection has occurred, with seeds from the 'outside' failing to develop on the heap and seeds from the resistant grasses known to be at some disadvantage in unpolluted soil. Despite the gene flow there are signs of divergence and thus genetic isolation between the two. Flowering times are now significantly different between resistant and non-resistant grasses.

2. The second possibility is that present-day hybrid zones arose through secondary contact. This appears to be the normal explanation for parapatric distributions, so that if subsequently the parapatric populations achieve full species status, they will have had a period of allopatric distribution before parapatric contact-and thus represent a case of allopatric speciation. This is almost certainly the situation with respect to those cases we have looked at in this book: the 'crow line' in central Europe, supported by similar distribution of other animal species; *Gryllus* crickets in the USA with their patchy mosaic zone; *Bombina* toads in central Europe; and 'area effects' in the banded snail *Cepaea nemoralis* on the Marlborough Downs. A phenomenon that emphasises the point is that of 'ring species'. In talking about prezygotic barriers earlier, we noted the two sympatric gull species-the herring gull, *Larus argentatus*, with a pale grey mantle formed from the wings and pink legs, and the lesser black-backed gull, *Larus fuscus*, with a near-black mantle and yellow legs. The two are sympatric in Britain and Scandinavia and are undoubtedly good separate species. But *Larus* gulls circle the North Pole. Going eastward they are distributed in northern Siberia to the eastern

Asian boundary of Russia, then across the Bering Strait and across northern North America, and finally back to northern Europe and the two sympatric species. But around the circle of distribution, there is a gradation of character from those of the black-backed to those of the herring gull -a circular cline of character whose ends happen to overlap in Britain. The gulls are somewhat arbitrarily divided into six species, but essentially form a continuum.

It is probable, once again, that the gull ring species underwent partial allopatric speciation in Ice Age refugia. But another intensively studied ring species appears to have a rather different explanation. *Ensatina eschacholtzii* (Figure 6.3) is a salamander whose overall distribution is along the western coastal range of (from north to south) the states of Washington, Oregon and California. In California the species's distribution circles the Central Valley along the Coastal Range in the west and the Sierra Nevada in the east. The western and eastern 'branches' meet to the south of the valley but do not interbreed. There are seven named subspecies in the complex, all strikingly different in appearance, but apart from the southern terminal pair, all adjacent pairs of subspecies interbreed freely. The accepted explanation is that the species spread from northern California down either side of the Central Valley, differentiating as it went, until the two branches met in the south. Studies of mitochondrial DNA corroborate this.

We referred to the various forms of *Ensatina* as 'subspecies', but in the case of the gulls *Larus argentus* and *Larus fuscus* are good species. The term subspecies is usually used to label allopatric populations agreed to be the same species, but

Figure 6.3 *Ensatina eschscholtzi*, a dramatic ring species demonstrating both variation and interbreeding. Credit Francesco Dall'acqua / EyeEm / Getty Images. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

distinguished by their distribution and appearance, but all sorts of other terms have been used, apart from subspecies to distinguish parapatric populations that are not quite separate species – terms such as 'semi-species', with 'superspecies' or 'species-group' to label the whole complex. As we know that evolution has occurred, it should come as no surprise to find that the biota is not neatly divided into clear distinct, easily recognised units.

The topic of subspecies, hybrid zones and ring species catches 'evolution in the making'. We may be halfway through the process of speciation here, not entirely there yet, but changes have happened, and reproductive barriers of some kind are present. Hybrid zones are narrow – both with the crows, the salamanders in Western America, and the fire bellied toads in Europe. If there were no barriers at all (and hybrid offspring had the same fitness as either parent) then the hybrid zone would expand and expand until either a cline was reached or until both groups melt together into one. This does not happen; instead the zone remains narrow. The zone itself may move (the black/hooded crow barrier has moved up North over time), but it remains narrow. The most likely explanation in most cases is that the hybrids have a lower fitness than either parent, either because of genetic defects stemming from their different parent genomes or because they are less well adapted than either parent. This can again open the door to reinforcement: in such a situation, it pays off to evolve characters that do not necessarily contribute to the bearer's fitness, but which help in making the 'correct' partner choice.

Sympatric Speciation

In looking for cases of sympatric speciation (apart from hybridisation and polyploidy in plants) two principal types of evidence might be expected: (1) historical records of a new species (or incipient species) appearing within the range of an existing closely related species, and (2) two or more closely related species coexisting in a restricted environment, and endemic in that environment, where no scenario can be suggested for an allopatric phase in the origin of those species. An example of the first case involves the 'true' (as contrasted with the *Drosophila* group) fruit fly *Rhagoletis pomonella*. The second case is illustrated by fishes that demonstrate the most spectacular example of adaptive radiation in the animal kingdom – the cichlids of African lakes.

Ironically the modern investigation of *Rhagoletis* as a possible example of sympatric speciation was initiated by a one-time graduate student of Ernst Mayr's, Guy Bush, though the history goes back to the time of Charles Darwin. In 1864 an American correspondent of Darwin's, Benjamin Walsh, wrote to him to say that a local farmer in the Hudson River Valley, New York State, had a new pest burrowing in his cultivated apples. These 'apple maggots' turned out to be the larvae of *Rhagoletis*, whose normal food was hawthorn berries. The fly was not known to parasitise the native North American crab apples, and Walsh actually suggested that *Rhagoletis* had changed its allegiance from hawthorn to apple and thus the apple flies were in the process of

becoming a new species. Darwin comments on the phenomenon in the sixth and last edition of the *Origin of Species* (pp. 35–36). A hundred years later, in the 1960s, Bush set out to investigate.

The important features of such a case are that the larvae feed on the host plant and that mating of the adults also takes place on the host. As with the case of grasses on mine spoil heaps, the timing of the reproductive cycle is different, but with a small time overlap. The 'new' apple race emerges from mid-June to the end of August, the hawthorn race from early August to mid-October: in each case about one month before the fruit is ripe. At first nothing was known about the genetic difference between the two races. In 1966 John Maynard Smith, at the University of Sussex, had produced a theoretical model in which at least two gene loci must have come to differ if the races were on the way to becoming separate species. One locus must condition host choice, and the other, survival on the 'correct' host. Selection for genetic linkage between the two should then occur (unless there was the unlikely mechanism that a single (pleiotropic) gene locus controlled both). It also had to be shown that the timing of emergence was under genetic control and that there was positive assortative mating, with each race preferentially mating with its own kind.

Subsequently it has been shown that the difference in emergence time between the two races is genetic and that given a choice in the laboratory, the races were largely faithful in their choice of larval foodplant. There were also significant differences in the genome of the two forms. But in the wild there is still some 6% gene flow between the two races in the same area, and other species of *Rhagoletis* are also in an incipient speciation state with *R. pomonella* producing viable hybrid offspring having their own food plant and being regarded as distinct species. It is not, of course known whether any pairs of races or species will ever achieve complete genetic isolation.

The Explosive Speciation of Cichlids

African megafauna has been rightly studied and appears to exemplify the biological diversity of that continent. Yet in just short of one hundred years the major lakes and the richness of their cichlid fish fauna have proved to be instrumental in our understanding of speciation in that these fish originated where we see them today.

Fishes of the family Cichlidae are chiefly known from Africa and Central and South America. They are perch-like fish with an elongate dorsal fin and a set of pharyngeal teeth in the throat, in addition to those in the normal jaw bones. Most are about 10–15°cm in length. They are freshwater forms, living in lakes and sluggish streams, but a few species are adapted to faster rivers and a few present in India and Sri Lanka are adapted to brackish water. In addition to those in smaller lakes and rivers in Africa there are some 1400 species of cichlid in the three Great Rift Valley lakes in East Africa: Lake Victoria, Lake Tanganyika and Lake Malawi.

The Great Lakes of East Africa are big, all three in the top ten largest lakes in the world, with a pronounced thermal stratification for much of the year. They vary in depth and in surrounding geology with shorelines differing from the steep and rocky

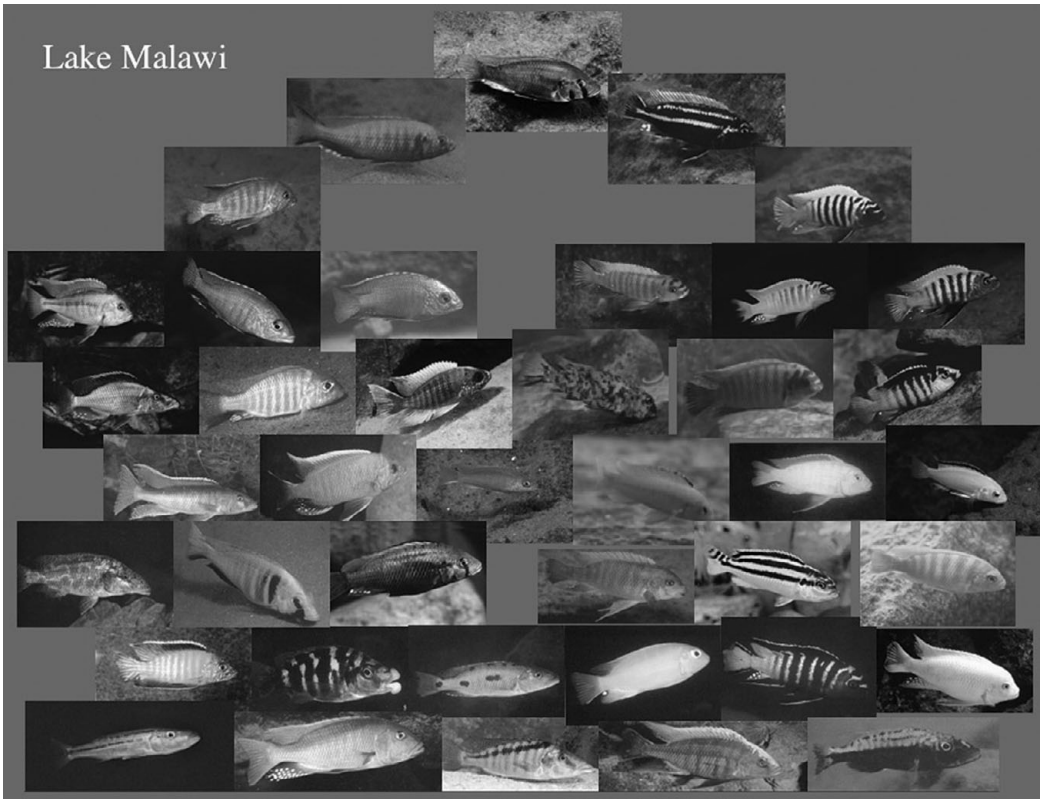


Figure 6.4 Cichlids of Lake Malawi. Photo credits: Ad Konings (Cichlid Press) and Justin Marshall. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

in the rift lakes of Malawi and Tanganyika to the shallow bays and swampy margins of Lake Victoria. The upshot of this is that varying physical and chemical differences provide a variety of habitats for fish and other organisms.

African cichlids are bony, perch-like fish (Figure 6.4), laterally compressed with a single pair of nostrils (most bony fish have two). A complex array of teeth is found both in the jaw and lower pharynx. Although there is a diversity of general body form (particularly colouration), it is often in the head region where physical contrast between the species is seen. There are around 700 species of Cichlidae; Lake Malawi alone has more than 200 species (Lake Victoria around 170 species and Lake Tanganyika 125+). Perhaps even more striking is that each lake has its own characteristic cichlid assemblage with most species confined to a single lake – not even found in the rivers that flow into them!

To explain such phenomenal diversity, it was suggested that the level of Lake Victoria had risen and fallen several times during the recent geological past, separating

off pools and streams which then allowed the differentiation of new species, followed by a rise in water level to flood the whole lake basin. Thus, there was a series of allopatric speciation events by **vicariance** or geographical separation. But it is now thought that Lake Victoria itself may not be more than about 12 400 years old (the age of terrestrial soils cored from the Lake bottom). There simply has not been enough elapsed time for several drying–flooding cycles, though one undoubtedly occurred.

Furthermore, there is a striking number of different modes of life among the Lake Victoria cichlids. There are algal scrapers, fish eaters, scale scrapers (feeding on other fish), mollusc-crushers, zooplankton feeders, paedophages (robbing the young fry from the mouths of other mouth brooding cichlids) and many others. Many of these forms and ways of life are replicated in Lake Malawi and Lake Tanganyika. It was therefore assumed that similar species from the three lakes owed their similarity to common ancestry, but that also has now proved not to be the case.

So, what is the cause of cichlid diversity? Both Lake Malawi and Lake Tanganyika are considerably older than Lake Victoria, with Malawi at 1– 2 Ma and Tanganyika 2-4 Ma. Meyer and colleagues have attempted to measure the times of divergence in cichlid phylogeny in the lakes using mitochondrial DNA sequencing. They discovered that some half a dozen separate stocks are present in Tanganyika, most of them endemic, but that both the Malawi and the Victoria 'species flocks' are derived from the same tribe represented in Tanganyika. In other words, all the species in the other two lakes radiated within their respective lakes and resemblances between closely similar species in different lakes are due to convergent evolution and not to close phylogenetic relationship. Within Victoria, however, there is very little difference in mitochondrial DNA between species despite their morphological diversity. The phylogeny reconstructed from DNA is very different from that based on morphology, and similarly for Malawi. The question then arises: could the species flock in either lake have arisen without sympatric speciation? The answer is probably yes; most species are very restricted in their environment within the lake, both in range of substrate (rocky or sandy, etc.) and depth. There have also been changes in water level in all three lakes, so that rocky outcrops become connected to the mainland and then islands. In 1992 Sturmbauer and Meyer published a study of the endemic *Trophius* genes in Lake Tanganyika. There are only six named species, yet they show twice as much genetic variation as the whole cichlid radiation in Lake Malawi and six times as much as in the species flock in Lake Victoria. *Trophius* are confined to a background of rocky slopes, and the authors suggest that speciation was hastened when the water level of the lake dropped and it was divided into three smaller water bodies. While the *Trophius* species are morphologically closely similar, there are more than 50 'races' within the six species, judged by colour, and it has been suggested that allopatric speciation was speeded up by colour and pattern variation spurred on by sexual selection in these and other cichlids.

While the rapid speciation of the African great lakes may have been confined to 'micro allopatric' speciation, there are examples in West Africa where the speciation could not have included an allopatric phase. In Cameroon there are a series of crater lakes, extinct volcanoes filled with water and, above the waterline, a rim. In 1972

Trewavas, Green and Corbet published an account of crater-lake *Tilapia* cichlids and concluded that the 11 species in one lake had differentiated within the lake (Trewavas et al., 1972). In 1994 Schliewen, Tauty and Paabo studied the same lakes using lists of mDNA for all the species and concluded that in each of the two lakes, the cichlids were monophyletic, having in each case a single common ancestral species (Schliewen et al., 1994). In one case, there were 11 species, in the other 9. Each species had a somewhat different ecology and there was no sign of hybridisation. Both lakes have a small outflow into local river systems but only one has an apparent inflow through the crater rim. There seems no other conclusion than that the radiation in each case was the result of sympatric speciation.

7 Taxonomy and the Diversity of Life

Diversity is a characteristic of life on Earth. However, in 1970, R. A. Crowson, then a lecturer in zoology at the University of Glasgow, wrote:

> There have been many authorities who have asserted that the basis of science lies in counting and measuring, i.e., in the use of mathematics. Neither counting nor measuring can however be the most fundamental processes in our study of the material universe – before you can do either to any purpose you must first select what you propose to count or measure, which presupposes a classification. Crowson (1970)

For the study of diversity to become more than a mere catalogue a conceptual approach is needed where patterns and relationships are identified in the search for order. Looking for patterns in the natural world appears to be a fundamental aspect of human development. And one could argue that to provide a classification is at the basis of all sciences (after all we classify materials and forces, rocks, soils and galaxies). A classification, however, provides more than a simple description and ordering - by naming objects and separating them into clusters, a *relationship* between groups and an *organising principle* (perhaps one of structural similarity or of origin) is implied.

It is not known for certain how many eukaryotic species currently inhabit our planet. The current textbook figure is around 1.5 million, but recently (Mora et al., 2011) using predictable patterns of taxonomic hierarchy, have suggested a figure of 8.7 million. However, even then, it is reckoned that only a fraction of the total number of species is represented. To these figures must be added those of prokaryotic bacteria – 40 000 recorded so far but bacterial DNA analyses in soil suggest that this figure could be nearer 400 million! If we also consider all the different species that have ever lived since life appeared around 350 billion years ago then the numbers become astronomical.

Human societies across the world from New Guinea to Western Europe have each developed their own **folk taxonomies**. In these simple classifications of organisms, individuals describe the natural order of their perceived world in terms of groups (we call them taxa) such as fish, trees, 'creepy-crawlies', etc. And such divisions are ever-present among different societies. There are also other divisions such as edible/inedible and resemblances to human body parts. Anthropologists argue for a ubiquity of classification among different societies as though it were inherent in humankind. Indeed, there are several instances of brain-damaged patients in Western hospitals who, on recovery, can recognise and name inanimate objects such as torch and pen but fail to recognise common animals and plants. Perhaps such category-specific

knowledge is in specific brain regions? Martin et al. (1996) found that although tools are recognised in the premotor cortex and animals in the occipital lobes, the temporal lobes were also activated at times indicating at least some plasticity of brain function.

As has been suggested, a classificatory scheme provides an organising principle, essential in the development of science. But there is something special about biological classification. Since the general acceptance of evolution, following the work of Darwin, Wallace, Lamarck and others, it has been recognised that a natural arrangement of organisms is 'out there' in the sense that there is a history that links all organisms by common ancestry. If that history were completely known, it could be presented as a diagram representing an irregular, inclusive and divergent hierarchy. *Irregular*, because it represents history, not just an organising principle. *Inclusive* in that, as in most classifications, the whole consists of a pattern of branching in which the terminal 'twigs' represent the things being classified, species in this case and *divergent* in that branching occurs. The important point is that organisms should bear some relationship to a natural order. A **phylogeny** results from the two processes of phyletic evolution, that is:

- change over time, and
- speciation, the splitting of one species into two or more types

In 1961, George Gaylord Simpson, the American palaeontologist, gave a series of definitions of terms used to characterise the various branches of Systematics (Simpson, 1961):

Systematics, he suggested, is the most general scientific field dealing with the diversity of organisms; 'Systematics is the scientific study of the kinds and diversity of organisms and of all relationships among them';

A rigorous study of the methods of classification is known as taxonomy (although some authors use 'a taxonomy' to mean 'a classification'): 'Taxonomy is the theoretical study of classification, including its bases, principles, procedures and rules';

'Nomenclature is the application of distinctive names to each of the groups recognised in any biological classification'.

Thus, we have four activities:

- **Classification** – ordering and organising objects (or organisms) into groups
- **Systematics** – that branch of biology dealing with relationships between groups of organisms
- **Taxonomy** – the scientific study of biological classification
- **Nomenclature** – naming organisms (both extant and extinct)

Linnaeus and Classification

The joint paper embodying the theory of natural selection was presented to the Linnean Society on behalf of Darwin and Wallace in 1858. One hundred years earlier,

1 January 1758 is fixed by the International Code of Zoological Nomenclature as the 'starting point' of zoological nomenclature. This was the year of publication of the 10th edition of Linnaeus' *Systema Naturae per regna Tria Naturae, Secundum Classes, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis* ('The Natural System on Three Kingdoms of Nature, according to Classes, Orders, Genera, Species, with characteristics, distinguishing features, synonyms, localities'). Scientific names of species and genera are valid (and have priority over later names for the same genera or species) if published after 1 January 1758 (with the odd exception of a Swedish work on spiders published at about the same time, which has priority over Linnaeus). The starting point for Botanical Nomenclature is 1753 for flowering plants and forms, the year of publication of Linnaeus' *Species Plantarum*.

It is a matter of some interest that the *Systema Naturae* mentions three kingdoms in its title: they were, in the familiar phrase, 'animal, vegetable and mineral'. Linnaeus attempted a hierarchical classification of minerals from his 1st edition (1735) and three volumes were projected for the 10th. But the 3rd volume, 'Regnum Lapideum', was never published. Linnaeus made further attempts to classify minerals in the 11th and 12th editions but ultimately failed. This failure in effect emphasised the special nature of the classification of organisms (including fossils!) as representing *actual relationships* rather than a convenient grouping.

Carl or Carolus Linnaeus (1707–1778) is often regarded as the founder of scientific classification of animals and plants ('Carl' is the anglicised and 'Carolus' the latinised version of Linnaeus' first name). Carl was Swedish, the son of a minister and keen gardener who taught him that all plants had names and fostered young Carl's interest in the natural world. Linnaeus studied medicine at Uppsala University where he was regularly to be found in the botanic gardens. He travelled widely collecting information on plants and animals (while making important contacts abroad). In 1741 he became a well-respected professor of botany. But in fact, Linnaeus' methodology goes back to the ancient Greeks. The idea of a *pattern* of classification derives from Plato (427 BC–377 BC) and Aristotle (384 BC–322 BC), while the *method* of classification derives from Aristotle. Linnaeus's intention though was different.

For example, Aristotle's method was intended to investigate the nature of living things rather than to produce a hierarchical classification. The group to be investigated, for instance all animals, would be designated the 'genos' (Latin genus). He would then divide the 'genos' into two or more groups, each labelled an 'eidos' (species); for example, animals with blood/ without blood. But he might use a different criterion for division, depending on his purpose at the time; for example, their mode of reproduction: viviparous/with perfect eggs or with imperfect eggs (which alter their size after being laid!), organisms with generative slime buds or spontaneous generation. Each of these categories is distinguished from all the others by a 'diafora' (Latin *differentia*). This was '*logical division per genus et differentia*'. Any 'eidos' (or species) could be characterised by its genus and its differentia. Thus, mankind was specified by its genus (animal) and its differentia (rational). Other characteristics, in addition to the differentia, were either properties or accidents. Properties could, according to Aristotle, be inferred from the differentia: (for man,

'being capable of learning grammar' was Aristotle's rather dubious example). Accidents were neither part of the overall definition, nor deducible from it and need not be permanent. 'In a sitting position' was Aristotle's example. The other important point was that the 'genos' could be at any categorical level as with (all) animals and man, or, in contrast, serpents divided into viviparous and oviparous.

Linnaeus took over from Plato the idea of fixed categories: empire (all entities), kingdom, class, order, genus, species and variety. Other categories, each occupying its own rank, such as phylum and family, were added later.

Linnaeus's contribution to taxonomy was essentially:

- A binomial system, in which every organism is identified by a generic name and a specific name.
- That every taxon should be characterised by a list of those features required for membership (derived from the idea of differentia).
- The establishment of a standardised hierarchy of categories.
- The production, in volume 1 of the 10th edition of *Systema*, of a much more comprehensive classification of animals than had been attempted before.

Apart from the ancient Greeks, Linnaeus did have forerunners who anticipated parts of his system, notably the English naturalist, John Ray (1627– 1705).

Lamarck and the Scala Naturae

In Chapter 2 when discussing the evidence of embryology for evolution, the concept of a scala naturae (ladder of nature) of organisms was noted. The idea is that all living things can be arranged in a linear series of increasing perfection, with mankind at the top and the simplest organisms at the bottom. There were variations: sometimes the series was extended further 'downwards' to inanimate objects, or further upwards to the hierarchy of angels and archangels or perhaps a philosopher or naturalist might postulate separate scalae for animals and plants. The concept of the scala is possibly attributable to Aristotle, but almost always it was accompanied by a second concept, that of plenitude (or 'completeness' of living forms). This doctrine asserted that if creation is perfect, it should contain no gaps, so the ascending series of the scala was unbroken: each species or genus merged into those above and below it. Apparent gaps were due to undiscovered forms.

The scala naturae was particularly popular, both with philosophers and naturalists, in the seventeenth and eighteenth centuries. It was even accepted by Linnaeus, and by Lamarck, for whom a preprogrammed ascent of the scala was the core of their evolutionary theory. At first this seems at odds with the claim that Linnaeus was the man who codified the data and techniques of modern hierarchical classification. This is because his claim for the naturalness of his classification depended not on the naturalness of the result, but on the correctness of the method.

This attitude also illuminates the origin of Lamarck's theory of evolution. He began with the scala (ladder) and, as it were, turned it into an *escalator*, so that from 1800 onwards, the mechanism was that of **orthogenesis** (belief in an 'impulse' pushing

organisms up the evolutionary ladder or scala until they reach perfection – that is, humankind). His corresponding systematic study was that of a '*distribution generale*' – arranging all organisms in their correct place on the scala naturae. Classification for Lamarck consisted of using the gaps in the known scala to produce the artificial arrangement of a hierarchical classification. Even though he is perhaps best known for the added complication of 'inheritance of acquired characteristics', he continued to insist on the distinction.

Jean-Baptiste Lamarck (1744–1829) was a botanist turned invertebrate zoologist in Paris and one of the first to champion a theory of organic evolution. In his great seven-volume work on the *Natural History of the Invertebrates* he looked to account for changes between fossil and living molluscs (he was an avid collector of shells) and began to formulate an idea regarding the development of life on Earth. Firstly, simple creatures arose spontaneously, thereafter diversification occurred through two processes: the 'impulse' that tends to make living things more complex (that is moving up the scala naturae) and the intervention of 'particular circumstances'. The latter process often referred to as the 'Inheritance of Acquired Characteristics' is the idea for which Lamarck is perhaps best known. He correctly identified the changing environment as a driving force in evolution but postulated that adaptive characters (such as larger teeth, longer necks, thicker fur) could be induced in organisms and thereafter inherited by their offspring. This mechanism for organic or biological evolution also involved the idea of 'use and disuse'; the notion that increasing use of an organ or body part would somehow strengthen it (and vice versa).

But despite the persistence of the scala naturae, the pattern rules of classification were settled in the nineteenth century. To provide a hierarchy, the groups to be classified (for example, species) were grouped into categories called **taxa** (singular taxon) at the next higher rank (in this case genera). Then the genera into families (or some intermediate category), families into orders, orders into classes, classes into phyla. Intermediate categories were inserted if thought to be necessary. All the taxa at the same level in the hierarchy occupy the same **rank** and are given the same category. Thus '*the rank of a taxon is that of the category of which it is a member*' (Simpson). We therefore construct a basic hierarchical system comprising:

KINGDOM (a basic, indeed fundamental, type of living thing such as an animal/ ANIMALIA, plant or fungus)
PHYLUM (characterised by a distinctive body plan or 'Bauplan' such as the ARTHROPODA)
CLASS (demonstrating the many variants of the 'Bauplan' such as INSECTA)
ORDER (a discrete and easily identifiable group within the class such as the beetles, COLEOPTERA in this insect example)
FAMILY (a closely related group such as the ladybird beetles, the COCCINELLIDAE)
GENUS (a characteristic group within the family such as the COCCINELLA)
SPECIES (the individual name given to the interbreeding unit for instance SEPTEMPUNCTATA, or seven-spotted ladybird)

The ladybird is a familiar and well-loved insect commonly portrayed in literature, art and children's nursery rhymes. It has several common names, e.g. ladybug, clock-leddy and red coat, alluding to its colour, its usefulness to farmers, its nature or its divine appearance (for instance reference to the mystical number seven). Ladybirds of course are said to bring luck, and their special status throughout the Christian world has provided many dozens of local names. But the beauty of Linnaean classification is that we can give our individual organism a binomial, or two-part, representative, scientific name applicable globally – *Coccinella septempunctata*. Moreover, the scientific name has meaning:

- It separates the seven-spot ladybird from the other 52 species of British ladybird
- It describes this insect perfectly – *Coccinella* (little red one) *septempunctata* (seven 'punctuations' or spots)
- It indicates the beetle family to which this insect belongs and thus its lineage within the Arthropod phylum

You might be aware though that the two-spot ladybird, *Adalia bipunctata*, belongs to a different genus to the seven-spot. This might therefore suggest a different lineage, maybe with different adaptations. The two-spot is smaller, more polymorphic, has different habits (more likely to be found overwintering) and is much less toxic than the seven-spot when fed to nestling blue tits. Indeed, it has been suggested that '2-spot ladybirds are largely-edible, polymorphic Batesian mimics of well-protected, monomorphic species such as the 7-spot ladybird' (Marples et al., 2008).

With practice it is easy to see how informative the naming of living things can be.

Classification and Evolution

> Our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation. The rules for classifying will no doubt become simpler when we have a definite object in view.
>
> Charles Darwin: *Origin of Species*, Chapter XIV.

Charles Darwin, in *Origin of Species*, and Alfred Russel Wallace in his 1855 paper, used the image of a tree to represent both classification and phylogeny. In the long last paragraph of chapter IV of *Origin of Species* Darwin states:

> The affinities of all 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. The limbs divide into great branches, and these into lesser and lesser branches, were themselves once, when the tree was small, budding twigs; and this connection of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinate to groups. Of the many twigs which flourished when the tree was a mere bush, only two or three, now grown into great branches, yet survive and . . . all the other

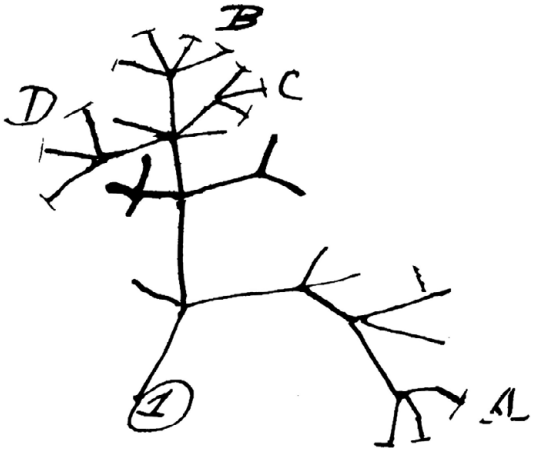


Figure 7.1 Darwin's depiction of branching evolution. The (evolutionary) tree is a familiar metaphor to us in the twenty-first century but Darwin's first (and only) phylogenetic tree diagram was a tentative affair (he headed the page in his notebook 'I think'). Drawn in 1837, this sketch emerges as a 'diagram' 22 years later with the publication of *Origin of Species*. He was a poor artist and it is probable that this original sketch was used by him to clarify his thoughts.

branches; so with the species which lived during long- past geological periods, very few now have living and modified descendants.

Both Wallace and Darwin (Figure 7.1) pictured the form of the Natural Classification as a tree, and thus as an irregular, inclusive (i.e. nested), divergent hierarchy. But they both also proposed that the form of the metaphorical tree represented the blood relationships of all the taxa embodied in it. However, recent evidence on crossbreeding in bacteria and plants show that crossbreeding is much more common than previously thought. Discrete lineages are therefore more blurred and the tree representation (at least for these organisms) is an oversimplification – we perhaps need to redraw the simile as a tangled thicket!

Chasing Ancestors

During the rest of the nineteenth century, and even more emphatically in the twentieth, knowledge of the fossil record expanded enormously and numerous attempts were made to incorporate fossils into the pattern of classification of living organisms. Unfortunately, this led, perhaps unconsciously, to the return of the 'ladder of life', the scala naturae. It was generally agreed that fossils, because they were ordered in sequence by geological stratigraphy, represented the possibility of direct evidence of evolution. Famous cases like the 'evolution of the horse' were interpreted as direct ancestor–descendant series. So palaeontological studies took the form of the search for ancestors – A gave rise to B, B gave rise to C, and so on. For surely the ideal evidence for evolution would be a series of fossils of diminishing geological age and apparent

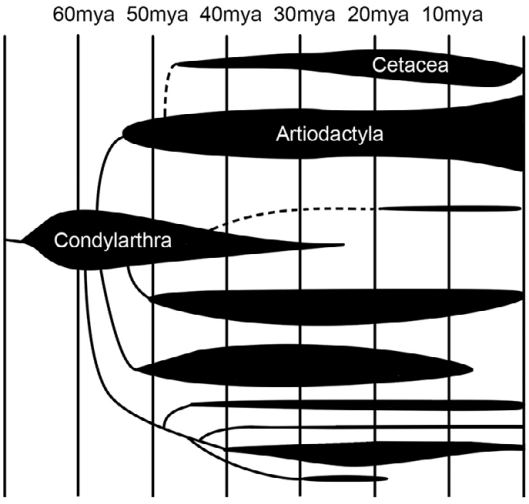


Figure 7.2 Spindle diagram showing the ungulates (hooved mammals). The width of the 'spindle' indicates the degree of diversity.

character change, with each specimen representing a species descendant of the one before it and an ancestor of the one after? But palaeontologists later realised that any fossil, or rather the once-living animal (or plant) it represented, was very unlikely indeed to be the actual ancestor of another fossil or living creature. It was unlikely except when the two were very close in time and space in an exceptionally complete fossil record that the species of one included the ancestor of the other.

So statements of ancestry became more vague – 'the reptiles gave rise to the birds' – and reconstructions of phylogeny tended towards a less linear pattern. Derivation of an archetype was tricky unless a hierarchical classification was employed. As a result, classification tended to be dictated by traditional groups. Reconstructed phylogenies were often ad hoc arrangements of high-level taxa, often represented by spindle diagrams (Figure 7.2) in which these taxa were represented by sausages in space, the length of a sausage being its duration and the variable width representing the estimated numbers of species at a particular time. There are several errors with this type of diagram. Firstly, the ungulates are not a natural phylogenetic group (some of the lineages are more closely related to other endemic African mammals). Secondly, the parent group, the *Condylarthra*, probably have several origins and the systematics of the *Artiodactyla* are now being extensively revised (hippos are probably more closely related to whales than other even-toed ungulates).

This state of affairs persisted for a hundred years, so that in 1961 Simpson emphasised what he saw as the subjective nature of classification:

> Taxonomy is a science, but its application to classification involves a great deal of human contrivance and ingenuity, in short, of art. In this art there is a leeway for personal taste, even foibles, but there are also canons that help to make some classifications better, more meaningful, more useful than others.

Developing a Modern, Biological Classification

Taxonomies are not simply abstract ordering; rather they represent the sum of our knowledge and our thinking at a moment in time.

All living things can be divided into relatively few groups or higher taxa called kingdoms. Historically animals and plants have been viewed as the major division of the natural world. Ancient writers such as Aristotle (384–322 BCE) and his pupil Theophrastus (371–287 BCE) described both the 'History of Animals' (Aristotle) and a 'Historia Plantarum' (Theophrastus). This, rather logical, bipartite division was continued in the eighteenth century by Carl Linnaeus who also included the minerals, Regnum Lapideum, as a third kingdom.

However, the two-kingdom scheme of animals and plants continued up until the mid-nineteenth century where, following the development of microscopy and observation of unicells (nominally included as either plants or animals), Ernst Haeckel (1834–1919) proposed a third kingdom, the Protista, for these novel unicellular forms. Development of the electron microscope in the mid-twentieth century illuminated major differences between bacteria (prokaryotic) and the remaining eukaryotic single-celled forms. Herbert Copeland (1902–1968) thus proposed a four-kingdom scheme with bacteria and blue-green algae (now called blue-green bacteria) elevated to the new kingdom Monera.

The Fungi had always been problematic. Their unique morphology, cell type and nutrition meant they had been placed both with plants (though they are heterotrophic not autotrophic) and protists (even though many are multicellular and have chitinous cell walls). The solution therefore was simple – create a new kingdom. And this was achieved by Robert Whittacker (1920–1980) in 1969 with his (now) five-kingdom scheme. The five-kingdom scheme then became biological orthodoxy, particularly following the publication of the book *Five Kingdoms* in 1982 by Lynne Margulis and Karlene Schwartz (Margulis and Schwartz, 1982).

Microbiologists often separate the true bacteria (Eubacteria) from ancient bacteria (Archaebacteria). Features such as cell walls (Archaebacteria lack a peptidoglycan layer), ribosomes (different RNA sequencing) and lipid chemistry (phytanol side chains not ester-linked in the Archaebacteria) resulted in Carl Woese (1928–2012) postulating a three-domain system comprising:

Domain Bacteria
Domain Archaea
Domain Eukaryota

Each of these higher groupings may then comprise several kingdoms.

A precise taxonomy though has not been agreed by biologists; it remains a 'work in progress'. However, North American high schools and colleges generally use a six-kingdom scheme (including the Eubacteria and Archaebacteria as separate kingdoms) while many schools and colleges in the UK retain the five-kingdom scheme. It is the latter that is used in the current text:

Kingdom Prokaryotae
Kingdom Protoctista
Kingdom Fungi
Kingdom Plantae
Kingdom Animalia

An Objective Classification?

It is surprising, especially in the light of the quotation from the first edition of *Origin of Species* cited earlier, that it took a hundred years for a method of classification that claimed to be objective to appear. Then, like the iconic London buses, one waited for a hundred years, and then two came along together! These have come to be known as **phenetics** (originally 'numerical taxonomy') and **cladistics** ('phylogenetic systematics'). The results of both methods can be presented as a **dendrogram** or tree diagram. If fully resolved, that dendrogram will consist of a series of branch points which are dichotomous, giving rise to two branches, and (conventionally at the top) representing the things to be classified (e.g. species). Both internal branch points and terminal points are nodes. The terminal nodes are referred to as OTU s ('operational taxonomic units') by pheneticists and 'terminal taxa' by cladists.

The decision as to how best to place organisms into groups involves judgements as to the relative importance of particular features. Does the presence of fur for instance take priority over the five-fingered limb or the tripartite brain in mammals? Ought we to consider the interconnectedness of body parts like Georges Cuvier in Paris? By studying both living and extinct forms Cuvier recognised natural groupings as distinct from the artificial scheme pioneered by Linnaeus earlier. Linnaeus's system was based on plant sexual parts, the number and arrangement of stamens, ovaries and so on. This approach, although useful as a tool for categorisation, is based on only one or a few plant characteristics as opposed to features from all parts of the organism.

Another problem in taxonomy is that of subjectivity. Should a scientific classification be open to interpretation or should it be purely objective and almost mathematical in its approach? In the next sections, we will investigate how both phenetics (a numerical classification) and cladistics (exploring relationships between organisms) aim to solve the problems of an objective classification.

Phenetics

Phenetics is a numerical technique that groups or clusters organisms by their overall physical similarity (think of phenotypes here). Phenetics developed out of several pioneering papers published in the late 1950s and early 1960s, significantly in parallel with the development of compact computers. The emphasis in phenetics was the use of a very large number of discrete morphological variations ('characters' or 'phenes') to be compared between the species or other taxon to be classified. For any character a

species would have a ‘character state’ of that character. A principle of phenetics was that all characters should count equally in determining relationships; in the jargon, they should be 'unweighted' (more correctly, ‘equally weighted’). The aim was to achieve a measure of difference between any two species (if it was species that were the OTUs), a so-called taxonomic distance. If two specimens, representing species to be classified, were similar in all the characters being used, the taxonomic distance between them would be zero, or, to look at it the other way round, the ‘overall similarity’ as it was termed (‘aggregate similarity’ is a better term) would be scored ‘one’ if two specimens differed only in the state of one character, then the aggregate similarity would be ‘*m*/*n*’ where *n* is the total number of characters studied and *m* is the number of matching characters. As an example, the vertebrate pectoral (shoulder) appendage might be used as a character, while ‘fin’, ‘five-fingered limb’ and ‘bird’s wing’ are states of that character; in other words, transformed homologues of one another. That, however, would be a very crude example. It is unlikely that a pheneticist would take the whole limb as his or her character. It would be split up into a whole series of characters, each with two or more states. This brings us to an obvious difficulty. An animal, if animals are being classified, cannot be analysed into a fixed series of independent characters. To take another of our previous examples, do the ear bones, the incus and malleus of mammals, which always occur together, represent states of one character (the quadratic–articular complex) or two (the quadrate and articular, respectively) or more? But this difficulty also afflicts cladistics, as we shall see. There is a series of techniques where the characters can be recognised as plausible units; however, that is where the data are derived from the sequencing of amino acids or DNA/RNA nucleotides.

Phenetic software programs are now often incorporated in mixed packages with other programs including cladistic ones (see section on ‘Cladistics’), but it is important to understand what is happening within the computer. Programs deal with binary data states hence are recorded as 0 or 1, in the simplest case, absent and present, respectively. There are then all sorts of rules to deal with multi-state characters, for instance leaves smooth/leaves slightly hairy/leaves very hairy or one/two/three/four/five fingers, to reduce them to binary coding. The next stage, inherent in the program, is to produce a character matrix or data matrix, which is a table listing all the objects (OTUs) along the top, and the *n* characters being studied down the side. The column under each OTU specifies the state of each character. With binary characters the distance between any two OTUs can then be calculated easily. The simplest matching coefficient can be represented by a two-by-two table and the simple matching coefficient is calculable.

To summarise, phenetics is a type of numerical taxonomy using observable features to provide a convenient taxonomy. Phenetics provides equal weighting to all the characters under discussion and uses a form of cluster analysis (a mathematical nearest neighbour analysis) to measure phenetic similarity. The use of a great many characters and its empirical nature (one only uses observable features) allows apparent phylogenetic or evolutionary inferences to be made from the taxonomic structure of the group under discussion.

Forming non-overlapping phenetic clusters solely based on similarity has its shortcomings:

- The underlying assumption is a correspondence between the degree of similarity and how recently the two groups may have diverged. Is it really true that the more similar organisms appear, the more recent the taxonomic separation?
- Is equal character weighting a desirable feature?
- There is no distinction between ancestral and derived states.
- It is difficult to construct a meaningful evolutionary history

We might also wish to consider convergent evolution where different organisms share the same character states by being exposed to the same environmental conditions. Convergence of body forms (due to similar environmental pressures) is commonly encountered both in the fossil record and in modern-day biota. **Convergence** can arise in sympatric associations (that is within the same geographical area). Examples of sympatric convergence include mimicry of harmful and poisonous snakes; the coral snake (venomous) is ably mimicked by the scarlet king snake (non-venomous) or harmful and dangerous insects (wasps and hoverflies are common examples). Organisms inhabiting the same type of environment but in different locations (allopatry) can also show convergence. Evolution of the dorsal fin in sharks and dolphins and spines in cacti and Euphorbias are both examples of allopatric convergence. A further example might include the fossil South American marsupial, the cat-like *Thylacosmilus*, and the North American sabre-toothed tiger, *Smilodon*. Both have evolved long, pointed canine teeth independently for the same purpose (that is predating thick-skinned prey). The structures observed are similar ***not*** because of common ancestry (that is homology) but exposure to common environmental conditions. We say the structures are analogous. The term **convergent evolution** is commonly employed to describe this process of achieving similarity over time.

Phenetic clustering can therefore be questionable in looking for explanations of ancestry. However, when coefficients, which are measures of similarity, have been calculated between each OTU and every other OTU, a similarity matrix can be drawn. This is like one of those distance tables that one finds at the back of motoring atlases. In the latter case, the vertical axis and the horizontal axis have the same list of towns in the same order, usually diverging from the corner where the lists meet. One can then read the distance from any town and any other town at the intersection of the appropriate row and column. This will of course be zero for the same town on row and column. The phenetic matrix has OTUs instead of towns and either similarity coefficients or distance measures (which we have not discussed) in the cells. Alternatively, resemblances between organisms are calculated and generalisations made using a per cent similarity (see Figure 7.3).

The important question from the point of view of evolutionary theory is to ask what the phenograms produced by pheneticists represent. The pheneticists' main claim is to objectivity. Given the data in the character matrix, all the subsequent procedures follow an agreed method with no intuitive component, so that any taxonomist should

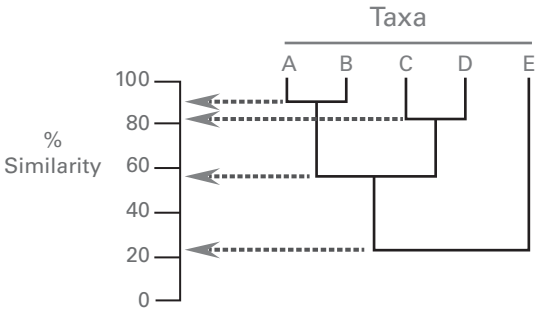


Figure 7.3 Example of a phenogram generated using numerical taxonomic methods.

get the same result. This claim is somewhat marred by the fact that there are many formulae for arriving at coefficients of similarity or distances and many clustering programs.

On the one hand the technique is both repeatable and objective in its computation. The quantitative nature of the technique leads to automated computations of many characters and such a rich data set provides greater discriminatory power. Similarly, a wide range of features can be included (provided they can be quantified).

However, there may be an issue with stability. It was initially thought that by using larger and larger data sets the taxonomy would become progressively more stable. But this was not found to be the case. The effects of **homoplasy** (similarity for any reason other than common ancestry) are more pronounced when using this technique. Finally, as this procedure is a mathematical and not biological device, it may not provide classification of 'natural groups' and so will not necessarily provide a natural classification.

A final issue is whether to interpret phenetic results in the same way as a phylogenetic 'tree'. Are the results 'real' in the sense that relatedness equates to common descent? We have already seen examples of mimicry where the mimic and its model are unrelated. Similarly, gulls and shorebirds may look the same although they do not share an immediate common ancestor. Or, with respect to characters, how might we deal with a character such as 'hair'? Is this the same in a cat and a bumblebee and what if the character (hair) goes 'missing' such as hair in the naked mole rat or a dolphin? A phenetic-derived diagram (phenogram) certainly promotes objectivity and clarity of thought, but does it provide meaning? The short answer is 'not always'.

Cladistics

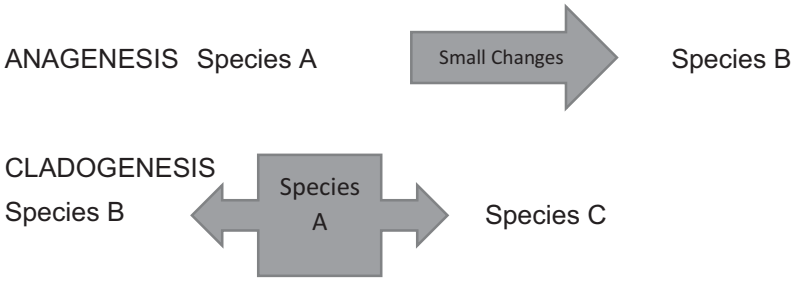
Cladistics is an approach to systematics in which taxa are grouped solely based on their most recent common ancestor. In cladistics the question is not simply one of sharing features but in determining which organisms share a common evolutionary history.

Cladistic methodology involves two basic precepts:

1. A **clade** represents the material or genuine evolutionary history of a group of organisms. A clade 'is a group of organisms that consists of a common ancestor and all its lineal descendants and represents a single branch' on the 'tree of life'' (Dupuis, 1984).
2. **Synapomorphies**, or shared derived characters (unique features not present in distant ancestors), form the basis for a cladistic analysis.

When a species splits during evolution (**cladogenesis**) it will form two similar **sister species**. A cladistic (sometimes also referred to as a phylogenetic) classification places these two taxa together and works 'backwards' examining ancestral relations before eventually constructing a hierarchy that resembles the familiar 'tree of life'.

An evolutionary lineage can be inferred by observing characteristics, such as brain size in primates, and describing both the rate and pattern of change. Evolution can therefore be described in terms of trajectory (or lineage) and change. The term **anagenesis** describes directional change within a single lineage between speciation events (gradually accumulating changes until the group becomes sufficiently distinct to call it a new species), while **cladogenesis** describes the branching of lineages through the act of speciation (one species splitting into two).



Suppose that one is studying two very closely related species of animal, so closely related that it is concluded that among living species they are more closely related to one another than either is to any other species; the cladistic term is 'sister species'. A clear example would be the two generally accepted species of living elephants (a few people claim that there are more than two). A whole series of characters, long trunk, large flapping ears, tusks, massive molar teeth, are uniquely shared by the Indian and African elephants. But they share many more homologous characters that are not unique to them (called **plesiomorphies**): both give birth to live fully-formed young and both have milk-producing females (they are mammals); both have limbs rather than paired fins (they are tetrapods); a skull and vertebral column (they are vertebrates) and so on. But of all these characters, only the uniquely shared ones (flapping ears, trunk, etc.) are useful in claiming the Indian and African elephants as sister species. These features are the shared or derived characters (synapomorphies) and the ones employed in cladistic analysis.

There are several differences between phenetics and cladistics but perhaps the most important is that of the features or characters employed. Evidence for phylogenetic (cladistic) relationships comes from what are called shared derived characters, which are features ***shared*** between members of groups but ***derived*** from the same common ancestor. A numerical, phenetic classification uses a combination of all characters regardless of their evolutionary origin. Cladistic or phylogenetic relationships are essentially ones of ancestral lineage while phenetic relationships are based on a more general similarity from which inferences might be made.

Within any evolutionary lineage, a feature might change substantially or less so. Very little change over evolutionary time gives rise to persistent ancestral or primitive characteristics, while recent change gives rise to derived characteristics. Thus, the human pentadactyl limb is ***ancestral*** while our large brain (compared with other primates) is ***derived***. The elephants (Order Proboscidea) are an ancient group first appearing in the Eocene but represented now by only two species. Features such as the ears and molar teeth separating these two groups are derived.

Returning then to our elephant example, all the evidence showing the mammalian nature of both is no help in deciding between an Indian elephant and an African elephant. However, the mammalian homologies do become useful when deciding that the bearers of live young (the Theria) are the sister-group of the egg-laying mammals such as platypus and echidnas (the monotremes) – both groups united as the class Mammalia.

Willi Hennig (1913–1976) was the first and most preeminent systematist to develop a classification based on evolutionary relationships. To develop a phylogenetic (evolutionary) reconstruction he developed a scheme based on lineage and ancestry. This contrasted with the prevailing view at the time that evolutionary relationships could be determined by looking at similarity in morphology, physiology and behaviour. Henning had realised that such similarities were interesting but only a shared ancestry would determine an evolutionary trajectory.

Hennig's ideas around classification stated that any grouping should be based on clear monophyletic groups (a single ancestor plus all its descendants). Other biologists such as Ernst Mayr disagreed stating that a mix of both evolutionary relationship and physical similarity (a compromise) was preferable. But Hennig's point of view was that a biological classification should be based on phylogeny only.

In cladistic methodologies, characters, or character states, can be thought of in two principal ways:

- **Plesiomorphic** (plesio = near related, morph = form) a primitive character state
- **Apomorphic** (apo = derived, morph = form) an evolutionarily advanced (or derived) character state

The long neck of a giraffe is said to be derived from its near relatives (it is apomorphic) while the original short neck of their distant ancestor is said to be plesiomorphic.

In this way, we might distinguish characteristics of the Indian and African elephants. Derived characters that uniquely define an OTU or terminal taxon are **apomorphic** as are characters uniquely shared between a pair of sister groups (e.g.

the molar tooth pattern or much larger ears of African elephants). An apomorphy is any distinctive derived trait handed down to its descendants.

Uniquely shared characters are termed synapomorphies; these are characters that represent an 'evolutionary innovation'. They can be traced back to the most recent common ancestor, but this character may not be shown by other closely related groups (e.g. the halteres in dipteran, two-winged, flies). Clusters of these derived characters can be used to construct phylogenetic trees. Synapomorphies emphasise the relatedness of species; for example, the opposable thumb is shared by humans and some primates but not the other mammals. The presence of organelles and rod-like chromosomes in eukaryotic cells is a synapomorphy not shared with the prokaryotes.

Characters that, while homologous between two taxa, are irrelevant to the task at hand, because they distinguish or unite groups at a higher rank, are known as plesiomorphic. Plesiomorphy is an ancestral state and in cladistics must be eliminated from the data for classification. So, for instance, in a sample comprising cat, lizard, chimp and human, we cannot group lizard and cat together simply because they share a tail because this feature (the tail) was inherited from a much earlier vertebrate ancestor. It is a plesiomorphy.

A cladogram therefore is based on a unique hierarchy of evolutionarily advanced, derived or apomorphic characters.

While phenetics owed its origin to the independent work of several groups of people, notably Robert Sokal and colleagues, then at University of Kansas, Arthur Cain, then at Oxford, and Peter Sneath, University of Leicester, cladistics is almost always credited to one man, Willi Hennig (1913–1976). Hennig's aim was to produce a 'Phylogenetic Systematics', the title of the 1966 English version of his book. Early opponents called his method 'cladism', later changed to the more polite cladistics. The job of the taxonomist, Hennig argued, was therefore to reconstruct the pattern of cladogenesis, which could be represented as a cladogram. He was not dogmatic about every speciation event being the splitting of one species into only two although some of his early followers were.

Thus, every species (if it were recognisable at all) would have one, or preferably more than one, unique (apomorphic) character. Any given species would then have a sister species and the two would be uniquely united by one or more synapomorphic characters. According to Hennig these latter shared characters would be diagnostic of the pair's (hypothetical) common ancestor. So that every internal node of the cladogram represents the common ancestor of the taxa that branch from it.

Later, in the 1980s, many cladists were to reject the hypothesis of ancestry as unnecessary and concentrate on the hierarchy of characters; so that their cladograms need not be interpreted as trees.

Quite frequently homoplasy (convergence or parallelism) rears its ugly head – similar structures in unrelated species not derived from a common ancestor. There is no trouble with obvious causes of homoplasy. The bird's wing and the bat's wing are so obviously homoplastic as wings in overall structure that no one would allow any similarity to override the obvious fact that the two creatures belong to different vertebrate classes judged by every other significant character.

In his original book, Hennig does not propose a clear method of dealing with incongruent characters, other than to suggest that contradictory characters be studied more carefully. Then cladists invoked the *principle of parsimony* (related to that of the fourteenth-century philosopher William of Ockham – 'Ockham's Razor'). A theory of parsimony is one that suggests that the simplest explanation to explain the data (for instance one requiring the least evolutionary change) is to be preferred. This form of logical inference is sometimes called cladistic parsimony. The principle of parsimony has been developed since then to be one of the cornerstones of cladistic practices.

In 'The strange case of the fish that wasn't' (chapter 1 in Carol Yoon's, 2009 book, *Naming Nature*) cladists are admonished for claiming that fish, as a group, do not exist! By concentrating on shared synapomorphic, or derived, characters the fish (along with zebras and moths) are not seen as evolutionarily cohesive groups. The fish-like characters of fins and gills and streamlined shape of fish exist because of the environment they find themselves in and are shared by all their fishy ancestors. Thus these (ancient) features are plesiomorphic and not to be included in our data sets. Thus, if we compare a salmon, lungfish and a cow, then surprisingly the chambered heart, internal nostrils and epiglottis of the lungfish make it more closely related to the cow than the salmon!

Do we have a situation therefore where strict adherence to a method makes no sense in the real world or have we not yet discovered characters where their 'value' is significant? In molecular biology there are such units which can claim to represent the 'amount' of evolution – the nucleotides that make up the functional parts of the double helix of DNA. These will be discussed in the next section.

Classifying vertebrates to satisfy both cladists and the Linnaean tradition is difficult. The phylogeny (because of its fossil record) is relatively clear but the taxonomy (classification) and nomenclature (naming) remains inconsistent. In general, biologists still use the Linnaean rankings. So, in the case of fish, few maintain the class Pisces, except at school/college level, but most accept the groupings within the phylum Chordata/subphylum Craniata as:

1. The jawless fish such as lampreys and hagfish ('agnathan' is a useful term but these animals constitute a diverse, paraphyletic group and do not form a coherent taxon)
2. Jawed vertebrates, the Gnathostomata (perhaps best considered as a super-class) comprising the remaining tetrapods and fish vertebrates which include the
   - Class Chondrichthyes – cartilaginous fish, sharks and rays
   - Class Osteichthyes – the bony fish such as salmon and eel, which includes:
     - Subclass Actinopterygii – ray-finned fish from the sturgeon to the herring
     - Subclass Sarcopterygii – lobefins and lungfish

In conclusion cladistics aims to 'identify and take account of only those shared characteristics which can be deduced to have originated in the common ancestor of a group of species during evolution, not those arising by convergence'. It has proven to be one of the most popular modern systematic approaches.

Molecular Taxonomy

If morphological characters are not of equal 'value', how might evolution be deduced? Which characteristics might exhibit evolutionary parity? There are units which can claim to represent the 'amount' of evolution. These are the nucleotides – functional parts of the DNA double helix which can be used to investigate hereditary differences in organisms.

There are two ways of investigating the linear structure of either a protein or DNA: (i) genetic distance measures and (ii) sequencing.

(i) Genetic distance is a measure of the genetic divergence between species or groups of organisms. By computing the variation between alleles at specific loci an estimate can be made as to when certain groups split from a lineage. So, if (i) splitting of lineages isolates the biochemistry of that group and (ii) that the longer the split has taken place the greater the divergence, we can estimate when cladogenesis or lineage splitting occurred. By looking at a specific protein, let's say cytochrome c, we might theorise that those animal groups that branched from the main vertebrate stem earlier will show a greater divergence. If we sequence part of the adult haemoglobin molecule (using another example), we notice a phylogenetic relationship (see Table 7.1). The accumulation of differences is the basis of **molecular phylogenetics**.

(ii) In the case of the sequencing of protein, actual characters are available for analysis. Looking at the codes (nucleotide sequences) and their products

Table 7.1 Genetic differences in the beta haemoglobin amino acid sequences of seven vertebrates expressed as a distance matrix

	Human	Baboon	Cow	Sheep	Mouse	Hamster	Chicken
Human		2	6	9	8	9	13
Baboon			7	10	7	10	13
Cow				3	11	12	16
Sheep					12	9	15
Mouse						7	16
Hamster							14
Chicken							

The numbers in the boxes refer to the number of amino acid differences in the haemoglobin protein sequences of the two animals being compared. It is apparent that the baboon sequence is very similar to that of the human, while the other, less related, mammals show increasing divergence. The chicken (a bird) shows the greatest divergence from that of human beings.

(polypeptides) there exists a limited number of combinations. All proteins have a basis of single or branched chains of amino acids (often with other non-amino acid units, such as the iron-based unit at the centre of globin molecules). But, generally, only 20 types of amino acids are found. And if we look at the transcription code (the DNA molecule), there are only four possible active bases each paired with another one of the four; like an alphabet with only four letters. This allows the possibility of 4^3 (= 64) words, more than adequate to code for only 20 or so possible amino acids. There is scope therefore for considerable 'degeneracy' in the code – an overproduction with amino acids possibly being encoded by more than one codon. Usually, but not in every case, the third base in a triplet can be any one of the possible four without affecting the resulting amino acid. Therefore, given the sequence of amino acids in the protein, the corresponding DNA sequence can be reconstructed, at least for the first two bases of each triplet, but now it is possible to sequence the DNA (or RNA) itself so that the individual bases become the states of the character between individual parts or complete genes. Also, comparison of sequences has become possible not only for nuclear genes, but also those of mitochondrial DNA (mDNA) and ribosomal RNA (rRNA). This method has its own complication however; with only four possible states of any base, homoplasy (the appearance of similar structures in unrelated species) is very common.

Another much-discussed problem in molecular taxonomy is that of the 'molecular clock'. In the 1960s, due to advances in technology such as gel electrophoresis and amino acid sequencing, it became possible to research the evolution of molecules.

A molecular clock depends upon the reliability of mutation rates of neutral mutations and is based on the presumption that for any given protein, the rate of molecular evolution is approximately constant over time for all lineages. This does not imply that all neutral mutations occur at the same rate. There is great variation among proteins. It is also known that genetic systems evolve at different rates and thus are useful for the reconstruction of phylogeny on different time scales. Vertebrate mitochondrial DNA evolves much more quickly than vertebrate nuclear DNA. The debate about the usefulness of the molecular clock concept concerns the constancy of rates of substitution within genes (and thus also applies to rates of insertion and deletion of nucleotides). Even within neutral genes, some substitutions are favoured over others. Among the four possible nucleotides, two (adenine and guanine) are purines, the other two (thymine and cytosine) are pyrimidines. For mechanical reasons mutations from one purine to the other purine or one pyrimidine to the other (transitions) are favoured over mutation from purine to pyrimidine or vice versa.

The concept of molecular clocks remains debatable to this day.

Exercises in (cladistic and phenetic) clustering of characters and dendrogram construction in molecular phylogeny have often garnered considerable controversy. This is even more emphatically the case when the dendrograms have been put on a time base by calculating a reference node using some dated geological event (going from a cladogram to a tree in cladistic terminology). All molecular techniques that claim to reconstruct

phylogeny are based on assumption of elapsed time for their correctness, but if they are calibrated to reconstruct the 'absolute dating' of internal nodes on the tree, they can directly challenge fossil or other geological evidence about the timing of phylogenetic events. Notoriously this has been the case with the dating of stages in human evolution (called 'transcendental cladism' by detractors), as we shall see later.

Nomenclature

The lasting contribution of Carolus Linnaeus to the discipline of taxonomy was noted earlier in the chapter:

- a binomial system for naming species (e.g. *Homo sapiens*);
- use of specific, biological characteristics for all species and higher taxa;
- a nested hierarchy of categories, each category occupying a particular rank in the hierarchy (class, order, family etc.);
- a zoological classification presented in the 10th edition of the *Systema Naturae*, which led to the year of publication (1758) being recognised as the 'Starting Point' for taxonomic names in zoology.

Thus was established the law of priority in zoological nomenclature. The *earliest* correct publication of a name for any taxon after that date is the first 'available name' for that taxon. However, in the early years of the nineteenth century, a time of exploration and the discovery of new species, with no firmly established rules, near chaos resulted in nomenclature, and a committee was set up to report to the British Association for the Advancement of Science. The distinguished panel included, among others, Edwin Strickland (chairman), Charles Darwin, Richard Owen and J. O. Westwood; their report was published as a 'Series of Propositions for Rendering the Nomenclature of Zoology Uniform and Permanent' and appeared in 1843.

There is a parallel to the history of the Zoological Code in that of the Botanical Code. In 1867 the French botanist, Alphonse de Candolle, edited the proceedings of a commission that discussed a series of 'Lois' or laws, proposed by him as Lois de la Nomenclature Botanique. The zoological and botanical initiatives then evolved in parallel as the International Code of Zoological Nomenclature (fourth edition, 1999) and the International Code of Botanical Nomenclature (eighth edition, 1994). A later arrival was the International Code of Nomenclature of Bacteria (1992) based on the Botanical Code but divergent from it.

All these codes have developed a mass of law, with some rules particularly contradictory between the zoological and botanical codes. But despite the differences among the three codes, they share what may be considered operative principles. Chief among these are those of (i) publication, (ii) typification and (iii) priority.

- *Publication*: For a name to be deemed to be properly published, and thus available, it must be published in a recognised and valid scientific journal in proper form. Some respectable scientific periodicals (e.g. *The Palaeontological Association Newsletter*) actually print in each number the following 'disclaimer': 'This

publication is not deemed to be valid for taxonomic/ nomenclature purposes (see article 8.2 of the International Code of Zoological Nomenclature (4th Edition 1999))', and there are further complications involving private circulation of preprints, and of course, in recent years, the status of computer-generated copies in various forms.

- *Typification*: If the new name is that of a species, the generic and specific names must be in the form of Latin, although they can be derived from non-Latin roots. Conventionally, generic and specific names are printed in italic type, with the generic name having an initial capital letter and the specific name a lower case letter (at least in the Zoological Code). The name is often followed by the name of its author, sometimes abbreviated, sometimes abbreviated and also including the date of publication, e.g. *Homo sapiens* Linnaeus (or Linn. or L.), 1758. If the species is now included in a genus different from that of the original author, that author (i.e. of the species name) is placed in parentheses, e.g. *Vanessa atalanta* (Linn.). Linnaeus placed the red admiral butterfly, *atalanta*, and most other butterflies in the genus *Papilio*.
- *Priority*: A newly published name must be accompanied by an adequate description if it is to be valid. The rules for adequacy have become successively stricter with succeeding editions of the Codes. In the nineteenth century many new species, some well known and well used, were hardly described. Matters improved during the twentieth century; and now a minimum should include the position of the new species in the taxonomic hierarchy, a diagnosis (following Linnaeus's original pattern), the origin of the new name, some acceptable illustration(s) of the organism, its geographical distribution and, for fossils, the geological horizon.

But the most important feature of a publication of a new species name is the designation of a **type** (or **type specimen**). This consists of one or more examples, which must normally be in a museum or other recognised institution and available for visiting systematists for study, as a reference to which the species name is always attached. A **holotype** is a single specimen, usually that illustrated in the description. Whatever the subsequent history of the nomenclature of the species, that specimen is the name-bearer for the species, and its locality is the type locality. If a series of specimens together are taken as the reference, they constitute a **syntypic series**, as is often the case with fossils, where one specimen does not always show all the diagnostic features. This, however, is unsatisfactory as the different specimens may not represent the same species. Under those suspected circumstances, a subsequent author may nominate one specimen to be designated as the type specimen – the lectotype. The remaining specimens are then paratypes. If the original holotype or lectotype is lost beyond tracing, then a neotype ('new' type) can be designated by an author who is revising the group including the given species. The information required is the same as that for the original description of a new species. If possible, a neotype should come from the same locality (and horizon fossils) as the original holotype.

So far, we have been talking about the type (and type specimens) of a species, but higher-ranking taxa also have types. The type of a genus is not a specimen but a

Table 7.2 Modern taxonomic ranks

Kingdom
Phylum
Class
Subclass
Infraclass
Order
Suborder
Superfamily
Family
Subfamily
Tribe
Genus
Species
Subspecies
Variety

species, usually the first species of that genus to be described: similarly, the type of a family is a genus. To avoid confusion this should be referred to as the 'type genus' not the 'genotype'! In the Zoological Code family names are derived from the name of the type genus, by taking the genus name root and adding the suffix '-idae'. For example, the butterfly family Lycaenidae (blues, coppers and hairstreaks) is derived from the genus *Lycaena* – the British and European small copper butterfly is *Lycaena phlaeas*. Categories immediately below and above the family ('family group names') are '-aidea' for superfamilies (above family) and '-ini' for tribes (below family). All taxa above the genus level begin with a capital letter but are not italicised. In the Botanical Code family names end in '-aceae'.

There are many other rules in all three codes, but for this summary section, the most significant is that of priority. The 'Starting Point' (1 January 1758 for the Zoological Code) has already been noted, but there are complications. All other things being equal, when two or more names apply to the same taxon, it is by the oldest one that it should properly be known. If two different species names are based on the same type, and this is clearly the case from their respective description, then the more recent name is an objective junior synonym of the older, and the older is the correct name. But if the two names are based on different types, it is a matter of expert opinion as to whether the two names represent the same species or not.

Biological nomenclature is thus a rule-based system of naming avoiding the inevitable confusion when using common names. Organisms are classified using a hierarchical system and assigned to a single taxonomic rank (see Table 7.2). Taxa at

the species level use a binomial (two-name) system such as *Homo sapiens* with classical Latin or Greek often providing the root of the name.

Classification and Big Data

At the time of writing, the Natural History Museum, London, one of the foremost institutions for the collection and research into biological specimens, is currently digitising 80 million specimens. This open access approach to sharing information includes data on everything from global bumblebees, taxonomic names of all UK species, from moss types to a catalogue of meteorites.

Big data is the name given to such large and complex data sets. Challenges with such large amounts of information include Volume (the amount of data), Variety (the types of data) and Velocity (speed of data transformation), often referred to as the three Vs.

The 'information explosion' is a term first used in 1941, describing the increasing volume and complexity of information gathering and information processing following the Second World War. In 1944 it was argued that in the United States, university libraries were doubling in size every 16 years while some 17 years later it was recognised that the amount of biological information (as recorded by the number of new scientific journals) was growing exponentially. In 1971 the Ministry of Post and Telecommunication in Japan found that information supply was growing faster than its demand (information in this case being the number of words) and by the new millennium (the year 2000) the world was producing 1.5 exabytes or 1.5×10^{18} bytes of new information per year; that is approximately 250 megabytes (10^6 bytes) for every individual on the planet!

To put this into perspective, one Sumerian clay tablet could code one symbol per cubic inch while the Gutenberg Press coded 500 symbols per cubic inch. And more recently computer RAM memories at the turn of the millennium stored 1.25×10^{11} bytes per square inch, and this figure continues to increase (see Gil Press, 2013 for a summary of the history of big data).

Bioinformatics is a multidisciplinary field that attempts to manage and understand large quantities of biological data such as pan-genomics (the full complement of genes in a clade), gene and protein expression, computational evolutionary biology and systems biology. To study cell processes or evolutionary relationships algorithms are needed along with the computational power to handle such data. Only in this way, it is argued, can complex biological processes be fully understood. Mathematicians and computer scientists have developed the tools needed to manage 'big data', while biologists evaluate the significance of their results.

As an example, computational biologists uncover evolutionary relationships through DNA and genome comparisons (changes in DNA over time) with systematists reconstructing evolutionary lineages (evolutionary relationships).

8 The History and Origins of Life on Earth

The origin and development of life on Earth may well be a unique event - although a study of **exobiology** (the biology of possible life outside planet Earth) is revealing several interesting ideas concerning how life might have originated elsewhere in the solar system.

To promote and sustain life three basic components are necessary:

1. *material* with which to make a body (organic proteins, lipids carbohydrates, minerals, etc.);
2. a sustainable source of *energy* to power that body (chemical, solar or geothermal); and
3. *environmental conditions* that will sustain complex molecular machinery and life processes (equable temperature, availability of a watery solvent, etc.).

And as discussed elsewhere in this book, life may be described as:

A self-sustaining chemical system capable of Darwinian evolution.

The anatomies of living organisms indicate that their bodies are essentially compact and cellular, composed of an organic (carbon-based) matrix with inorganic additions. Within a cell, jelly-like cytoplasm provides a matrix for metabolic activities (cell chemistry), while selectively permeable membranes provide both an internal and external surface on which to base biochemical machinery. Exchange of materials also takes place through these membranes. An energy supply is either physically acquired (as in **heterotrophic** organisms) or, in the case of green plants, synthesised using an external energy source such as the sun (**autotrophic**). Stored energy in food molecules together with a biochemical electron transport chain transfer this energy into a useable form. It is perhaps convenient to think of stored energy as being like water within a large storage tank; and when needed a hole opens in the side allowing a stream of water to flow out and drive a small 'turbine'. This biochemical machinery (a proton pump) eventually forms ATP. Finally, the 'Goldilocks' nature of planet Earth, that is, not too hot, not too cold (particularly in view of the protein nature of catalytic enzymes), ensures that environmental conditions promote continued chemical activity and replication of living organisms.

Following the 'Big Bang' at the beginning of the universe, all the elements necessary for life, carbon, oxygen, hydrogen, iron etc., came into being. A profusion of stars powered by nuclear fusion provided energy while elemental forces of gravity and energy transfer helped form galaxies and solar systems.

According to current estimates the universe is around 12–13 billion years old. Some 4.6 billion years ago, in our solar system dust particles began to stick together ('accretions') by electrostatic and gravitational forces forming substantial solid bodies approximately one kilometre in diameter. These structures continued to coalesce forming a variety of rocky objects including the asteroids and planets including the Earth. The young Earth was not capable of sustaining life. Heat generated internally together with cosmic radiation would have severely compromised the stability of macromolecules such as proteins and nucleic acids. Also, colossal bombardment by rock fragments left over from the formation of the solar system would have vaporised any oceans creating a disturbed and fractured planetary surface.

Planetary surfaces however determine the likelihood of life developing. The planet Mercury, although volcanic, cooled quickly early in its history and is now completely solid. Its small size and weak gravitational field also left it devoid of an atmosphere. Mercury is now cold and airless – a most unsuitable planet. Venus, although about the same size as the Earth, has a dense atmosphere of carbon and sulphur gases promoting a runaway greenhouse effect and surface temperatures well in excess of 400°C. Its proximity to the sun and its corrosive (sulphuric acid) atmosphere also make this an unsuitable home for living things as we know them. Mars is smaller than the Earth but further away from the Sun. It is large enough to retain an atmosphere (mainly of CO_2) and may have had surface water, but Mars today is cold, barren and windswept. Only the Earth it seems is suitable for complex life – not too hot, not too cold with accessible minerals, liquid water and a protective atmosphere.

When did life on Earth originate? Geologists report that the early bombardment of the Earth ended around 3.9 billion years ago. The consequence of these cosmic impacts was to supply additional minerals and, most importantly, surface water from the cometary and asteroid debris. The world's oldest known rocks are 3.8 billion years old and located at a site in Western Greenland called Isua. A study of tiny pieces of graphite found in apatite crystals at Isua also reveals evidence of a very early carbon-based life form. The oldest known fossils perhaps are found in rocks in Western Australia and Canada are around three and a half billion years old (see Figure 8.1). Life therefore arose rapidly just under one billion years following the Earth's formation.

What Is Life: Characteristics of Living Things

Being able to recognise living entities is not simply a philosophical or academic enterprise. Biologists still struggle with the question 'are viruses alive?' and the rise of Artificial Intelligence has brought sharply into focus the question of life and consciousness. Perhaps not surprisingly this question requires the expertise of several bio-specialists:

- Anatomists and histologists to answer the question WHAT constitutes a living organism
- Physiologists and animal behaviourists to explore HOW living things operate

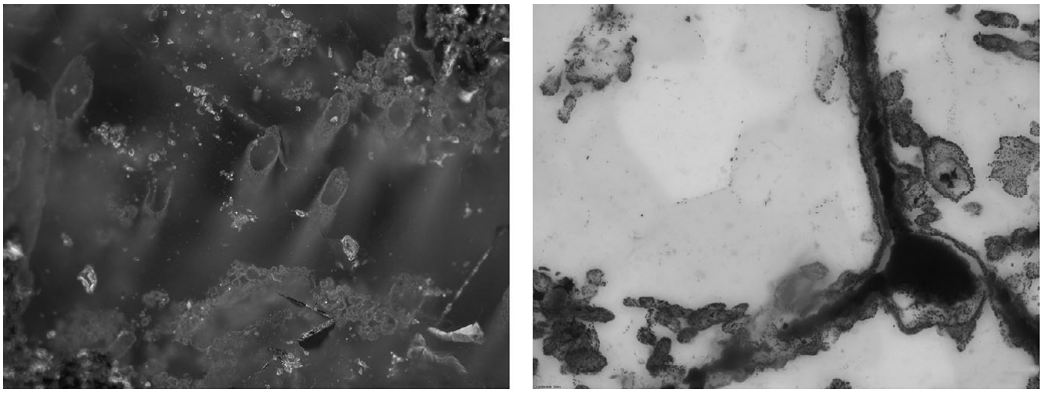


Figure 8.1 The World's oldest fossils? These Canadian microfossils are thought to date from around 3.77–4.28 billion years ago. The haematite tubes (left) and haematite filament attached to clumps of iron (right) are thought to be the remains of filamentous bacteria up to half a millimetre in length and the thickness of a human hair. Like their present-day relatives, they are thought to have inhabited hydrothermal vents in the early oceans. There is debate though as to this interpretation. Photo credit: Matt Dodd with the specimens of Dominic Papineau. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

- Ecologists to study WHERE organisms occur
- Developmental biologists to look at questions of WHEN structures begin to form
- And evolutionary biologists to answer the WHY questions; why so much diversity and why so well adapted.

The vitalism/mechanism debate is discredited as life processes can be increasingly explained through the action of physical and chemical systems. But living things are still characterised by essential features; for instance, living things need:

✓ To acquire food (a nutritional requirement)
✓ To transfer energy from 'food' molecules, that is to respire
✓ To excrete metabolic (cell) waste
✓ To exchange gases between the organism and its environment
✓ To coordinate the very many metabolic and physiological processes within the body
✓ To grow in a particular way
✓ To achieve a degree of mobility at some stage during the life cycle
✓ To produce genetic copies of oneself – to reproduce

To this list however one might add:

✓ A self-regulating physiology and biochemistry
✓ An adaptation to the environment; either within a short space of time (behavioural and physiological adaptation) or over longer, geological time spans
✓ And the process of evolution itself

A final, and philosophical, question looks at the possibility of reducing living things to their basic components. Can life be explained simply by the macromolecules and inherent biochemical machinery within the bodies of living things (a materialist view) or can we take a non-reductionist view that there is an *emergence* of properties due to the complexity of biological systems? For instance, can we explain the properties of water (its liquidity for example) simply by looking at the hydrogen and oxygen atoms? Both reductionist and non-reductionist views are represented in the literature, but the concept of *function* is important in biology and in evolution (less so in chemistry and physics).

Origins of Life

Over the centuries, several theories have been proposed to account for the relatively rapid emergence of living organisms – the development of animate matter from the inanimate:

- COSMOZOAN THEORY – the proposal that life arose elsewhere in the universe and was transported to Earth by meteorites, comets, etc.
- SPONTANEOUS GENERATION – the automatic and inevitable production of animate matter from mineral sources
- CREATIONISM – the intervention of a deity or supernatural being causing life to come into existence
- BIOCHEMICAL ORIGINS – the assumption that organic compounds were formed naturally from simple inorganic precursors becoming integrated into protein-based protocells

Evidence that the Earth was 'seeded' by life forms from outside the planet is sketchy. The **Cosmozoan theory** (also called the theory of panspermia) was popular in the nineteenth century and more recently in the twentieth century following the discovery of interstellar molecules in space with the presence of hydrocarbons possible indicators of organic chemistry. A meteorite falling in 1969 in Murchison, Australia was found to contain both hydrocarbons and simple amino acids, the building blocks of life. Tests carried out have shown that not only can amino acids survive the intense temperatures and pressures resulting from their entry and impact on the Earth's surface, the molecules do in fact polymerise on impact forming simple polypeptides. It is quite possible therefore that life's precursors came from outer space; but there is yet no direct evidence of any organised life outside our own planet and so the Cosmozoan theory remains speculative.

Bread left out for several days goes mouldy, meat in hot climates rapidly becomes infested with maggots, animal carcasses likewise. Such observations gave rise to the theory that life (often verminous) could arise spontaneously given the right conditions. **Spontaneous generation** was a theory common to many ancient civilisations as well as medieval Europe where it coexisted with theories of special creation.

Later, European science disproved spontaneous generation in favour of **biogenesis** – the notion that life can only arise from preexisting life forms. In 1688,

Francesco Redi observed that little white worms on decaying flesh were in fact fly larvae while Lazzaro Spallanzani (1765) found that boiling and sealing animal and vegetable broths prevented the generation of further life forms. The later work of Louis Pasteur and others confirmed the existence of microbes contaminating organic material.

Special creation is a theory upheld by most of the World's religions. It relies on the belief in a deity or God creating humankind and all other organisms for a divine purpose. Creationists often take sacred texts as their source of reference and incorporate these within a personal belief system relying on faith and revelation. Arguments against a literal translation of texts such as the Christian Bible continue within both the scientific and ecclesiastical establishments. This topic will be addressed later.

A **biochemical origin** of life was suggested by Oparin in Russia and Haldane in England independently in the 1920s. Essentially, they argued that in the early, chemically diverse, prebiotic environment of early Earth, energy supplied by lightning or UV light can cause the synthesis of a variety of simple organic molecules from inorganic precursors. The early atmosphere would not have contained much oxygen since this element combines readily with hydrogen.

The Oparin–Haldane theory proposed:

1. a synthesis of complex biomolecules from inorganic forms
2. a structured organisation of organic molecules into protocells
3. early protocells secured an energy source by consuming other protocells/ macromolecules in this prebiotic 'soup', i.e. they were heterotrophic

As scientific knowledge increased, the biochemical theory became refined by Harold Urey and Stanley Miller, a graduate student in Urey's laboratory (Miller and Urey, 1959). They were curious about the kinds of reactions that might occur in the early reducing atmosphere of the Earth. Consequently, they created an 'atmosphere' of hydrogen, methane, ammonia and water in a sealed glass container. Through these gases they passed a continual electrical discharge (see Figure 8.2). In a typical experiment, the reaction could proceed for a week or so. Progress was monitored by sampling the reaction vessel. Careful analysis revealed a possible sequence of early biochemistry:

1. first, aldehydes and hydrogen cyanide were synthesised,
2. on combination with ammonia and chemical intermediates such as the aminonitriles,
3. interaction with water (as in the prebiotic oceans) then gave rise to simple amino acids such as glycine, alanine, glutamic and aspartic acids.

Almost all naturally occurring amino acids have been discovered as were many isomeric forms not found in proteins today and are not therefore designated by the universal genetic code of terrestrial life. Another cautionary note is that equal amounts of (D- and L-) optical isomers were found in the Urey–Miller experiments. Except for certain bacteria, living organisms today incorporate only L-amino acids.

Thus, simple chemistry may provide building blocks for proteins. Ribose and deoxyribose sugars (needed for formation of DNA and RNA) can be easily built up

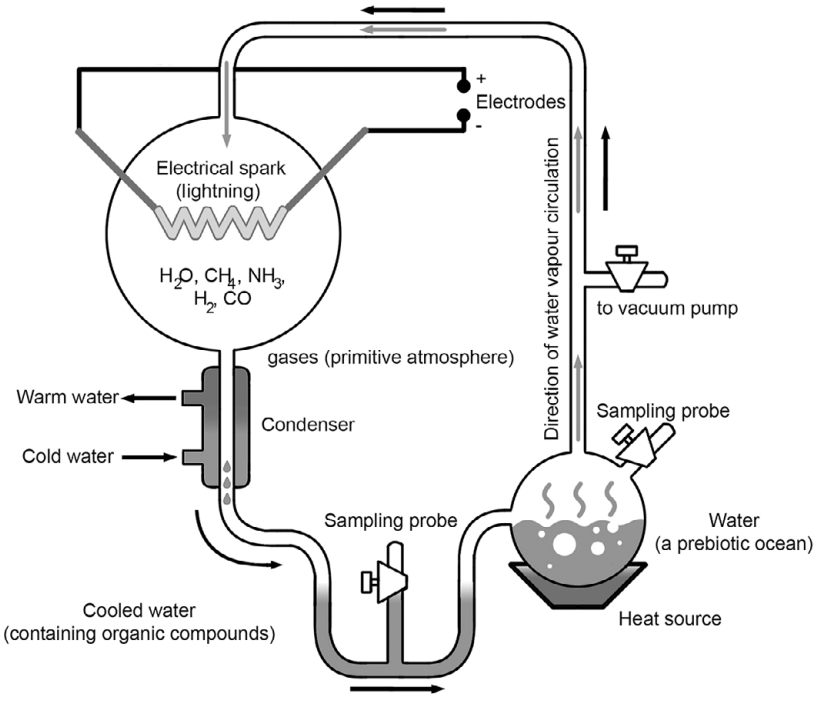


Figure 8.2 The biochemical origins of life, the Urey–Miller experiment. The investigation looked at materials present in the early Earth's atmosphere (water (H_2O), methane (CH_4), ammonia (NH_3) and hydrogen (H_2)) and the effect of electrical discharge from lightning storms. At the end of one week's continuous running, up to 10% of the carbon within the system was now in the form of simple organic compounds.

from the condensation products of formaldehyde (during the formose reaction). It is also possible to account for the appearance of the pyrimidine and purine bases in DNA and RNA.

The next chemical step was polymerisation – the joining of simple molecules (monomers) into the biologically active protein and nucleic acid molecules (polymers). The energy to drive polymerisation in living cells comes from ATP. On the prebiotic Earth such functions could have been carried out by molecules such as carbodiimides that possess lots of free energy. In order that only the 'correct' polymers were formed (e.g. abnormal nucleotides would have interfered with normal ones in DNA synthesis), an inorganic catalyst is postulated. Given the challenges of producing plausible nucleic acids under primitive conditions, another argument is that perhaps a simpler replicating system evolved first, only to be succeeded by RNA and DNA later. Several investigators have begun the search for alternative genetic materials.

Living cells are distinct from their surroundings. A membrane barrier delineates the interior and the exterior of the cell. Alexander Oparin (1894–1980) found that aqueous

solutions of polymers naturally coalesce forming **coacervates** (polymer-rich colloidal droplets suspended in aqueous solution). Macromolecules formed in the prebiotic Earth might also form coacervates. Oparin also noticed that a barrier of sorts often forms around such coacervates and that molecules (for example he added phosphatase enzyme to an aqueous solution) are preferentially concentrated in the colloidal phase (equivalent to the cell's cytoplasm?). Lipid molecules naturally form monolayers and bilayers in solution and such conditions may favour the formation of membrane-bound droplets. Dispersed droplets, perhaps containing simple catalysts (and thus a simple 'metabolism'), can be visualised forming, growing, splitting and breaking down in a primitive ocean. The crucial step in the formation of protocells, however, is the evolution of genetic machinery to (1) instigate cell replication and (2) order and coordinate the simple metabolism.

Other possible pathways for the development of cellular life have been proposed. Sidney Fox in 1950 suggested a theory of protocell formation where proteinoid microspheres (spherical structures with a diameter of around 2 μm) are formed through rapid thermal polymerisation (see Fox and Dose, 1977). Polypeptides are produced in hot aqueous conditions not dissimilar to those found on the early surface of the planet (and in hot springs and oceanic thermal vents today). Cairns-Smith (1990) while looking at the difficulty in constructing a nucleic acid replicating system proposed the idea of replicating clays. He argued that electrically charged clay particles could act as a replicating template concentrating and organising organic molecules on their surface. The cellular information was therefore stored not as a nucleotide sequence on DNA molecules but as a specific distribution of electrical charge on clay particles. Another idea gaining ground in the 1980s was the notion that early life forms would have been autotrophic ('self-feeding') not heterotrophic. It seems unlikely that autotrophs could have evolved from heterotrophs in the short time span indicated by the prokaryotic fossil record; similarly, the abundance of iron-rich clays would provide a ready source of (chemical, oxidation) energy.

Quite how these protocells or microspheres or organic replicating droplets became living cells is not clear. Certainly, the evolution of a genetic machinery is crucial and one in which there are no laboratory models. The first stable cells were undoubtedly bacteria-like. They would have possessed a simple metabolism perhaps even lacking enzymes. Nucleic acids are autocatalytic and probably played a dual role of acting as a template for proteins and a replicating agent. The proteins themselves probably had a dual role too: both structural and protective. The biochemical theory on the origin of life presupposes a natural aggregation of important biomolecules slowly developing the ability to replicate and control an internal chemistry. In a changing environment the ability to persist and to replicate provided a springboard to develop the earliest forms of life on Earth.

To summarise, the earliest life forms needed to perform two basic actions: to replicate (in order that life be self-sustaining) and to develop an ordered biological chemistry from the disordered chemical 'soup' found in the early environment.

A self-copying molecule was discovered in 1953 with Watson and Crick's paper on the structure of DNA. But several bacteriophages use RNA as their genetic material

(rather than DNA), and so the earliest replicators may have developed in an 'RNA world'. But a paradox exists here. For RNA to copy itself an enzyme (RNA replicase) is needed; but if nucleic acids code for proteins (like RNA replicase) and proteins are needed to enable the copying then we have an impasse. The solution it seems comes from the discovery that RNA itself also has catalytic properties. Therefore, this molecule can serve both as enzyme and replicator in what Gilbert (1986) refers to as an RNA world.

An ordered biological chemistry is seen in the *metabolism* of even the simplest organisms. The question as to whether metabolism arose before replication has never been fully answered, but the consensus now is that the **metabolism-first hypothesis** is the most favoured. Current models suggest that before the development of macromolecules smaller molecular units harnessed energy from their surroundings in a self-sustaining system. Following the development of catalytic action, simple, slow molecular behaviours were radically speeded up, leading ultimately to the formation of autocatalytic processes and feedback cycles

The Earth is 4.6 billion years old with the oldest rocks to date seen to be around 3.9 billion years old. The Earth initially had a molten surface suffering continual bombardment as it cooled. Subsequent metamorphosis due to heat and pressure has removed any early fossil evidence, though evidence of graphite indicates that organic life might have existed around this time ('chemical fossils'). The first recognisable fossil evidence occurs in rocks three and a half billion years old. What looks like filamentous bacteria have been found in rocks in Western Australia from around this time. Also, ancient, fossilised mats of stromatolites (prokaryotes still found today in salt marshes and warm lagoons) were and are found in Australia. Another type of bacteria-like prokaryote is found fossilised in the remains of hydrothermal vents that existed 3.2 billion years ago. From these early prokaryotes it takes another three billion years before the first animals and plants are seen.

The First Organisms

A simple thought experiment suggests that we can work out what early life was like by working backwards in time to deduce the last universal common ancestor, LUCA (Longstaff, 2015). LUCA would have been the ancestor of the simplest (prokaryote) organisms, the true bacteria (Eubacteria) and the archaea (or Archaebacteria). Although it is believed that both the bacteria and archaea evolved independently, they share certain features that presumably originate in our earliest common ancestor, namely:

- A protein matrix
- Nucleic acids of DNA and RNA
- A universal genetic code
- Ribosomes, transcription and translation
- ATP and ATP synthase
- Chemiosmosis and a proton gradient
- The ability to evolve (slowly)

Hydrothermal vents on the deep-sea floor are likely candidates for biogenesis. They were probably more common in the early Earth (due to increased geothermal heat flow), and the 'black smokers' (vents with an outgassing of hydrogen sulphide, methane and carbon dioxide) are likely to have provided the basic nutrients for metabolic systems. Because of the acidity and high temperatures of these vents, LUCA was almost certainly an **extremophile**.

In comparing the bacteria and the archaea we note different mechanisms for nucleic acid replication and fermentation processes. Their membrane lipids differ. Perhaps we might conclude that LUCA did not possess plasma membranes and copied its DNA in a different way to that which we see today (Longstaff, 2015).

Origins of the Eukaryotes and the Evolution of Sex

Prokaryotic (bacteria-like) life dominated the Earth for 1.5 billion years. During this time, simple prokaryotic cells diverged into both autotrophic and heterotrophic forms occupying most terrestrial and aquatic environments. A survey of current prokaryotic diversity reveals two major domains: the true bacteria (Eubacteria) and the Archaea (or Archaebacteria). Molecular systematics has designated these two main prokaryotic lineages: the Archaea generally found in extreme environments (organisms in such 'difficult' environments are called extremophiles) and the true bacteria found in an enormous range of habitats and environmental conditions.

Photosynthesis probably evolved early in prokaryotic history; blue-green bacteria or Cyanobacteria are found in stromatolites 3.5 billion years old. With geological evidence for a build-up of atmospheric oxygen at least 2.7 billion years ago the Cyanobacteria must be a very ancient group. Oxygenic photosynthesis (splitting water to release oxygen) is a complex process requiring two photosystems. Some groups of modern prokaryotes are non-oxygenic using a single photosystem to remove electrons from compounds such as H_2S. A logical inference is that the Cyanobacteria evolved from ancestors, perhaps a single common ancestor, with simpler non-oxygenic photosynthesis. It is possible that photosynthesis evolved independently on several occasions, but given the metabolic complexity of this process, the likelihood is that photosynthesis originated once in a common ancestor.

Simple eukaryotic cells resembling unicellular algae are found in rocks 1.5 billion years old. Eukaryotic cells are larger and more complex than prokaryotes (Figure 8.3) combining features of both the Archaebacteria and the true bacteria. The first **eukaryotes** probably formed through a fusion or symbiosis of the two main bacterial types; recent genomic analysis confirms the presence of both archaebacterial and eubacterial features.

The origin of internally membraned, nucleated cells – the Eukaryota – was arguably the most important event in the evolution of life on Earth. Up until that point prokaryotes dealt with environmental change through mutation. Genetic variability was ensured by a large population of cells dividing rapidly and replication 'mistakes' providing a sufficiently large gene pool to allow natural selection to take place and

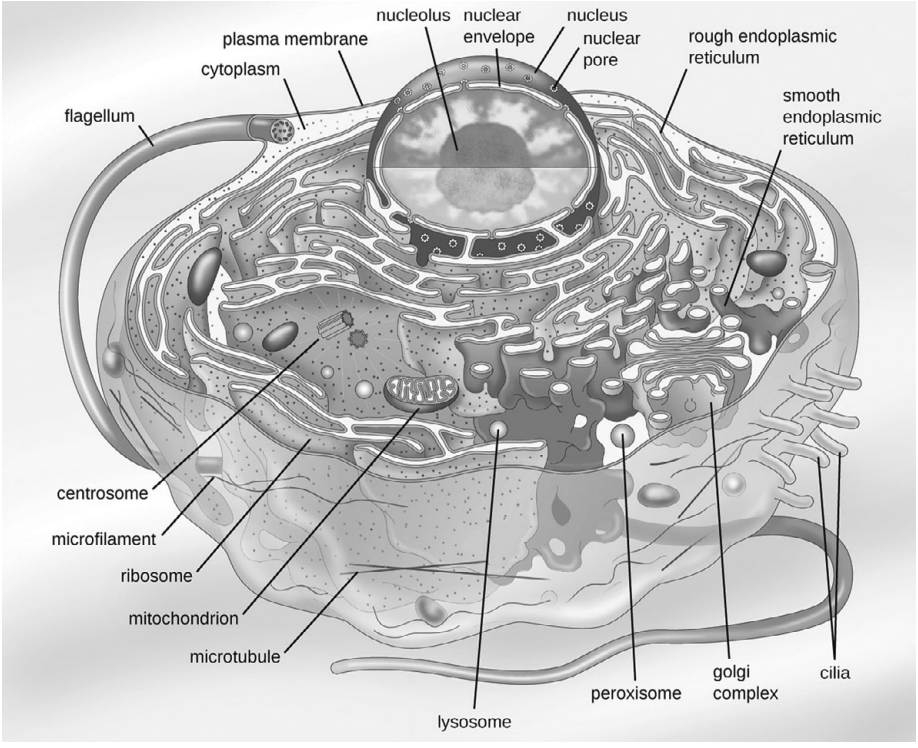


Figure 8.3 The eukaryotic cell. Note the structural complexity of the eukaryotic cell: with membrane-bound organelles, flexible flagella, encapsulated nuclear material, an internal membrane matrix and greater size, etc. Source: https://openstax.org/books/microbiology/pages/3-4-unique-characteristics-of-eukaryotic-cells (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

accommodate any environmental perturbation. This situation of course is satisfactory only up to a point. The evolution of complexity in living things was brought about by the ability to exchange genetic information. Such genetic recombination popularly known as 'sex' provided a distinct selective advantage to organisms. **Desirable features could be shared between organisms allowing the build-up of complex metabolic pathways and structural systems**. Bacteria can share genetic information through lateral transfer, but it is only through sex that true genetic diversity is achieved.

Chromosomes are found in all living organisms allowing linkage of genes and the transmission of gene 'sets'. Prior to the evolution of chromosomes genes presumably replicated autonomously. The advantage of a synchronous replication of gene sets is that competition and conflict between genes is reduced. Gene sets or linked groups allow complex activities to occur within organisms. Metabolic pathways, A –> B –> C –> D, etc., can develop through establishing a succession of genes producing relevant enzymes. Linked genes on chromosomes also allow an orderly segregation of chromosomes during cell division. Daughter cells will maintain a complete genome following cell division or **cytokinesis** (cytoplasmic cell division). Genomic conflict

however arises when there is a bias in the transmission of genes. One example might occur when genes in mitochondrial DNA segregate differently to those in nuclear DNA. Another example occurs in jumping genes or **transposons**, pieces of DNA that can move from one location in the chromosome to another. As genes 'jump' from one piece of DNA to another, genetic disruption can occur. The equitable segregation of genes within the structure of a linear chromosome has been the mechanism of choice (i.e. provides a distinct selective advantage) for sexually reproducing organisms.

Several suggestions have been put forward to explain the advantage of sexual reproduction. Sex is an advantage to the population through increasing its genetic diversity to cope with environmental crises. Sex also confers an advantage by speeding up evolution and providing a range of possible phenotypes for future selection. However, most biologists would argue that selection operates at the level of the individual (or even the gene) not at the group level. The topic of group selection is controversial and discussed later. Sexual reproduction though is successful in biological terms, and several other suggestions have been put forward to explain its selective advantage to individuals:

- Sexual reproduction is more successful in removing dangerous mutations than asexual reproduction. The asexual lineage reproduces parental genomes and mutations accurately (offspring are clones of their parent) whereas sex is the result of a mixing of parental genes and so only a small proportion of the offspring (one half in the first generation, a quarter in the second and so on) will carry the deleterious gene.
- In combating parasitic infections, it is an advantage to remain 'one step ahead' in the evolutionary arms race. Therefore, as sexual reproduction speeds up the rate of evolution, this fact will provide a selective advantage to the host in avoiding parasitic infection. This argument works for both host and parasite.
- Sex can improve the survivorship of offspring either by enabling parental choice (female choice or male choice selecting the best partner) or through the simple fact that two parents are better than one (clearly biparental care is restricted solely to certain animal species only).

Perhaps the earliest fossil eukaryote is a spiral, filamentous alga (*Grypania*) found in Michigan, USA, in rocks 2.1 billion years old. However, chemical signatures of eukaryotes (the presence of steranes derived from sterol in cell membranes) can be detected in rocks 2.7 billion years of age. This time correlates well with the accumulation of oxygen in the atmosphere.

We can be certain that oxygen was not present in the early atmosphere; it is not found in the outgassing of fissures and volcanoes and is not found combined with other elements in rocks of that age. Oxygen, it seems, emerged as a by-product of oxygenic photosynthesis; initially by prokaryotic and photosynthetic cyanobacteria and a few hundred million years later by eukaryotic algae. Evidence for oxygen at this time is seen in the red beds (banded iron formations) of 'rusted' iron-bearing rocks dating back over two and a half billion years ago. At that time, the Earth's environments were changing dramatically. The presence of chloroplasts in eukaryotic cells may help explain an increased oxygen production while the presence of mitochondria

and development of aerobic respiration suggests an intense period of activity within early life forms capitalising on the increased energy efficiency of the cell. Using oxygen to help harness stored energy (aerobic respiration) provides a selective advantage sufficient to counter the disadvantages of an atmosphere with a chemically reactive and corrosive (oxygen) gas. Interestingly, the present atmospheric oxygen concentration (20.95%) is just below that in which planet Earth would have a highly flammable (and hence very unstable!) atmosphere. Eukaryotes are generally aerobic.

The **endosymbiotic theory** proposes a mechanism by which early eukaryotic cells may have developed from prokaryotic ancestors. Essentially early cells imbibed or incorporated other smaller cells into their bodies; these smaller cells then became 'fixed' providing a useful and specific function. Candidates for such 'introduced' structures include organelles such as chloroplasts and mitochondria. The first step would seem to be the development of a **chimaera** or fusion of an Archaebacterium and Eubacterium. So, for instance, a *Spirochaete* bacterium could have provided undulipodia (flagella, cilia, etc.), while a *Thermoplasma* archaebacterium contributed other cellular features such as membrane-bound enzymes. Recent evidence suggests that up to five different bacterial genomes are present in a simple eukaryote such as *Amoeba*.

Cell organelles (mitochondria and cell plastids), it is argued, are derived from bacteria forming intimate relationships with early eukaryotes. Bacteria are eventually incorporated within the cell and subsume their independence to the new, fused cell body. Photosynthetic cyanobacteria may be the original chloroplasts in early protists and algal cells, with aerobic bacteria taking their energy liberating machinery inside cells – eventually forming mitochondria. Evidence for the endosymbiotic theory (a form of internal symbiosis) comes from these organelles having their own genetic material separate from the nuclear DNA of the host. Mitochondrial DNA is very different from that in the nucleus and more like bacterial DNA. Moreover, mitochondria and chloroplasts may behave autonomously within the cell dividing independently of the nucleus. A modern equivalent of this mutualistic relationship is seen in lichens and corals where certain species of unicellular algae inhabit host cells. Similarly, the protozoan *Paramecium bursaria* may contain numerous unicellular algae (*Chlorella* sp.) within its cytoplasm. The presence of intracellular symbionts, such as mitochondria and chloroplasts, in eukaryotic cells might have originated thus:

- bacterial cells ingested by early eukaryotes
- or incorporation due to the relatively elastic and porous nature of early eukaryotic cell walls
- remaining as permanent intracellular parasites

Multicellularity and the Higher Taxa

Just over a billion years ago the stage was set for an amazing burst of diversity within living organisms. Eukaryotic cells increased both in size and complexity resulting in colonial forms and a division of labour within cell aggregates. That is the first

multicellular organisms were formed. Multicellularity originated repeatedly during evolution resulting in the great variety of size and form seen in present-day eukaryotes. Algae, fungi, plants and animals are all descended from these early ancestors. Algae (belonging to the Phylum Protoctista) are morphologically the simplest group forming unicellular, colonial, filamentous and macroscopic forms. The fungi comprise both unicellular and multicellular groups, while animals and plants are exclusively multicellular.

Molecular clocks place the common ancestor of multicellular eukaryotes back to around 1.5 billion years ago. Fossil evidence though is limited. On Somerset Island, Canada, there are remains of a primitive multicellular alga (1.2 billion years old) with what looks like a bilobed holdfast at its base, while larger animal forms such as jellyfishes are found around 600 million (0.6 billion) years ago. In the late Precambrian era multicellular organisms seem to be relatively scarce; few fossils are found. One possible explanation is that a series of extensive ice ages meant that glaciers and sea ice covered much of the Earth's surface during the late Precambrian limiting multicellular, eukaryotic life to only one or two localities such as hot springs and hydrothermal vents. This scenario, called the 'Snowball Earth' hypothesis only came to an end with the gradual thawing of the planet thus allowing organisms to increase their distribution and diversify.

It is only relatively recently however that the significance of cell structure has been used in the classification of organisms. In the 1930s the terms prokaryote and eukaryote were used for the first time to describe those cells with and without a nucleus (or karyon). In the 1970s Carl Woese at the University of Illinois made a profound discovery in the molecular machinery of what had hitherto been called simply 'bacteria'. He suggested that two distinct groups exist, the Archaebacteria (extreme thermophiles with distinct RNA and lipid molecules) and the Eubacteria (a diverse group containing the familiar Gram-negative and Gram-positive forms). Therefore, Woese proposed a new classificatory ranking above the level of kingdom. Three **domains** were proposed, the Archaebacteria (the Archaea or ancient forms), Eubacteria (true bacteria or simply Bacteria) and the Eukaryota (the Eukarya or eukaryotic forms). Divisions between the two prokaryotic domains, Archaea and Bacteria, are at least as great as that between the previous two and the Eukarya.

Interestingly, the domain Eukarya includes forms as diverse as single-celled protists, seaweeds, fungi, flowering plants, insects and human beings. The world of the eukaryote is, of course, varied yet still reasonably familiar. It can come as something of a shock therefore to realise that at least two-thirds and maybe up to 90% of all life on Earth belong to other microscopic, prokaryotic forms!

The Eukarya possess a complex cell machinery enabling them to inhabit most aquatic and terrestrial habitats as well as packaging genetic material effectively and conveniently in the form of chromosomes. The nucleus is the most obvious difference between the two main cell lines, present in a eukaryote but not in a prokaryote. The nucleus contains the genetic material, the DNA, wrapped around a core of protein (histone) molecules. Bacterial cells (I use the word loosely here and not in its taxonomic sense) lack the strengthening proteins and therefore pack the DNA loosely

within the cytoplasm and not within chromosomes. Some archaea though do possess histones and demonstrate their affinity to eukaryotic forms. Other underlying differences between eukaryotic and the 'simpler' prokaryotic cell include the existence of a structural cytoskeleton and contractile proteins in eukaryotes. The cytoskeleton provides shape and a 'scaffold' for the cell's metabolism while contractile proteins allow movement in motile forms such as *Amoeba*. Cell division (mitosis and meiosis) is also unique in the Eukarya using precise chromosome movements to ensure an exact replication of genetic material. Cell division in prokaryotes is a much more haphazard affair.

Further differences between prokaryote and eukaryotic cells are given in Table 8.1.

Colin Tudge (2000) in his comprehensive work *The Variety of Life* recognises the complexity of the Eukarya by describing the large, more apparent forms as 'mega-eukaryotes' with 'fungoids' and 'protists' making up the remainder of this domain. The traditional five-kingdom scheme of Margulis and Schwartz (1988) is still respected by many biologists but professional systematists often use one which describes 21 extant (living) kingdoms including the three, more familiar, fungal, plant and animal kingdoms (Margulis and Schwartz, 1982).

In considering the origins of multicellularity, three models have been proposed:

- *Mutualism model*: by living together in a symbiotic arrangement unicellular forms may become increasingly obligated to one another and share tasks within this permanent association.
- *Colonial model*: following cell division, daughter cells retain a physical connection thereby forming a many-celled structure.
- *Syncytial model*: cells form a syncytium where the nucleus divides but not the cytoplasm. The multinucleate **syncytium** may then progress towards multicellularity.

Multicellularity is seen to be an ancient condition of life on Earth with current, living forms showing evidence for all three approaches:

- mutualistic arrangements are seen in lichens;
- colonial forms are evident in algae such as *Volvox* and *Pandorina*;
- slime moulds regularly form syncytia.

And of course, multicellularity has advantages:

- by their size (in competition for resources, overcoming the limits of diffusion and antipredator strategies);
- as well as by the complexity of multicellular organisms (possessing varied life cycles, cell differentiation, effective division of labour, etc.)

All of which provides a stimulus both for genetic diversity and adaptive radiation.

Table 8.1 A brief summary of the differences between prokaryotic and eukaryotic organisms

Feature	**Prokaryotes**	Eukaryotes
Occurrence	Just about everywhere including extreme environments (found in the atmosphere more than 30 km above the Earth and in rock more than 1 km below ground)	Ubiquitous on the Earth's surface except the most extreme environments
Cell size	All are microbial with small cells 1–10 μm	Formed of much larger (and more complex) cells 10–100 μm.
Nucleus	Absent; a nuclear region within the cell contains the genetic material	A discrete, membrane-bound nucleus is seen
Nucleoli	Absent	Present
Internal membranes such as endoplasmic reticulum	Absent	Commonly found, often with ribosomes
Plasmids such as mitochondria and chloroplasts	Absent	Present (chloroplasts only found in plants and some protoctists)
Streaming movement of the cytoplasm (cyclosis)	Absent	Commonly seen
Nucleic acids	Lack a histone strengthening element	DNA coiled around a histone protein core forming a chromosome
Duration of the cell cycle	Very short, typically 20–60 minutes	Longer, taking around 10–24 hours
Flagellum	Simple construction composed of a structural protein, flagellin, powered by a proton pump	A more complex structure comprising outer (90) and inner (2) microtubules powered by ATP within the basal body
Flagella motion	Rotatory	Undulatory
Contractile proteins within the cytoplasm	Actin and tubulin rare. Cannot alter cell shape; nutrients absorbed directly	Actin and tubulin common allowing amoeboid movement and cell actions such as phagocytosis
Cell division	Direct, by binary/multiple fission or by budding. No centrioles	Genetic division through the precise actions of meiosis and mitosis.
Metabolism	Highly diverse; varied sources of energy, carbon and electrons	Consistent patterns of glucose oxidation, Kreb's cycle, cytochrome electron transport chains
Respiration	A full range of anaerobiosis and aerobic organisms	Generally aerobic respiration
Development	Lack of tissues and differentiation. Some colonial forms	Extensive development of tissues and organ systems in some types. Multicellularity common

The Evolution of Animals

Multicellularity developed repeatedly during evolution. Colonial prokaryotes such as bacterial mats are commonplace; the algae include many colonial and filamentous forms. But perhaps the greatest expression of multicellularity occurs in the animal kingdom. Around 35 phyla have been described and fossil evidence suggests that many more basic forms or body plans were tried out.

Animals may conveniently be described as heterotrophic, multicellular eukaryotes. They are characterised as simple cells lacking plastids and cell walls with unique structural proteins (like collagen) and intercellular junctions. Animals are generally motile with a rounded body form comprising contractile (muscle) and coordinating (nerve) cells. Animals may also be distinguished by their reproduction and life history. Animals usually reproduce sexually with a diploid stage dominating the life cycle. The fertilised egg cell or zygote then undergoes mitotic cleavage resulting in a hollow ball of cells (the blastula) followed by the process of cell infolding or gastrulation.

Sponges are the simplest of all animals. They consist of relatively few cell types (called choanocytes) loosely bound together and supported by spicules. They do not form tissues or organs and they have no basement membranes. Sponges do not possess a symmetry; indeed, it is difficult to derive any other animal form from this group. But sponges are useful in that they suggest a possible origin for animals.

Most biologists agree that the Animalia are a **monophyletic group**, that is, lineages can be traced back to a single, common ancestor. The choanoflagellates, for example, are a group of protists demonstrating an uncanny similarity to the basic cell type of the sponge (see Figure 8.4). As explained earlier, there are three possible ways in which multicellular animals theoretically might evolve from protist ancestors: they may form a composite organism with different cell types fused together (rather like lichens and corals); cells could divide but remain together forming a colonial structure; or a multinucleate protist might develop internal cell divisions. The second, (colonial-origin) mechanism is that favoured by most animal biologists.

It has been postulated that the animal kingdom probably evolved from a colonial, flagellated protist like modern-day choanoflagellates (King, 2004), and that some 700 million years ago a colonial choanoflagellate (see Figure 8.4) developed into

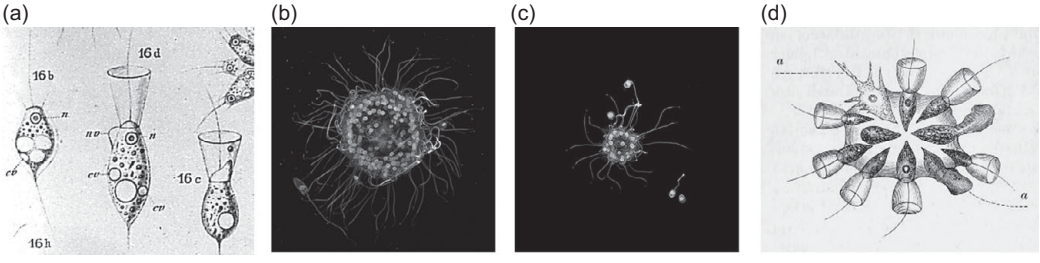


Figure 8.4 (a–d) The choanoflagellates. Photograph of large and small colonies. Photo courtesy of Kayley Hake for images b and c

the first proto animal. The current classification of animals is complex. The sponges and placozoans (sometimes referred to as the Parazoa) seem to exist as almost autonomous units. If these organisms are broken up, each small fragment will easily regenerate in a similar way to plant tissue culture. The true multicellular animals (or Metazoa) are symmetrical, coordinated with distinct body tissue layers. How then might this diverse group of organisms be defined as a true **clade** (i.e. they are all derived from a common ancestor)? The answer lies not in defining animals by exclusion – they do not photosynthesise, they do not have cell walls, etc. – but using **synapomorphies**, features that all animals possess but have been derived from a common ancestor. A possible chemical feature might be the presence of collagen, but perhaps the best line of evidence lies, not surprisingly, in the genes.

Geologists recognise different periods in the evolution of the Earth and it is in rocks of the Cambrian period, dating back 545 million years, that a positive explosion of animal types is seen.

The earliest true animals, the Metazoans, appear as fossils in what is known as the Vendian period, in the Precambrian, between 620 and 550 million years ago. Discovered in the Flinders Range in South Australia, these unusual soft-bodied animals occur as assemblages in sandstone rocks. They are referred to as Ediacaran fauna taking their name from the Ediacaran hills. These animals, however, present palaeontologists with a puzzle. How were these soft-bodied animals preserved, and do they relate to any living animal group? Perhaps the Ediacaran animals (with forms like jellyfish and sea pens) had thicker cuticles than modern forms? Perhaps there were fewer scavengers to consume the soft parts? Perhaps these animals were not buried and so were less affected by decomposers within the seabed sediments? Either way their preservation is remarkable and yet mirrored in different parts of the world (Ediacaran fossils have also been found in Africa, Europe, North America and Asia). As for their affinities with present-day forms, a bold theory by Adolf Seilacher suggests that these animals are unique, a sort of evolutionary experiment. The Ediacaran fauna, he argues, bears no relation to present-day phyla.

Simon Conway Morris (1998) describes a walk through the Flinders Range where deep gulleys and river gorges expose layers of rock deposited over hundreds of millions of years. In the oldest rocks at the bottom no fossils are seen. Slightly higher up the gorge (as the rocks get younger) Ediacaran fossils are seen in quantity. Following the walk as younger rocks are exposed, the Ediacaran fossils disappear only to be replaced by distinct and recognisable aquatic invertebrate forms, often more complex than their Ediacaran forebears. In particular, animals appear with skeletons.

Skeletons are the hard parts of animals. They create a hard, protective exterior; they permit muscle attachment and effect coordinated movement; they act as a reservoir of minerals. The ‘skeletisation’ of previous soft-bodied forms is a profound event in animal evolution and one which marks the beginning of the next period in the Earth’s history – the Cambrian.

Earth’s geological history can be divided into periods, eras and aeons. The four billion years from the Earth’s formation to the explosion of multicellular life in the Cambrian period is generally referred to as the **Precambrian**. Geologists though like

to subdivide the Precambrian into the *Hadean* (the oldest rocks), the *Archean* (where life first appeared) and the *Proterozoic* (with an oxygen-rich atmosphere). Following the arrival of complex multicellular life around half a billion years ago the Earth's history is conveniently divided into 11 periods starting with the Cambrian (the first skeletonised animals) running through to the Carboniferous (characterised by coal measure swamps), the Jurassic (the age of the dinosaurs) and finally the Quaternary (and the arrival of humankind). These 11 geological periods can be grouped into four eras and a single aeon, the Phanerozoic.

Table 8.2 provides a summary history of life on Earth along with the major geophysical events shaping the land surface.

Table 8.2 A history of life on Earth (mapped against geological periods)

Age millions of years ago	Geological era	Major historical period	Illustrative environments[a]	Notes on the evolution of life
0.01 10 000 years ago	**Quaternary**	**HOLOCENE**	The period since the last Ice Age characterised by various anthropogenic activities including deforestation, desertification, industrial pollution and, most recently, climate change. The influence of humans on the planet has led to calls that our current epoch be called the **Anthropocene**	The biota is characterised by habitat destruction, spread of agriculture and an increasing extinction of once common species. It is estimated that 30% of current species may become extinct in the next 100 years – a sixth extinction, **Holocene mass extinction**, is predicted by some
1.64		**PLEISTOCENE**	Climates and temperatures shifted dramatically. Characterised by the advance and retreat of glaciers, Pleistocene glaciation both eroded and deposited huge amounts of material on to the continents. Ice core evidence shows several	Human evolution was moving apace. 1.8 million years ago *Paranthropus* was tool-making in present-day Tanzania while early (*Homo*) Europeans are seen 780 000 years ago. The first human cave art is seen in South Africa (75 000 years ago) and *Neanderthals* existed in central Europe up

Table 8.2 (*cont.*)

Age millions of years ago	Geological era	Major historical period	Illustrative environments[a]	Notes on the evolution of life
			glacial and (warmer) interglacial periods	to around 28 000 years ago. Wildlife in the interglacial periods comprised *megafauna* such as large cats, mammoths, bison and large flightless birds in New Zealand
5.2	(***Neogene***) **Tertiary** ***Palaeogene***	**PLIOCENE**	Cooling and a colder climate in the late tertiary cause ice caps to thicken and sea levels to fall. Continents in the Neogene were close to their current positions but falling sea levels created several land bridges allowing greater animal and plant radiation. The end of the Neogene comprises the first of the Ice Ages	Insect and plant communities coevolve with large (hippo-like) mammals. There are many songbirds. Early Ape evolution occurs on the sides of the Himalayas and in Africa. An early human ancestor, *Sahelanthropus*, is seen in the African Rift valley around 7 million years ago and (bipedal) *Australopithecus* around 3.6 million years ago
23.3		**MIOCENE**		
35.4		**OLIGOCENE**	Collisions between continents resulted in mountain chains such as the Alps forming. Rapid global warming saw a 4°C temp. rise, developing a warm subtropical climate. Animals and plants took millions of years to recover from the K-T (Cretaceous–Tertiary) extinction	Following the removal of the dinosaurs there was an explosion of small placental mammal types. Lake sediments show abundant fish. Terrestrial environments show great diversity of invertebrate types with lush vegetation. The first savannah grass community occurring in the Oligocene. Birds are becoming common along with the first appearance of anthropoid primates
56.5		**EOCENE**		
65		**PALAEOCENE**		

Table 8.2 (*cont.*)

Age millions of years ago	Geological era	Major historical period	Illustrative environments[a]	Notes on the evolution of life
145	**Mesozoic**	**CRETACEOUS**	The global climate becomes cooler and the breaking up of Pangea forms several smaller continents. There were frequent volcanoes with ash falls with both Northern and Southern hot arid belts **The K-T extinction** event at the end of this division (maybe volcanic, maybe meteorite impact) removed 60% of all species, particularly marine forms such as Foraminifera, Ammonites and Echinoderms	Large dinosaurs and a variety of small mammals are typical of terrestrial habitats. Also of significance is the development of flowering plants (oaks, lilies and sunflowers) corresponding with a raid increase in insect diversity. Ants, butterflies and grasshoppers all appear in the Cretaceous showing an insight into their coevolution with plants The **K-T extinction** removed all the large and non-avian dinosaurs. Birds and mammals therefore flourished
208		**JURASSIC**	Characterised as 'The Age of the Dinosaurs', the Jurassic had a warm, temperate climate following the break-up of Pangea. Sedimentary rocks such as limestone, sandstone and shale indicate warm seas and coastal plains with effective preservation of animal remains. Volcanic episodes and major tectonic activity (basaltic	Ichthyosaurs, cartilaginous fish and cephalopods dominate the seas. On land, early mammals, small and shrew-like, some with beaver tails, developed alongside giant sauropod dinosaurs. In the late Jurassic *Archaeopteryx* heralded the development of the bird-like reptiles The mass extinction event at the end of the Triassic saw a

Table 8.2 (*cont.*)

Age millions of years ago	Geological era	Major historical period	Illustrative environments[a]	Notes on the evolution of life
			floods) in the final 18 million years of the Triassic led to climate change and two or three phases of the **Triassic–Jurassic mass extinction**	dramatic reduction in marine reptiles, large amphibia and cephalopods. Roughly one half of all animal species became extinct (but few plants!)
245		**TRIASSIC**	Massive tectonic events resulting in the break-up of Pangea forming Gondwana in the South and Laurasia in the Northern Hemisphere separated by the Tethys sea. A tropical, equatorial Northern climate becoming hot and seasonal in the South	Following **the Permian–Triassic mass extinction event** modern species assemblages such as coniferous forests (plus increasing insect diversity) together with large marine reptiles (in the Tethys sea) are found. A transition was taking place between the archosaurs (crocodiles, pterosaur, etc.) and the newly emerging dinosaurs
290	**Palaeozoic**	**PERMIAN**	Equatorial climate, strongly seasonal with regular sea level fluctuations. Crustal plates fused forming the supercontinent **Pangea** (with a hot dry interior). Major volcanism at the end of the Permian together with release of methane from the seabed triggered pulses of	This period shows how reptiles threatened amphibian tetrapods on land. Ammonites and brachiopods were dominant in the seas and are used to accurately date rock strata. The **Permian–Triassic mass extinction** was particularly severe; 96% of marine and 70% of terrestrial

Table 8.2 (*cont.*)

Age millions of years ago	Geological era	Major historical period	Illustrative environments[a]	Notes on the evolution of life
			extinction at the end of the Permian	species became extinct
362.5		**CARBONIFEROUS**	Coal-bearing (carbo-) rocks indicating a tropical humid climate with high summer temperatures. Seasons were indistinct (few tree rings) and warm shallow seas covered much of the land	Coal measure swamps housed tree-size clubmosses along with a diverse range of (often giant) arthropods. Several lizard-like amphibians are found with reptiles sporting terrestrial adaptations such as scales, lungs and even the first appearance of the amniote egg
408		**DEVONIAN**	Two large supercontinents were surrounded by tropical waters and giant reefs. The climate is tropical with seasonal rainfall. A **late Devonian extinction** occurs either through reduced sea levels or meteorite impact	Peat bogs and the continuing evolution of (jawed) fish resulting in lobe-finned groups. Non-vascular plants remained on land with the arrival of the first tetrapods at the end of the Devonian
438		**SILURIAN**	Melting of the glaciers and raising of sea levels. Orogenic events (formation of mountain chains) plus development of tropical reefs	Rapid development of shallow reefs with radiation of crinoids and graptolites. Colonisation of the land with early arthropods and simple mosses
505		**ORDOVICIAN**	Northern hemisphere mainly shallow seas with land forming a supercontinent (Gondwana)	A diverse range of marine invertebrates with the appearance of jawless fish **Mass extinction** due to glaciers forming at

Table 8.2 (*cont.*)

Age millions of years ago	Geological era	Major historical period	Illustrative environments[a]	Notes on the evolution of life
			moving towards the South pole	the South pole and draining of the shallow seas
543		**CAMBRIAN**	Fragmentation of the main super continent. A mild climate with sedimentation in the plentiful seas	The sudden appearance of a wide variety of fossil types representing most animal groups. Trilobites are common
2500	**Precambrian**	**PROTEROZOIC**	First evidence of the build-up of oxygen in the atmosphere. Global glaciation	Stromatolite diversity. Soft-bodied Ediacran fossils
3500		**ARCHAEAN**	Volcanic with tropical climate	Prokaryotic microbes/ stromatolites
4550		**(HADEAN)**	Period before the earliest known rocks on Earth. Characterised by a partially molten surface and frequent planetary collisions	Some (dated) zircon crystals have been found dated around 4 billion years ago with traces of carbon minerals (biotic?) dated around 3.5 billion years ago

To provide a more continuous narrative, mass extinction events are highlighted in **bold** text and the formation (and break-up) of supercontinents in ***bold italics***. The arrival of major animal and plant groups is underscored.
[a] As generally found in the Northern Hemisphere.

The **Cambrian explosion** is a term used to describe the dramatic radiation in animal fossils seen 540 million years ago. Over a 20-million-year period many animal body plans were seen for the first time; the Chordata, for example, are first seen in the mid-Cambrian. What we now know is that the 35 or so main animal phyla evolved during this period. Of significance are the molluscs, echinoderms and arthropods as exemplified by the brachiopod molluscs and trilobite arthropods typical of this time period.

We are unsure though as to how dramatic the Cambrian events really were. There is evidence to suggest that ancestors of the Cambrian fauna could have lived in Ediacaran times. Studies of developmental genes controlling the eyes, brains and axial patterning suggest that the body plans seen so clearly in the Cambrian may have developed some time before; only the difficulties of fossilising soft body parts prevent

us from witnessing this. The great complexity of some of the Cambrian fossils also presents a case that their origins might be found within the Precambrian.

Events taking place within the Cambrian have both ecological and phylogenetic origins. Three possibilities have been put forward to explain the diversification of animal types at this time (the so-called Cambrian explosion):

- *Ecological causes*: Animals are soft bodied and, perhaps due to a burrowing habit, some forms develop a hard outer covering enabling them to increase their distribution and grow larger in size. Alternatively, the development of predators and predation led to a change in the dynamics of ecological communities inducing selection for better protected and faster forms. It is well known that effective predators maintain diversity in a community (remove a top predator and diversity decreases). However, recent feeling is that predators may cause additional diversity.
- *Phylogenetic causes*: Because of differences in the Hox complex of regulatory genes, several metazoan lineages occurred just before and into the Cambrian. Maybe genetic control was unusually flexible at this time. Such a radiation of form (divergent evolution) found full expression in the warm shallow seas of the Cambrian period.
- *Geological causes*: Although there were no great changes in sea chemistry, perhaps increased oxygen levels provided the greater (metabolic) energy required for the diverse activities of the Cambrian fauna. It is suggested that a thick cuticle or shell would hinder the diffusion of oxygen; therefore, this characteristic could only have arisen in oxygen-rich waters (for these are marine sediments). It is also suggested that the development of animal guts promoted carbon fixation as faecal pellets rapidly became buried in the sediments.

The Cambrian diversification is of interest both to evolutionary biologists and developmental biologists. The new field of **evo-devo**, the synthesis of evolution and development, looks carefully at these genetic imperatives.

Perhaps the greatest Cambrian fossil assemblage ever found is that of the Burgess Shale. This unique fossil collection was found in rocks in British Columbia, Canada, on 31 August 1909. The diary records of Charles Doolittle Walcott, eminent American geologist and Director of the Smithsonian Institute, tells us that the small area of land (now named Walcott quarry in his honour) yielded thousands of pieces of fine shale and mudstone in which were preserved, in exquisite detail, the soft parts of animals hitherto unknown. There were representatives of animals found alive today, but 18 types of fossil bear little resemblance to any living animal. The aptly named *Hallucigenia* was thought to be a worm-like animal walking on what resembled stilts with tentacles along its back. It is now assumed to be an armoured lobopod (Phylum Onychophora), related to the velvet worms walking on paired rows of legs with dorsal spines. *Opabinia* is thought to be an ancestor of the arthropods; it was a soft-bodied animal 5–6 cm in length and believed to be a carnivore (Figure 8.5). Walcott attempted to interpret the Burgess fauna in terms of present-day forms. The current

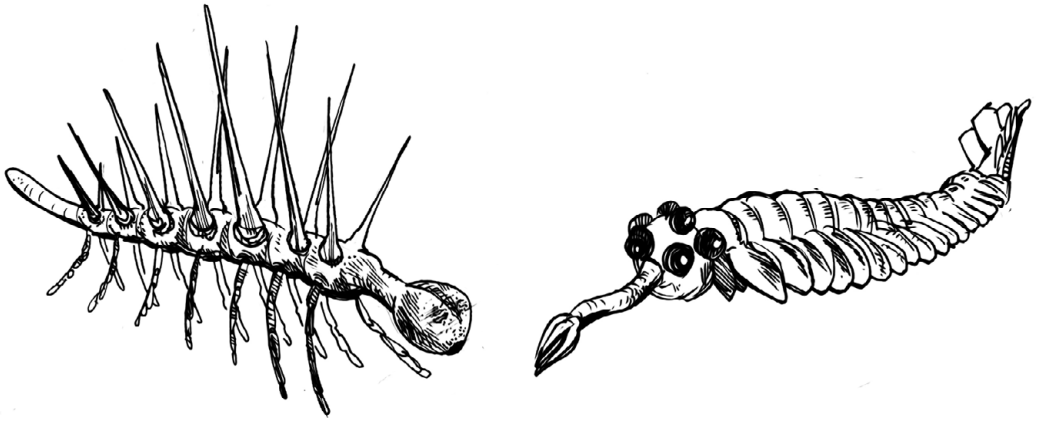


Figure 8.5 *Hallucigenia* and *Opabinia* fossils found within the famous Burgess shales in the Yoho National Park, Canada. *Opabinia* (right) has a proboscis about one third of its body length; its name is derived from the Opabin Pass in British Columbia, Canada. Lobes on the side of the body are believed to be gills or perhaps biramous limbs. *Hallucigenia* (left) is a spiny worm-like animal. It is thought that the extended portion is the head, but this is unclear, and that it has paired walking legs and protective spines.

thinking is that many of these unusual types were the result of a tremendous adaptive radiation at that time with evolutionary 'experiments' determining successful and unsuccessful lineages.

The Evolution of Plants

Land plants (we shall call them land plants even though some have secondarily returned to water) are important in evolution as they have managed to modify both the biotic and abiotic components of their environment. Plants modify both the microclimate and the substratum in which they grow. They transfer energy from the sun through photosynthesis and form complex relationships with animals. The evolution of plants has created a rich, many-layered community establishing a diversity of habitats and ecological niches.

Plants are multicellular, eukaryotic, photosynthetic autotrophs. They possess cellulose cell walls and a variety of plastids (e.g. chloroplasts). Plants are not necessarily characterised by their mode of nutrition (autotrophic), for this feature is shared by many prokaryotes, protists and the algae. Rather it is their life cycles (featuring embryonic development, non-reproductive tissues and alternation of generations) together with specialist cell features (peroxisome enzymes and specialist cellulose-synthesising proteins within plasma membranes) that distinguish this major eukaryotic kingdom.

The major colonisation of the land by plants began 410 million years ago at the end of the Silurian period. Early plants were without roots, stems, leaves or a rigid cell

structure, like upright seaweeds. Life on land requires support systems (not needed in aquatic environments) and some mechanisms to prevent desiccation or drying out. The first plants probably evolved close to the ground, possibly something like the ancestral mosses. But taller plants had a selective advantage in spore dispersal and light capture and thus stimulated the development of strengthened cell walls and a vascular (or transport) system.

It is likely that land plants are derived from multicellular algae. The Plant Kingdom is therefore **monophyletic**. The nearest ancestor to the land plants is an algal group called the Charophycea. The following homologies link modern land plants to the Charophycea:

- the presence of cellulose-synthesising proteins (rosette cellulose-synthesising complexes) in the plasma membrane
- peroxisome enzymes associated with the chloroplasts (preventing organic losses due to photorespiration)
- similar flagellated male gametes (algal gametes are very similar to the antherozoids of the Bryophytes)
- a similarity in the production of new cell cross walls during cell division (only land plants and some of the more complex Charophycea possess phragmoplasts responsible for the alignment of cytoskeletal elements across the developing cell wall)

One of the earliest plant adaptations to life on land was the development of a transport or vascular system. What we now recognise as xylem and phloem originated from ancestral meristematic tissue of the plants' moss-like ancestor. *Cooksonia* (found in Silurian fossils) is the oldest known vascular plant (Figure 8.6). It possessed small, lignified, xylem-like cells and sporangia (spore-producing units) at the ends of its branches. By the mid-Devonian a wide range of vascular plants had evolved including relatives of the modern pteridophytes (an informal term for all the seedless vascular plants notably the ferns and horsetails). *Cooksonia* taxonomy is problematic (Gonez and Gerrienne, 2010), but as one of the earliest tracheophytes, its delineation is critical for this important plant clade.

The Carboniferous period (360 Mya) is characterised by tropical swamp conditions containing tree ferns and giant club mosses, giving rise to what we now know as the coal measures. The later Mesozoic was dominated by the conifers, gingkoes and cycads, while the flowering plants, the angiosperms, developed even later around 100 million years ago in the Cretaceous.

The first plants were non-flowering and reproduced by means of wind-blown spores. Later seed-bearing plants (the Spermatophyta) increased the efficiency of reproduction where the seed was able to protect the female gametophyte and nourish the developing embryo. The development of pollen obviated the need for water and a motile male gamete (i.e. 'sperm-like cells' not needed), while the evolution of the fruit helped in seed dispersal.

The two main groups of seed plants are the gymnosperms (conifers, etc.) and the angiosperms (flowering plants). True seed plants probably arose from an extinct group of ancestral plants, the Progymnosperms. Research data support the view of a single

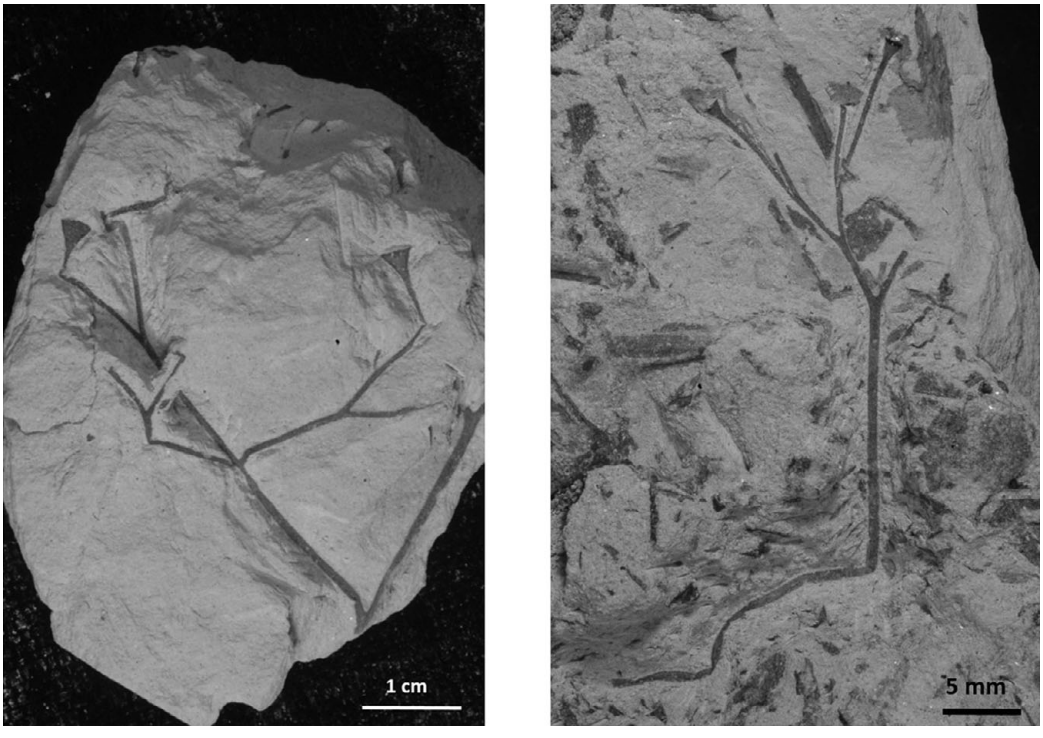


Figure 8.6 *Cooksonia paranensis* fossil specimens. Photo courtesy of Philippe Gerrienne

evolutionary event leading to the Progymnosperms (the seed plants therefore originated as a clade) followed by two separate and independent evolutionary events forming the two main (monophyletic) branches.

Movement onto Land

Life on Earth had witnessed three major macroevolutionary events some billion years or so since its origin. The transition:

1. from prokaryote to eukaryote,
2. from unicellular to multicellular and
3. from an aquatic to a terrestrial existence.

The transition from water onto land occurred independently in the main kingdoms of living organisms and was made relatively quickly following the development of complex multicellular forms.

The advantages of a terrestrial existence are clear:

- ❖ greater levels of available oxygen for energy transfer
- ❖ higher light levels for photosynthesis

- abundant and localised nutrients
- a solid substratum for attachment
- ease of movement through a less dense medium (air)
- opportunity to exploit new environments

The disadvantages of life on land though are also apparent:

- the risk of desiccation
- the need for body support
- difficulties in gamete dispersal and fertilisation
- protection against incoming solar radiation
- greater variations in (air) temperature and pressure

The colonisation of the land began in the Silurian period and seems to have been consolidated around the time of the Carboniferous. The first land plants were the primitive mosses with early vascular plants such as *Cooksonia* seen in the late Silurian. The first land animals were probably detritus-feeding myriapods, their hard, arthropod exoskeleton providing both support and waterproofing. Early peat bog communities (such as that of Rhynie in Scotland, 408 million years ago) also show evidence of fast-moving carnivores, such as the centipede *Crussolum*, together with sap-sucking arthropods.

Because of the relatively high concentration of ('salty') body fluids found in animals today, it is assumed that animals colonised the land directly from the sea rather than take the freshwater route. Animal colonisation of the land, by and large, took place in the intertidal zone. Colonisation of freshwater habitats was largely accomplished by animals already adapted to terrestrial conditions. However, it is thought that vertebrates and some molluscs may have taken the less popular freshwater route onto land.

Some animals, although terrestrial, have never lost their dependence on water. Nematode worms and little 'water bears' or tardigrades inhabit water films in the soil or on the surface of moss plants. They are terrestrial in name only; their microhabitat is entirely aquatic. Similarly, animals like the isopod crustaceans show a transition from purely marine aquatic forms (e.g. the benthic form, *Bathyomus*, at half a metre in length the largest isopod) through transitional forms (e.g. *Ligia*, generally found in crevices in sea cliffs) to what is normally considered a truly terrestrial form (the woodlouse, *Oniscus*). The emphasis of macroevolutionary change has shifted from the seas to the land over the past 400 million years. Land animals are now the dominant animals on Earth in terms of numbers of species.

In plants it is thought that adaptations to life in shallow water preadapted plants for life on land. Environmental features such as increased light levels, increased nutrients and increased carbon dioxide concentrations gave plants a selective advantage. Marginal plants have adaptations to prevent desiccation such as tougher cuticles and more resistant spores. Apertures or stomata are present to encourage gas exchange while the sporophytes of many land plants develop via embryos to confer protection. Some of these chemical adaptations (e.g. sporopollenin) are seen in Charophycean algae, the ancestors of land plants.

Other plant terrestrial adaptations include:

- meristematic tissue
- apical and lateral meristems to define shape
- multicellular embryos
- alternation of generations
- thick-walled spores
- a waterproof outer cuticle
- development of vascular tissue
- stomata to enable gas exchange
- secondary plant products for defence

All of these are common to the three major groups of land plants (bryophytes, pteridophytes and spermatophytes) and demonstrate a remarkable adaptive radiation to available conditions. A final feature of the evolution of land plants is the remarkable joint evolution or coevolution between plants and animals (especially insects). This is covered further in later chapters.

9 Molecules and Evolution

Evolution has been described as 'the product of the differential reproductive success of genetic variants' (Stearns and Hoekstra 2000); another admirably concise definition.

Multicellular organisms though operate on various levels from the molecular to the cellular; whole organism to population. These organisational layers are all susceptible to change; indeed, the ability to demonstrate that molecules have also evolved is one of the great achievements of twentieth-century molecular biology. A multilevel selection therefore operates at all levels shaping the development and evolution of both genotype and its expressed phenotype. But what if there is a clash between the interests, say, of a protein molecule (perhaps better suited to a warm environment) and the entire organism (adapted for life in a colder climate). We can see that a potential consequence of multilevel evolution is an internal conflict within the genome – a **genome conflict**. This chapter looks at the early evolution of organic molecules together with the molecular basis of adaptation and the recent discipline of **molecular phylogenetics**.

What cosmologists call the *Big Bang* is thought to have created our known universe – the cosmic structures and elements found within it. And so, 10 microseconds after the explosive birth of our universe, a super-hot, super-dense 'soup' of elementary particles existed in both basic physics and spacetime. There followed the production of a plasma (it was too hot to be gaseous) and the elements helium and hydrogen began to form. This took only around 100 seconds, so after approximately a minute or so after the *Big Bang*, all the building blocks of stars, planets and ultimately life were present in our rudimentary universe. The evolving universe is a story more accurately told by cosmologists, but suffice it to say that our Sun (a relatively young star) formed about 4.57 billion years ago and planet Earth around 4.54 billion years ago (formed through condensation of dust and gas from a solar nebula into proto-planetary bodies).

The Early Earth

The Earth's atmosphere (more accurately referred to as its secondary atmosphere as the first hydrogen/helium mix was lost through solar winds and the lower gravity of the young Earth) was formed through volcanic outgassing. Roughly 4.2–3.8 million

Table 9.1 Elemental composition of the Earth's atmosphere by volume (taken from various sources)

Gas	Percentage volume	ppmv (parts per million by volume)	Notes
Nitrogen	78.10	781 000	Formed by outgassing in the early Earth
Oxygen	20.95	209 000	Formed by early photosynthesis
Argon	0.934	9350	An inert gas
Carbon dioxide (CO_2)	0.041	397	Much of the early CO_2 was locked away as carbonates (now increasing of course due to anthropogenic activity)
Neon	0.002	18	An inert gas
Helium	0.0005	5	Most escaped from the Earth's proto-atmosphere
Methane (CH_4)	0.0002	2	A greenhouse gas formed by early bacteria (and compounded by anthropogenic activity)
Krypton	0.0001	1	An inert gas
Hydrogen	0.00006	<1	Most escaped from the Earth's proto-atmosphere
Ozone (O_3)	0.002–0.005	2–5	Only found in the stratosphere (the ozone layer)

years ago, the Earth's early atmosphere comprised ammonia, carbon dioxide, hydrogen, hydrochloric acid, hydrogen sulphide, methane, nitrogen and some water. A noxious mixture! As our young planet evolved, the Earth's surface temperature cooled allowing carbon dioxide to form carbonates in the rocks. But if we look at the present-day composition of the atmosphere (Table 9.1), we notice a preponderance of nitrogen and oxygen with the other gases in significantly smaller quantities.

Evidence indicates that compositional changes in the atmosphere were brought about by early prokaryotic life forms, **methanogenic** (methane-producing) bacteria and oxygen-producing **cyanobacteria** around 3.5 million years ago. The major effect of all this was a move from a strongly reducing atmosphere to that of an oxidising atmosphere (as is well illustrated in rock strata of those times). Some oxygen is produced by photochemical dissociation, that is the breakdown of water by UV radiation, but by far the greatest source of atmospheric oxygen is through the chemistry of photosynthesis. The evolution of metabolic pathways incorporating electron transfer and light-driven proton pumps allowed early prokaryotes to reverse the (respiratory) ATP → ADP reaction and to fix carbon (and sulphur) sources releasing the dissociated oxygen as a by-product. Mulkidjanian et al. (2006) analysed 15 complete cyanobacterial genome sequences revealing a conformity of 'photosynthetic gene sets'. They noticed significant lateral gene transfer but concluded that ancestors of cyanobacteria are the most plausible candidates for the first photosynthetic organisms.

The earliest fossil evidence for cyanobacteria is around 2.7 billion years ago though oxygen did not start to build up in the environment until around 2.3 billion years ago. The action of deep ocean vents and the weathering of volcanic rocks released large amounts of iron into the oceans. Photosynthesising cyanobacteria also released oxygen into the water, which reacted with the iron, forming an iron oxide, magnetite (Fe_3O_4). As the magnetite was deposited on the ocean floor, it ultimately formed iron-rich rocks ('red beds') that betray the oxygen-rich conditions on the sea floor. However, once dissolved, iron was used up in the oceans, oxygen was then released, in quantity, into the atmosphere. Oxygen is a reactive gas and combines with several compounds. It is taken up by iron-rich basaltic rocks on land forming the characteristic red beds of terrestrial habits (the red colour here emerging from the reaction product haematite, Fe_2O_3). These terrestrial red beds appear in rock strata between 2.0 and 1.8 billion years ago.

The early molecular world between 4.5 billion and 3 billion years ago consisted of simple macromolecules formed through natural processes, such as the catalytic effects of metals on simple organic compounds such as methane along with the physical effects of heat, sunlight and pressure. Current thinking suggests that the first organisms to appear on the primitive Earth would have been anaerobic heterotrophs – anaerobic due to the lack of free oxygen and heterotrophic due to the simplicity of their nutrition. This hypothesis presupposes the existence of abiotic, organic compounds on which to feed. In order to investigate the production of organic materials from inorganic sources (a point alluded to by Charles Darwin in a letter to Joseph Hooker where he would like to conceive of a 'warm little pond' in which 'conditions for the production of a living being are now present' – Letter 7471 in the Darwin Collection at Cambridge) several investigations have been undertaken. Friedrich Wohler in 1820 demonstrated that high yields of urea could be produced by reacting cyanogen with liquid ammonia and then heating the ammonium cyanate, while Adolph Strecker, 30 years later, synthesised alanine from a mixture of ammonia, ethanal and hydrogen cyanide. Later in the mid-twentieth century Stanley Miller produced amino acids, hydroxyl acids and urea from a mainly methane/ammonia chemical mixture and an electrical discharge (see Figure 8.2).

More recently, several hypotheses have been advanced indicating how the early asteroid and cometary bombardment of the early Earth 4.1 billion to 3.8 billion years ago might have:

1. Brought organic molecules to Earth thereby 'seeding' the early environment
2. Created simple organic compounds through the high temperatures and pressures created on impact
3. Punctured the Earth's crust producing volcanically driven geothermal vents within which life could more easily form (craters thus formed would also act as convenient receptacles for life's 'experiments'!)

Chapter 8 deals more fully with the origins and subsequent early development of life on Earth. The origins of replication and the transition from an RNA to a DNA world are considered next.

Replication and the RNA World

Biologists still struggle to understand the transition from an abiotic (non-living) to a biotic (living) world. The appearance of macromolecules capable of replication and catalysis of other chemical reactions must have marked the beginnings of life on Earth. The discovery of catalytically active RNA molecules together with their role in heredity strongly suggests that this particular nucleic acid must have been among the earliest precursors of living things. Ribonucleic acid (RNA) is a well-known replicator with a key role in protein synthesis. It is a single-stranded polynucleotide, each nucleotide comprising a ribose sugar, a nitrogenous base and a phosphate group. Functionally, there are three main types of RNA:

- Messenger (mRNA), the template for translating the genetic code on DNA into polypeptides, carries the information to the ribosome (translation)
- Transfer (tRNA) transfers amino acids to the ribosome during translation (transcription)
- Ribosomal (rRNA), a major component of the ribosome (60% by weight), together with ribosomal proteins catalyses the assembly of amino acids into the polypeptide chain

Ribosomal RNA is one of only a few gene products that are found in all cells. For that reason, they are used to delineate taxonomic groups and determine species divergence – many complete RNA sequences have now been identified.

The suggestion that living entities first appeared in an 'RNA world' was proposed by Walter Gilbert in 1986; incidentally, it was Francis Crick (codiscoverer of the structure of DNA) who first suggested that RNA might be the first genetic molecule. Until recently protein *enzymes* were thought to be the only biological molecules capable of catalysing other biochemical reactions. However, work by Sidney Altman and Thomas Cech (for which they received their Nobel Prize for Chemistry in 1989) provided strong evidence for the suggestion that RNA molecules can also act like enzymes. Their studies also showed that RNA could edit parts of the genetic message it was carrying; the molecule was therefore acting both as an enzyme and an informational molecule (a **ribozyme**). The discovery of ribozymes supported the idea of an RNA World (sometimes referred to as the 'RNA World Hypothesis').

There are several laboratory models of early self-replicating entities, but nucleic acids and their analogues such as peptide nucleic acid (PNA) and threose nucleic acid (TNA) form the likeliest candidates. Both PNA and TNA have the familiar 'backbone' + 'nitrogenous base' structure and both form a double helical structure. TNA seems a likely early candidate because the 4-carbon sugar threose is readily synthesised and is more durable than the relatively unstable ribose sugar found in RNA. However, to provide a chiral sugar component into the TNA it has been suggested that PNA was a precursor incorporating chiral sugar dinucleotides at the end of a PNA chain.

It has been suggested that the evolution of the RNA world might have arisen with the possible sequence:

PNA → TNA → RNA

Chirality describes the situation where identically constituted molecules are mirror images of one another (also referred to as **stereoisomers**), and this type of molecular symmetry is important in the origins of life – the chirality of a molecule determines how a molecule behaves within a cell. Organic macromolecules show a distinct 'handedness' in nature, sugars can twist light to the left or the right, amino acids generally twist light to the left, while nucleic acids are often right-handed molecules. So how did this situation arise in nature? There are two questions biochemists need to answer:

1. How did molecular 'handedness' evolve?
2. Why did right-handed molecules of RNA emerge?

Two main theories emerged describing this facet of the biological world. Firstly, cosmological theories suggest that these biased molecules came to Earth via meteorite showers (there is a slight bias towards left-handed amino acids) or that polarising radiation induced the formation of left- and right-handed molecules on Earth. Most biochemists though favour a second option whereby chance events in prebiotic chemistry (chance accumulations perhaps) favoured the current disequilibrium. The preponderance of right-handed RNA can only be postulated. However, Gerald Joyce, at the Scripps Research Institute in the USA, has been looking both at the chemistry and the biology of RNA molecules for three decades. He built right-handed RNA molecules from right-handed building blocks but when left-handed building blocks were introduced, the bias then fell apart. But more recently Joyce and colleagues have selected and isolated ribozymes that can catalyse particular forms of RNA isomer. Current research elsewhere in the USA is attempting to synthesise both mirror images of the RNA molecule and determine which ones are biologically 'superior' in certain situations – in other words to answer the question as to why left or right handedness matters.

The existence of an RNA molecule with the capability of both catalysing proteins and self-replication is only the first step in producing a viable, prebiotic life form. A single molecule cannot carry out both functions simultaneously; a complex of molecules (some acting as gene templates and others as an RNA replicase) is needed within some form of discrete space. A protocell here is usually visualised as a membrane-bound sac composed of insoluble lipids with internal membranes allowing specific biochemical reactions to occur efficiently and simultaneously (what Jack Szostak, another Nobel Prize winner in 2009, referred to as self-replicating vesicles). Ribozymes might also generate lipids for growth, in which case we have a growing reproducing cell-like structure. If the cells show differential survival (hence evolution), then perhaps we might consider these protocells alive?

Gene Trees

Genetic material (nucleic acids) are composed of linear polynucleotide sequences. The specific sequence (of say DNA bases) conveys the information needed by the cell.

Table 9.2 Immunological distances between primate species (various sources)

	Albumins obtained from		
Species tested	**Chimpanzee**	**Gibbon**	**Human**
Human	3.7	11.1	0
Gorilla	6.8	11.7	3.7
Orang-utan	9.3	11.1	8.6
Gibbon	9.7	0	10.7
Chimpanzee	0	14.6	5.7
Sumatran siamang	9.7	2.9	11.4

Large-scale genomic sequencing now generates vast amounts of chemical data available for interpretation; data that biologists can use to determine function and data that can infer evolutionary history. Molecular evolution is the study of how and why such polymer sequences change over time; the accumulation of differences forms the basis of a **molecular phylogeny**.

At this point it is worth contrasting a species with its molecular phylogeny. A **species tree** attempts to reconstruct the evolutionary history of a particular species lineage, whereas a **gene tree** uses the same principles to reconstruct a *molecular* lineage. However, there may not be an exact correspondence between these two as genetic polymorphisms, especially in ancestral species, may not affect the actual (phenotypic) evolutionary pathway, particularly when the divergence time between different species is short.

The first generation of comparative molecular phylogenies involved immunological studies (antigen–antibody responses) within a host animal (usually the rabbit). Antibodies are produced in the host in response to the introduction of specific protein antigens. If protein A yields antibody B, then this antibody will react to protein A in a very specific way, usually agglutination or precipitation. We can then measure the antibody response to antigens from different species – if the reactions are similar, then we can conclude that the two species are closely related. The strength of the reaction, in different species, is often referred to as antigenic or immunological distance and describes the degree of relationship.

One example is the degree of similarity between proteins from different Old-World and New-World primates. Separate antibodies were obtained against albumin obtained from chimpanzee, gibbon and human subjects. These three antibodies were then reacted with albumins from other primate species (Table 9.2).

Based on these data we can see that **immunological distances** vary among species, the smaller the number, the less intense the reaction and the smaller the immunological distance, and that, on close inspection, humans appear to be most closely related to gorilla (shortest immunological distance). The next ‘closest’ is

chimpanzee, then orang-utan, gibbon and siamang (the Sumatran siamang is a type of large gibbon). This study provides useful evidence regarding phylogenetic relationships among primates, but how compelling is it? For instance, there is little reciprocity; the human–chimpanzee results (5.7) are different from the chimpanzee–human (3.7). This is also true of the gibbon data. Additional studies have been carried out with an additional protein antigen – lysozyme. And here results were not consistent with those of the albumin studies. So, we need to be cautious when interpreting single studies.

Another technique applied in the early days of gene tree studies is that of amino acid sequencing. Haemoglobin was one of the first proteins to yield its amino acid sequence. Haemoglobins are found widely in nature (in animals, plants and protists) indicating their establishment early in evolutionary history. The animal haemoglobin molecule comprises four globin polypeptide chains connected to a central iron–porphyrin (haem) unit. The molecule reversibly binds with oxygen thus aiding its transport. Different species produce different types of haemoglobin. These differences exist between species and even within species (human adult haemoglobin for instance can differ among individuals and differs significantly from human embryo haemoglobin). Plants also use haemoglobins to bind oxygen during the respiration process; it is similarly found in protists, fungi and prokaryotes – all of which indicates that this molecule has a remarkably long evolutionary history.

Following amino acid sequencing, the next task for evolutionary biologists was to estimate the degree of similarity between molecular structures (in this case amino acid sequences). Several analytical methods may be employed here. Often a variety of methods are used to generate a gene tree (and thereby deduce evolutionary relationships). The most commonly used methods include:

Numerical methods: calculating the number of differences between each sequence pair.

Parsimony methods: exploring sequences to find the minimum number of mutations to account for the available information.

Likelihood methods: comparing data with a theoretical model to determine which data set is most probable if sequences are (i) closely related or (ii) distantly related.

Using numerical methods ‘distance’ between a pair of amino acid sequences can be calculated. When comparing every sequence pair, a **distance matrix** can be displayed (see Table 9.3a) resulting in the construction of a **gene tree**. It is through consideration of such molecular gene trees that we can infer evolutionary relationships. In Table 9.3(a) a common lineage is found between mouse and hamster then between cows and sheep and another common lineage between human and baboon. These six mammals then share an earlier ancestry.

When looking at the relatedness table, Table 9.3(b), one can see that Human and Baboon are closely related; more so than cow and sheep, which in turn appear more related than mouse and hamster. Chickens are a totally separate group.

An examination of several human haemoglobin/amino acid sequences suggests that rather than arising from different genes, converging and assuming similar functions,

Table 9.3(a) A distance matrix to compare the amino acid sequences of vertebrate haemoglobin; each value represents the number of amino acid differences between the two haemoglobin sequences

	Human	Baboon	Cow	Sheep	Mouse	Hamster	Chicken
Human		2	6	9	8	9	13
Baboon			7	10	7	10	13
Cow				3	11	12	16
Sheep					12	9	15
Mouse						7	16
Hamster							14
Chicken							

Adapted from Hartl and Jones (2009).

Table 9.3(b) A table of inferred relatedness taken from the amino acid sequences of vertebrate haemoglobin

Apparent relatedness (inferred)		
Vertebrate	**Closest distance**	**Distance value**
Human	*baboon*	2
Baboon	*human*	2
Cow	*sheep*	3
Sheep	*cow*	3
Mouse	*hamster*	7
Hamster	*mouse*	7
Chicken	*?????*	13+

all the different globin chains arose from a single, ancestral globin gene. It is likely that **gene duplication** gave rise to the seven different globin-type proteins we see today – alpha, zeta, epsilon, gamma, delta, beta and myoglobin chains. Phylogenetically, these all arose from an ancestral myoglobin-like molecule around 500 million years ago.

DNA and RNA Phylogenies

It is possible to splice together single DNA strands to produce the double-stranded helix. The ease with which this can be achieved between species (that is forming 'hybrid' DNA) is a measure of the 'relatedness' of the two species and can be used to estimate how homologous the different DNA strands might be.

Essentially single-stranded DNA from two different species can re-associate into a hybrid form at the appropriate temperature. The DNA hybrid is then heated until the double strand disassociates and forms the original single strands. The temperature at which the double strand separates corresponds to the stability of the double-stranded hybrid. The greater the nucleotide match (the greater the similarity between the polynucleotide sequences), the greater the temperature needed to get them to separate.

So, the greater the mismatch between the nucleotide strands, the lower the stability of the hybrid DNA and the lower the temperature needed to separate them. It is reckoned that for each 1% difference in polynucleotide composition the thermal stability of the DNA hybrid is lowered by 1°C. Work by Sibley and Ahlquist in 1984 used DNA–DNA hybridisation to infer the phylogeny of primates and, again, the close similarity of humans and chimpanzees. This work was reanalysed later (Sibley et al., 1990) where their original assumption was supported, 'the branching order of the living hominoid lineages, from oldest to most recent, was gibbons, orang-utan, gorilla, chimpanzees, and human . . . a chimpanzee–human clade (is) indicated, rather than the chimpanzee–gorilla clade usually suggested from morphological evidence'.

A second technique used to compare DNA samples is that of **restriction fragment** length polymorphisms. **Restriction enzymes** are used to identify and cut DNA molecules at specific loci. Calculating differences in the resulting fragment patterns allows molecular biologists to estimate genetic variation which, in turn, can be used to determine lineages.

Of importance when considering nucleic acid phylogenies are two specific types of DNA:

- ✓ Mitochondrial DNA – evolves rapidly and is relatively easily isolated. It is particularly useful when used by molecular biologists to study a narrow range of related organisms or when species have only recently diverged. **Mitochondrial DNA sequencing** has been particularly successful in studying the divergence of cichlid fish in East African lakes.
- ✓ Microsatellites – tandem repeats of short nucleotide sequences often found in non-coding DNA. The number of repeats is variable both within populations of DNA and within individual alleles (hence the term variable number of tandem repeats or **VNTRs**). **Microsatellite analysis** is commonly used in genetics to trace inheritance patterns and engage in linkage analysis.
  Evolutionary biologists have also used this technique to infer phylogenetic relationships

Deoxyribonucleic acid, DNA, is just about universal in the living world. And the existence of DNA homologues between species is particularly strong evidence for the

unity of life. We discussed earlier in this chapter an 'RNA world' in which a catalytic, replicating, information-carrying molecule (RNA) may well have been one of the first living entities. An RNA world would have had a diverse range of RNA molecules perhaps operating in concert with one another (laboratory-based experiments have shown that ribozymes, catalytic RNA molecules, have the capacity to carry out a wide array of biochemical activities). So, can we ask the question what caused the transition from an RNA world to a largely DNA world?

Protein synthesis is generally associated with the DNA molecule, but several of the protein biosynthesis mechanisms are also catalysed by ribozymes. The similarity of DNA protein synthesis and RNA synthetic mechanisms strongly suggests a common origin, probably in the RNA world. However, the main limitation of the RNA molecule is its extreme instability. Thus, a transition to the more stable DNA molecule would seem likely particularly when the increased stability allows for longer polynucleotide sequences and therefore greater information storage capacity. Following increased synthesis of organic compounds in the early Earth, it is a short step then to the likelihood that only in the DNA/protein world would we witness encapsulation and the formation of membrane-bound structures as seen in protocells.

Rates of Molecular Evolution

In 2009 a British–Chinese research team sequenced 10 million base pairs on the Y chromosomes of two distantly related Chinese men. And, in the first-ever direct measurement of the human mutation rate, they came up with a figure of 100–200 mutations every time DNA is passed from one generation to the next. This translates as one mutation for every 30 million base pairs.

Because the Y chromosome does not readily mix with other chromosomes, estimating its mutation rate is easier; but this does confirm that some DNA sequences evolve at much faster rates than others. For example, non-functional polypeptides (such as the C peptide discarded during the formation of insulin) evolve at much faster rates than their more functionally constrained counterparts. Thus during the formation of human insulin the C peptide has a mean substitution rate of 0.47 nucleotide differences per (codon 1+2+3) site whereas the functional A and B peptides have a mean substitution rate of only 0.17 nucleotide differences (after Kimura 1983). Within the histone proteins it is also known that H3 and H4 evolve very slowly, yet others, such as the antiviral protein gamma interferon, evolve particularly rapidly. Gamma interferon (at 5×10^{-9} amino acid substitutions per site per year) is changing four times faster than beta globulin and significantly faster than H4 histone.

So how do we calculate the speed or rate of molecular change? The most direct route perhaps is to observe changes in visible phenotypes (particularly in 'closed' laboratory populations). The rate of visible mutations within laboratory species is summarised in Table 9.4 (taken from Ridley, 2003).

The general figure of gene mutation is seen to be around 1×10^{-6} changes per locus per generation. But this figure shows great variation both between and within

Table 9.4 Mutation rates (per gene locus per generation) as observed directly in laboratory species

Species	Character/gene	Mutation rate
T2 bacteriophage	Lysis inhibition	1×10^{-6}
E. coli bacterium	Lactose fermentation	2×10^{-7}
Chlamydomonas reinardi (alga)	Streptomycin sensitivity	1×10^{-6}
Zea mays (corn)	Shrunken seeds	1×10^{-5}
D. melanogaster (fruit fly)	White eye	4×10^{-5}
Mus musculis (mouse)	Piebald coat	3×10^{-5}
Human	Normal/albino	3×10^{-5}

species. It can depend upon the type of mutation (simple point mutations are more common than deletions) or on the environment of the cell (UV light can cause specific mutations in yeast while in bacteria caffeine is a **mutagen**).

Both proteins and nucleic acids can alter their structure and their functioning over time but there are basic differences between these two classes of molecule. Both are polymers but there are only four DNA bases compared to the 20 or so amino acids in proteins. This implies that changes at nucleotide sites are more likely than changes at amino acid sites, and that two sequential changes at a nucleotide site is more likely to result in a return to its original state than two sequential changes at an amino acid site. Some of the fastest evolving DNA sequences are the pseudogenes, so called because they are duplicate genes that have since lost their function, while genes that code for ribosomal RNA (rRNA) are among the slowest evolving genes. By using slowly evolving genes evolutionary relationships between major taxonomic groups (such as the Archaea, Bacteria and Eukaryotes) that diverged more than 2 billion years ago can be elucidated. Rapidly evolving molecules such as the fibrinopeptides involved in blood clotting can be used to investigate the relatively rapid evolution of closely related groups, such as within the primates. Use of proteins and nucleic acids provides information not only on lineages and patterns of branching from a common ancestor (cladogenesis) but also about the amount of genetic change that has occurred (anagenesis).

Molecular Clocks

A clock is a timepiece that uses a constant and uniform event to measure change. In evolutionary biology molecular clocks utilise the same principle of constant rates of change to calculate the approximate ages of specific lineages. So, for example, the degree of difference in the fine structure of a protein molecule between two species is proportionate to the time that they last shared a common ancestor.

In 1996 Greg Wray, a Duke University biologist, and his colleagues, using molecular evidence, calculated the divergence of major animal groups as 1200 million

years ago. This provided a major shock to evolutionary biologists who, using fossil evidence, assumed that the start of the Cambrian era (around 650 million years ago) mirrored the diversification of major animal groups. Wray was using *molecular* evidence for evolution rather than the more traditional geological (*fossil* evidence) and his technique virtually doubled the age of the earliest animals.

A molecular clock of evolution employs the premise that nucleotide sequences in DNA change in a constant fashion and that the number of accumulated changes then correspond to the time elapsed. This elegant theory can then be used to attach a time scale to a phylogenetic tree. Molecular clocks were first proposed by Emile Zuckerandl and Linus Pauling in the 1960s based on empirical observation. Corroboration followed in 1968 when Motoo Kimura developed his **neutral theory of evolution** which suggested that nucleotide alterations could be effectively neutral, that is not altering the fitness of the organism. Neutral changes would then accumulate and indicate the evolutionary past.

The notion of a constant molecular clock is however thought to be rather simplistic. Criticism of Greg Wray's early date for animal radiation came from several sources. It was stated for example that Wray had found an unusually early date because he had used vertebrate molecular clocks, and vertebrate mutation rates are slower than those of other animals. Kimura was also criticised when it became clear that rates of molecular evolution can vary significantly among species. There is also evidence that substitution rates within organisms can vary according to metabolic rate. Finally, it has been shown that statistically molecular estimates are skewed because underestimation is grouped (it is a bounded error – cannot be smaller than zero) while overestimation errors are unbounded and therefore form a longer 'tail' on the frequency distribution graph. More recently more accurate methods have been employed to calibrate the molecular clock (generally using fossil evidence to accurately plot dates of lineage splitting). Molecular biologists have also developed a more 'relaxed' molecular clock that allows molecular evolution rates to vary within limits.

This section began by using the analogy of a molecular clock as some sort of watch or clock accurately measuring the passage of time. But molecular clocks are not metronomic – they do not measure absolute time. Rather they are *stochastic*, one whose state is randomly determined. They measure the probability of change in much the same way as we can measure the probability of radioactive decay.

Phylogenomics and Transposable Elements

Phylogenomics is the trans-disciplinary study that attempts to reconstruct evolutionary relationships through a comparison of individual genomes. It is an emerging science with relevance to descriptions and explanations of macroevolutionary trends.

For instance, the evolutionary history of birds has long been debated. How did flight evolve, and what are the advantages of homeothermy and the laying of hard-shelled eggs – all these are questions still being debated. In order to rise to this challenge a team from nine universities in five countries set out to describe the

genomes of 48 bird species representing most of the avian orders (Zhang et al., 2014). Thirty-eight bird genomes were sequenced using a whole genome shotgun strategy and assembled along with previously acquired genomes. The result was a library of avian genomes including duck, peregrine falcon, pigeon, chicken, zebra finch, Adelie penguin and many, many more. From this and other studies it is hoped that evolutionary biologists will now have the tools to answer some of these questions, to compare bird genomes with those of other vertebrates and address the relative paucity of the avian fossil record.

Genomes are not simply sequences of nucleotide bases coding for proteins. Rather they are a complex array of functional and non-functional (or function not known) DNA with regions of highly repetitive DNA sections (tandem repeats). The inventory of a typical eukaryotic genome comprises (after Lesk, 2007):

- Dispersed gene families
- Genes in tandem
- Genes without known functions
  - Short interspersed elements (SINEs)
  - Long interspersed elements (LINEs)
- Pseudogenes
- Minisatellites
- Microsatellites
- Telomeres

In humans, for instance, only 2–3% of the genome codes for proteins while repeated elements of unknown function (SINEs and LINEs) account for 13% and 21%, respectively.

Transposable elements are mobile segments of DNA found in all organisms. The term covers a wide range of genes and characteristics, but when they move to a different location within the genome, they generally leave a copy of themselves behind. A transposable element therefore is an allele that (though moving within a genome) can increase in frequency in a population and can also be transmitted from parents to offspring. Sometimes called 'jumping genes' or transposons these DNA segments were initially regarded as non-functional or 'junk' DNA, but more recently evidence has been found that gives them a role both in regulating gene expression and in cell differentiation.

In the 1940s maize geneticist Barbara McClintock noticed that mottling in corn ears had a genetic component. She discovered a genetic element that both controlled mottling and contributed to chromosome breakage and called the gene *Dissociation* (*Ds*) noticing that breaking of the chromosome always occurred at or near this gene. The gene was also unusual in that it often moved to a new location (**transposition**) causing the chromosome to break at the new site. Interestingly, a second genetic element (*Activator*, *Ac*) is found within the same genome, and it too is transposable affecting gene regulation. Several families of transposable elements have since been described and are often related to some of the repetitive sequences (SINEs and LINEs) found within the genome.

Transposable elements can have an advantageous or a deleterious effect within the genome. In humans, for instance, they have been implicated in tumour formation and haemophilia. The simple bulk of this additional (transposed) material can also burden the host genome. For this reason, transposable elements have been described as 'genetic parasites'. So, carrying them in large numbers (up to 45% of the total human genome!) would seem maladaptive; so why do they exist in virtually every organism and why are they such an ancient component of the genome (Japanese studies have shown that V-SINE transposable elements are approximately 540 million years old)? The answer lies in the relative costs to the organism and has important theoretical implications for the on-going debate regarding levels of selection (see Chapter 4). For if selection occurs at the level of the organism, their genetic burden would provide a negative selection pressure and fitness would be reduced. However, at the level of the gene their duplication and rapid accumulation within the gene pool can offset a slightly reduced fitness. According to models devised by biologists, transposable elements in sexually reproducing organisms (new targets for transposition) that replicate themselves efficiently and with least cost to the host organism are favoured by natural selection and tend to spread.

Transposable elements perhaps at best seem to be a mixed blessing. As a 'genomic parasite' they can transmit themselves at their host's expense. But can organisms protect themselves from this so-called parasite? The answer seems to be that they can. Although neutral mutations can be fixed in the genome by genetic drift, deleterious mutations can be eliminated by natural selection (sometimes referred to as negative or purifying selection). Furthermore, several researchers have suggested an active process, DNA methylation, as a chemical means of denying gene expression in these introduced elements. Yet transposable elements can also have a positive influence. Antibiotic resistance was observed in certain strains of bacteria (conferred by plasmid-borne transposons), and, more recently, deliberate insertion of engineered transposons into eukaryotic cells (notably in rice and vertebrate immune systems) has also demonstrated fitness benefits.

Lateral Gene Transfer

Many animal genomes have acquired prokaryotic genes over the course of their evolution through a process of lateral or horizontal gene transfer. Exploring the genomes of fruit flies, nematodes, primates and humans, researchers found evidence to suggest that some of these genes may even be functional. The extent to which horizontal transfer is implicated is evidenced in a study by Crisp et al. (2015) where 40 animal genomes were analysed for prokaryotic sequences. Around half of the sequences examined had 'foreign' DNA indicating transfer of bacterial DNA into the animal (including human) genome. Some of these 'foreign' (not really foreign of course as now they are incorporated) sequences coded for functional enzymes.

Vertical transfer of genes is represented through meiosis (**gametogenesis)** in the familiar passage of genes from parents to offspring. But a lateral or horizontal transfer

can also occur, particularly in prokaryotes; this sideways transfer occurs between peers within the same generation. Mechanisms for horizontal transfer include:

- *Transformation* (changes in the host's genome through uptake of foreign genetic material)
- *Transduction* (DNA is transported between hosts by an intermediary, usually a virus)
- *Conjugation* (a process in bacteria whereby a growth 'tube' physically joins two cells allowing material to pass through)
- *Transposable elements* (a mobile segment of DNA moving nucleotide sequences within the cell)

Although these processes have been recognised as a major factor in prokaryote evolution for some time, it has only recently been acknowledged that a similar process also exists in eukaryotes.

Based on subunit rRNA genes it is possible to draw up a phylogenetic tree representing common lineages for mitochondria and chloroplast DNA. This is the strongest evidence yet for the **endosymbiotic theory**, which presupposes that bacteria were incorporated into early eukaryotic cells eventually forming the organelles mitochondria and chloroplasts. With their own DNA and double membranes, physical evidence such as size can now be corroborated with extra-eukaryotic DNA sequences.

Important evolutionary consequences accrue from the actions of lateral gene transfer. Bacterial cells, particularly those in extreme environments, contain genes found in other similarly adapted forms. For example, *Thermoplasma acidophilum* lives in aquatic environments with temperatures as high as 60°C and acidity levels as high as pH=2. This (Archaean) bacterial cell shares about 17% of its genome with the distantly related extremophile *Sulfolobus solfataricus*, which thrives in a remarkably similar habitat. And in eukaryotes new metabolic capabilities were similarly endowed by lateral gene transfer.

Genomics and 'Big Science'

Genomes are the site of information storage and expression and, as such, play a pivotal role in biological evolution. It should come as no surprise therefore to discover that genomes themselves can evolve. The Human Genome Project (2001), the Mouse Genome Sequencing Project (2002) and the Arabidopsis Genome Initiative (2001) are all testament to the explosive growth in the study of genomics. The use of **comparative genomics** has been instrumental in recognising the three major Divisions of living things (Archaea, Bacteria and Eukaryota) along with elucidating major events in the evolution of life on Earth and, of course, what makes us human!

In 1997 the US Department of Energy (DOE) set up the Joint Genome Institute (JGI) in California to study 'genomes of non-medical microbes, microbial communities, plants, fungi and other targets relevant to DOE missions in energy, climate, and environment'. Collaborators from around the world (958 in 2015) now have access to

large-scale DNA sequencing facilities to explore gene functioning in a range of organisms. The DOE's main mission areas are bioenergetics and biogeochemistry applications, but under the umbrella of the Genomic Encyclopaedia of Bacteria and Archaea (GEBA), the DOE/JGI is currently embarking on a raft of projects exploring prokaryotic genome diversity. And in the same way that taxonomists use type specimens as a reference point for further analysis then microbiologists who are part of the GEBA project are generating type strains of bacteria and archaea, once again to establish a phylogenetic baseline on the tree of life. In a pilot study, 56 diverse prokaryotic genomes were sequenced to establish a rigorous taxonomy. More recently, a phylum-level GEBA study, the CyanoGEBA effort, has 'sequenced the genomes of approximately 50 phylogenetically diverse cyanobacterial strains from all five morphological sections' (Shih et al., 2013). Therefore, in the GEBA project comparative genomics has harnessed the work of bioscientists in order to explore topics such as nitrogen fixation in root nodule bacteria, metagenome functions in microbial communities and, of course, bacterial classification and evolution.

Studies of transposable elements have shown that genomes are not static entities but dynamic, evolving structures. A further example of that dynamism is the phenomenon of lateral (or horizontal) gene transfer. Eukaryotic cells therefore are a mosaic of original and acquired DNA sequences with genomic change both very ancient and ongoing.

Genes and their genomes can adapt. Parasites, for instance, have remarkably small genomes which perhaps fits in well with their restricted lifestyle. They also have what has been termed virulence genes which when 'switched off' artificially cause a bacterium to become much less virulent. Interestingly, vertebrate parasites contain many genes that code for variants of membrane proteins (the malarial parasite in mice for instance has 806 genes coding for membrane glycoprotein variants). Parasites are adapted morphologically and physiologically to their way of life; we can now see that they are also adapted genomically – a molecular basis for adaptation.

10 Human Evolution

Twelve years after *Origin*, Charles Darwin published his first account of human evolution: the *Descent of Man and Selection in Relation to Sex* (1871). A year later *The Expression of the Emotion in Man and Animal*' was published. So why did Darwin wait so long to consider more fully human evolution? There are many possible reasons:

- His ill health
- He did not want to add to the prejudice and scandal he thought was being heaped upon his theory of evolution
- The ridicule he personally received such as the numerous caricatures of Darwin and lower life forms, particularly after the publication of *Descent* in 1871
- The social instability in England at that time including issues of slavery, social justice and treatment of the poor
- A lack of adequate fossil evidence for humans
- Other books written on the topic such as Charles Lyell's *Antiquity of Man* (1863) and Thomas Huxley's *Evidence as to Man's Place in Nature* published the same year.
- He needed time to develop a theory of sexual selection in order to explain human races
- The uncomfortably close links between humans and the great apes that might discomfort some people (he had first seen Jenny, an orang-utan, at London Zoo in 1838)

It is logical from Darwin's premise in *Origin* that evolution must be universal. The case for evolution by natural selection, his 'one long argument', was cogently and coherently presented in his 1859 text. The *Descent of Man and Selection in Relation to Sex* (1871) is a relatively short book, partly because of the argument (comparative embryologies and human/ape homologies) had already been made and partly because of a dearth (at that time, not now) of human fossil evidence. 'Descent of Man' is split into two parts, Part I exploring affinities and genealogies and Part II looking at sexual selection as a crucial selective mechanism

It was clear to Charles Darwin and his contemporaries that (physically at least) humans shared a very close common ancestor with the great apes. Ernst Haeckel imagined and named a series of intermediate forms from ape to Man, but the 'ape-man theory' was seriously challenged well into the twentieth century. Some thought our

last common ancestor was monkey-like rather than ape-like, others thought the tarsier was the most likely last common ancestor while other biologists postulated a pre-ape ancestor with long fingers and modified upper body. But it was the application of molecular biology, particularly immunological studies, that provided the first real insight into primate evolutionary relationships.

The recent history of studying human evolution is one of comparison – human fossils with living primates plus DNA analyses with our closest ape relatives. It was known that we were part of the ape family, but for much of the late twentieth century it was assumed that humans were a special branch or offshoot of that lineage. Then in the 1980s genetic information demonstrated that we were not a subfamily of apes in general but a subfamily of a group of apes that include chimpanzee and gorilla. Fossils from East Africa also point out that modern humans evolved not in a single lineage, typically: Australopithecus ➔ Homo erectus ➔ Neanderthal man ➔ modern man, but rather our human forebears are separate branches on that same tree. Moreover, our hominin ancestors probably shared the planet many times in the past three or four million years making the story of 'where we came from' much more interesting.

Looking at Mammals

Humans are mammals (see human classification, Table 10.1) and, as such, possess the following characteristics:

- ❖ Possession of milk-producing mammary glands (from which the group gets its name)
- ❖ A skin covered in hair (not scales, not feathers but thin hairs growing from follicles)
- ❖ They are homeothermic (sometimes erroneously called warm-blooded) controlling body temperature through both behavioural and physiological means
- ❖ Possession of a diaphragm to help ventilate the lungs
- ❖ Internal fertilisation with the young born alive (by this we mean that the young are born relatively fully independent, they do not hatch out of an egg). This form of birth is referred to as **viviparity** (compared with oviparity or egg-laying)
- ❖ Generally have larger brains with a sophisticated behavioural repertoire involving extended parental care and far-reaching learned behaviours
- ❖ Differentiation of teeth and remodelled jaw allows for a wide range of diet

Mammals are a rather species-poor group (4327 recorded species in 1991) but include some of the largest (the baleen whale, larger even than the dinosaurs), the fastest (the cheetah) and most inventive (humans and chimpanzees) animals on the planet. In general, and for good ecological reasons, megafauna (large animals) generate fewer species – compare mammals to insects for example. But species numbers can vary over time – rhinoceros and elephant have few extant, or living, species (five and two, respectively), but the fossil records show between 100 and 200 species of each!

Figure 10.1 Fossil skull of *Cynognathus crateronotus*, a mammal-like reptile. *Cynognathus* lived during the Triassic period and was approximately two metres in length. Mammal-like features include a less reptilian lower jaw (dominated by the dentary bone) together with well-differentiated teeth such as incisors and canines. A secondary palate (separating the mouth from the nasal cavity) is typical of the later, mammal-like, synapsid reptiles. Picture courtesy of Daederot, Wikimedia Commons

Mammals evolved from reptilian stock in the Triassic period around 230 million years ago; here Class Reptilia and early mammals probably coexisted. The dinosaurs, diapsid reptiles, were initially dominant. This group (the Diapsida, part of the larger Sauropsida) is the largest and most complex reptilian group and includes the dinosaurs together with all living reptiles except tortoises and turtles. The synapsid reptiles included the sail-backs like *Dimetrodon* and the early mammal-like reptiles like *Cynognathus* (see Figure 10.1 for a more complete description). An extensive collection of fossils from the Triassic and Permian connects mammals with their therapsid (part of the Synapsida) cousins. The actual course of mammalian evolution is still somewhat contentious but undoubtedly involved the possession of homeothermy (incorrectly also termed warm-bloodedness), which allowed them to forage at night away from their larger reptilian neighbours, together with their developing dentition and powerful jaw muscles.

The story of mammalian life on Earth begins in the Jurassic period almost 200 million years ago. Although mainly thought to be small, nocturnal, shrew-like creatures, we now see that there was also a radiation of forms from the 50-cm long, swimming, beaver-like *Castorocauda* to the gliding *Volaticotherium* to a new burrowing, egg-laying monotreme *Pseudotribos*. During the late Jurassic a new group, the multituberculates, arose. Named because of their complex cheek teeth, these highly successful rodent-like mammals survived up to around 40 million years ago (when they were probably superseded by the evolution of true rodents). And by the early Cretaceous a new type of mammal appeared on the scene - the therians, the non-egg-laying forms. Therians were much more like modern mammals with a flexible ankle joint and shoulder blade for increased mobility, more complex cheek teeth for a

wider variety of food items and viviparity. Viviparity involves the formation of embryos protected within the body and the transfer of nutrients from the mother to the offspring thereby maximising survival of the young.

In late Jurassic waterlogged forests (for example in what is now Guimarota, Portugal) more than 26 species of small mammal have been found, while in Northern China one of the early mammals was a small badger-like creature known as *Repenomamus*. Fossils found in China dating around 125 million years ago (early Cretaceous) clearly demonstrate that mammals and dinosaurs overlapped; for in the fossilised stomach of *Repenomamus* are found the remains of a small dinosaur hatchling. The early Cretaceous similarly saw the rise of small mammals. In Mongolia soviet scientists discovered the fossils of 17 small mammal species in fluvial (associated with streams and rivers) deposits.

Later mammalian evolution is characterised by an increase in size and further adaptive radiation due to both climate change and the break-up of the super continents. It should be remembered also that habitats such as the polar ice cap and the desertification of North Africa are relatively recent events (within the last 10 million years) and thus many of our characteristic and specialised mammal types are also new (in a geological sense) arrivals.

The class Mammalia is divided into two groups: the **Prototheria** containing the monotremes, the egg-laying mammals, and the **Theria** containing those giving birth to live young (**viviparous**). It is debatable whether the Prototheria can be recognised as a formal taxon (it includes most of the early shrew-like mammals), but for convenience here, we recognise three current subclasses of mammal:

- *Prototheria* (egg-laying mammals producing milk for the young, e.g. duck-billed platypus)
- *Metatheria* (pouched mammals whose young are born in an immature state, e.g. kangaroos and opossums)
- *Eutheria* (true placental mammals including most of the familiar groups together with humans)

The path to becoming human can be seen in current mammalian classification. For a human phylogeny can be discerned if we explore mammalian relationships along with their fossil history. If we were to attempt an imaginary journey backwards in time, we would encounter our ancestors and witness the splitting of human and mammalian lineages (Dawkins, 2004). For example, around 6 million years ago the 'Human' lineage would have split from that of the chimpanzee; around 7 million years ago we would divert from the gorilla and 14 million years ago the (combined) ape line would have split from the orang-utan. Our journey would then take us back to when our lineage split from even more remote ancestors: gibbons (18 million years ago), Old-World monkeys (25 million years ago) and New-World monkeys (40 million years ago or MYA). Thereafter we might trace our ancestry back 70 million years to the Cretaceous witnessing the emergence of the tree shrews and further back to the rodents (75 MYA), the ancient armadillos and sloths (95 MYA) and some of the very first placental mammals (aardvarks and manatees, 105 MYA). Even further back in

time we would observe the monotremes (egg-laying mammals such as duck-billed platypus) together with other egg-layers, the mammal-like reptiles.

The amniotes constitute a **clade** (group of species all having a common ancestor) comprising the reptiles, birds and mammals. Amniotes are generally tetrapods having an embryo equipped with an amnion (an adaptation for life on land and arose in the Carboniferous period around 320 million years ago). The sauropsids include most of the early reptiles, including dinosaurs, and birds. Mammals and their ancestors belong to the other major division, the synapsids. The sauropsids include those animals commonly known as reptiles (lizards, snakes, turtles and the large bodied dinosaurs), while the synapsid group contained the Therapsida, the mammal-like reptiles. Therapsids are a success story of the Permo-Triassic with legs slung vertically underneath their bodies, a range of clearly differentiated teeth and, of course, endothermy, an ability to regulate body temperature by metabolic means. Many therapsids died out during the Permo-Triassic mass extinction. Mammals are the only living therapsids.

Becoming Human

Within the true placental mammals (the **Eutheria**) it is the **primates** that most clearly illustrate our human ancestry through both a superficial physical resemblance and a more profound biochemical similarity. Why do humans belong to the primates? Well we are not lagomorphs (rabbits and hares) or rodents, we are not hooved quadrupeds (artiodactyls) neither are we part of the Carnivora (dogs and cats) or Insectivora (moles and shrews). We certainly do not fly (Chiroptera, bats) or live in water (Cetacea, whales and dolphins). But we cannot define a taxonomic grouping through exclusion – so what are the characteristics of primates that enable us to place ourselves within that taxon?

Although relatively easy to recognise, primates are difficult to define unambiguously:

- ❖ They have relatively large brains (but so do dolphins)
- ❖ Their eyes face forwards and are surrounded by a bony socket (but they are not unique in this)
- ❖ They have two mammary glands on the chest (but so do elephants)
- ❖ They have flat nails, not claws, on the end of their digits (some do have claws, but this is probably the most unique feature)
- ❖ They have sensitive skin ridges on their fingers (but so do tree shrews)
- ❖ They have highly mobile feet and hands (squirrels also have mobile ankles)

and the feature most often described

- ❖ They have an opposable thumb (but actually not all primates do)

Unlike the other mammals, primates appear not to have become specialised to a particular way of life. And it is this generality that is perhaps the secret of their success. They have retained the basic mammalian features of large brain, excellent

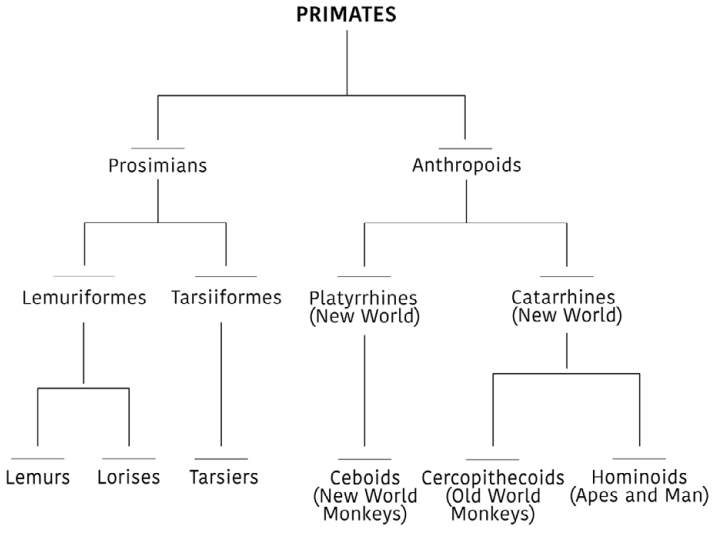


Figure 10.2 A simplified outline classification of the primates.

vision, nimbleness and varied dentition in order to become supremely arboreal (tree-dwelling) or indeed for life on the ground. The earliest primate fossils (lemurs and tarsiers) are found 55 million years ago, but several authors consider them to be much older, perhaps found up to 70 million years ago, which makes them one of the oldest groups of placental mammals. Figure 10.2 provides a summary classification.

Two main groups of primates are recognised (though modern zoologists recognise three or even four grades), and these two are:

- The *Prosimians* ('pre-monkeys') including lemurs and tarsiers, perhaps the group most closely resembling our early arboreal primate ancestors
- The *Anthropoidea* (or simians, the monkeys) with more intricate social lives and bigger brains; these primates arose in the Eocene diverging into two groups, the *New-World monkeys* of South America (the marmosets, spider monkeys, etc.) and the *Old-World monkeys* of Africa (chimps, macaques and baboons)

The apes (brachiate primates, lacking tails), including humans, arose from the Old-World monkeys at the end of the Oligocene (24 million years ago) and radiated in Africa in the Miocene. One of the earliest of the apes, *Proconsul africanus*, was found by Louis Leakey near Lake Victoria (Africa) in 1948 (Figure 10.3). It was evidently of stocky build, had no tail and had a large braincase like present-day chimps. It ran about on the ground on all fours and ate fruit. Fossil pronconsulids now comprise four species ranging in weight from 17 kg to 50 kg and growing up to a metre in length. They lived around 18 million years ago in wooded flood plains surrounded by volcanic highlands.

The apes then spread from Africa into the Middle East, Asia and Southern Europe. Molecular evidence suggests that Asian gibbons are the most primitive ape having

Figure 10.3 Skull of *Proconsul africanus*. With ape-like canine teeth and a rather human forehead *Proconsul* is seen as being ancestral to both chimpanzee and the apes (Consul was a performing 'intelligent' chimp featuring in London Zoo at the time). Picture courtesy of Don Hitchcock

branched off from the other Anthropoids about 25 million years ago. The focus of ape (and human) evolution though remained in Africa.

Within the apes (Hominoidea) only five genera are found today compared with the dozen or so in the fossil record:

- *Hylobates* (gibbons)
- *Pongo* (orang-utan)
- *Pan* (chimpanzee)
- *Gorilla* (gorilla)
- *Homo* (humans)

But the nomenclature (naming) and classification (ordering) of the apes can be complex. Therefore, within the monkeys and apes (Anthropoidea) the following system is used here:

Order: Primates

An outline classification (based on so-called natural groupings) has already been provided in Figure 10.2.

Suborder: Prosimii (comprising extinct 'stem primates' such as the adapids and onomyids along with the lorises, lemurs and tarsiers).

Suborder: Anthropoidea (the 'simians' or monkeys and apes – comprising New-World monkeys, Old-World monkeys, apes and humans).

The tarsiers are closely related to the monkeys, which provides taxonomists with a dilemma as whether to more formally separate the tarsiers from the loris/lemur group.

Laying within the anthropoid group are several superfamilies including:

Superfamily: *Cercopithecoidea* (including Old-World monkeys; macaques, colobus, mandrill, etc.)

Superfamily: *Hominoidea* (the man-like apes including gibbon, chimp and humans)

The gibbons are generally split off as a separate group and humans with their (extinct) relatives placed in another. The remaining three groups of apes were put together as the *Pongidae*. However, molecular studies have shown humans and chimps to be very closely (98%) related and humans are similarly closely related to gorillas. So, the question is do we choose to put humans into a separate family based on their unique features or do we place all the great apes together as one family? Some authors choose to put them into separate families – a convention that has been followed in this book. Figure 10.4 below uses molecular evidence (immunological distance) to illustrate this point.

Thus, the apes include:

- Family: Hylobatidae (gibbons and siamangs)
- Family: Pongidae (gorillas, chimpanzees and orang-utans)
- Family: Hominidae (humans and human ancestors)

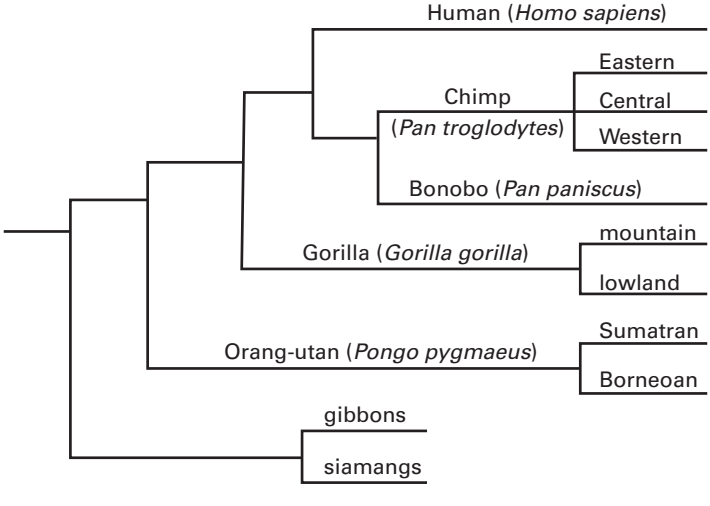


Figure 10.4 Suggested relationship between major primate groups based on immunological distance.

A more modern classification now looks like:

ORDER		Primates			
		|			
SUBORDER	Prosimii		Anthropoidea		
			|		
SUPERFAMILY		Cercopithecoidea		Hominoidea	
				|	
FAMILY			Hylobatidae	Pongidae	Hominidae

Most of the proto-humans are of course extinct, but they include the oldest known specimens (*Ardipithecus*), the australopithecines (including the famous fossil 'Lucy') which it is believed gave rise to a heavy-jawed version of *Australopithecus* called *Paranthropus*. Tudge (2000) reiterates that the term 'hominid' was first used to describe human beings together with their immediate ancestors (a convention followed in this book) and . . . that the group of humans we describe are intrinsically different from the other apes:

- With flatter faces
- Naturally bipedal (walking upright on two legs)
- Development of speech and sophisticated language
- Larger brains and more complex social behaviours
- Absence of a penile bone (os penis)
- Nakedness (weak hair and low density of hair follicles) perhaps to reduce ectoparasite load

In many texts, the family **Hominidae**, in the strict sense, refers only to the genera related to our own genus *Homo*. However, in the current text, the term 'hominid' (lower case letter h) is used to denote the general notion of a man-like ape whereas 'Hominid' (upper case letter H) describes that specific family of Primates which also includes Ardipithecus, Australopithecus, Paranthropus and the *Homo* group.

Palaeobiology and the Human Lineage

From teeth to skulls, full skeletons and human footprints, the human fossil record now comprises around 6000 specimens and the richness of this record allows reasonable confidence in reconstructing human evolutionary history. And, as with most large animals, the human lineage does not comprise a linear sequence of one species after another but rather a branching 'tree' of early human species. Often several species coexisted at the same time.

Four main groups (or clades) are represented in the human family tree (Smithsonian Institute, 2015):

- Ardipithecus
- Australopithecus
- Paranthropus group
- *Homo* group

But the earliest known unambiguous ape is *Proconsul*. Based in the early Miocene, about 18 million years ago, *Proconsul* was tailless (as evidenced by morphology of

the sacrum); it did not possess a particularly large brain, nor did it have the limb mobility of present-day animals. However, *Proconsul* did have greater limb mobility than the other monkeys. Thus, *Proconsul* is considered as an early ape but retaining several monkey-like features suggesting that it moved on all fours in the tops of trees rather than hanging from branches. When compared to today's great apes *Proconsul*:

- Has a smaller brain
- Scapulae (shoulder blades) are on the side not the back and the shoulder girdle is less mobile
- The elbow joint is limited and cannot extend fully
- Arms and legs are the same length (in present-day apes arms are longer allowing them to suspend themselves from trees)
- Has lateral vertebral processes (projections) whereas modern apes have backward pointing processes to stiffen the spine in order to support a bipedal (two-legged) gait

Currently four species of *Proconsul* are recognised.

By the end of the Miocene, however, there is evidence for great apes in Europe, for example *Dryopithecus*, suggesting a migration out of Africa into Eurasia (this is still debated). Specimens of *Dryopithecus* discovered by Lartet in 1856 and Begun (in 2004) show:

- A large-brained animal (like a chimpanzee)
- Slow-growing teeth suggesting that it was long-lived
- A fully extendable elbow joint (for hanging from branches)
- Flatter nasal region
- A downward pointing face (unlike *Proconsul* and gibbons that possess an upward pointing profile)

All of which indicates a close resemblance to African apes and the human lineage.

At the same time as *Dryopithecus* was inhabiting the (then) lush European forests a close relative, *Sivapithecus,* was living in Asia. Both species were long-lived with a dentition that suggested a diet of fruit. *Sivapithecus* locomotion was partly suspensory but it is unclear exactly how its mobility relates to that of other apes (perhaps it had a unique locomotion?). However, a molecular/phylogenetic analysis suggests that *Sivapithecus* lived in what is now Turkey/India/China and is most closely related to the present-day orang-utan.

Moving on to more hominid (man-like) fossils, *Sahelanthropus tchadensis* is thought to have lived around 7 million years ago and to be part of a possible chimp–human transition. Discovered in 2002 in lakeshore sands and clays in Northern Chad, this metre-sized ape combined human features with an ape-like skull. The single, partial skull found has a flat face and heavy brow ridges but the lack of postcranial (below the skull) features means that it is impossible to determine if the animal was bipedal. Whether *Sahelanthropus* was an ancestor of humans, chimps or both is still debated. However, its location away from the African Rift valley (where most of the other early hominid fossils were found) perhaps indicates that early hominids had a much wider distribution than previously thought.

But getting back to our original four clades making up the human family tree, the *Ardipithecus* group (initially placed within the genus *Australopithecus*) are thought perhaps to be the earliest truly Hominid fossils (White et al., 1994). *Ardipithecus ramidus* lived around 4.4 million years ago (the late Miocene) with specimens discovered in the Afar region of Ethiopia. The dentition in general appears to be ape-like; however, small canines and thin enamel point to a Hominid ancestry. Pieces of the fossil cranium indicate an anteriorly positioned foramen magnum indicating a bipedal gait, while the small brain is roughly 20% of that of modern man. A relatively complete *A. ramidus* skeleton was found in 2009. It was nicknamed 'Ardi' and judging by the pelvis and big toe (hallux), this man-like ape was a **facultative biped**, in other words able to walk on two legs, although this was not obligatory. Walking on the ground was probably rather simple and short term; while in trees, Ardi would move around in a quadruped fashion.

Structures such as the teeth, wrist bones and skull organisation suggest a possible human lineage, whereas its long toes, facial appearance and small brain provide more ape-like origins for *Ardipithecus*. It is too young to be a common ancestor of chimps and humans, but studies of teeth growth and jaw patterns suggest a social behaviour more akin to that of humans. The *Ardipithecus* trajectory seems to occupy a unique place in Hominid evolution, neither chimp nor human but showing the beginnings of a more sophisticated social organisation.

Around 3.5 million years ago two human ancestors about, a metre tall were walking side by side in volcanic ash and mud in a dry riverbed in what is now Tanzania. These tracks were probably made by *Australopithecus afarensis*, 'Lucy's people'.

Lucy (or AL288–1) is a pivotal Hominid fossil discovered in 1973 by Donald Johansson and Tom Gray within the Hadar formation of Ethiopia. With several hundred bones and more than 40% of a complete skeleton it soon became apparent that this specimen showed distinct human features. Using argon–argon radiometric dating technology, ash from around the fossil was estimated as 3.22–3.18 million years of age establishing Lucy as the oldest Hominid fossil found. Characteristic human features included:

- A 'valgus knee', ankle bones and lumbar curve indicating an upright (bipedal) gait
- A pelvic girdle like that of modern human females (though the acetabulum where the thigh bone articulates was small and ape-like)
- The position of the femur indicating an upright posture
- A conical rib cage indicating a long intestine for digesting plant matter
- Teeth indicating a diet of fruits and leaves but more brittle foods too

It was another four years before Lucy was fully described as a new species, *Australopithecus afarensis*. But this specimen was not the first australopithecine found; that honour goes to Raymond Dart who studied a hominid child's fossil found in South Africa. The 'Taung Child' (*Australopithecus africanus*) was discovered in 1925. This specimen had human teeth and a spinal articulation with the skull that indicated an upright gait. With the fossil dated at 2.2 million years of age Dart's interpretation was disputed at the time and largely ignored by the

Figure 10.5 A family group of australopithecines.

scientific community. But later finds by Robert Broom in the limestone caves of the Sterkfontein valley displayed hominins with an ape-like sloping face but a very human spine and pelvis. With increasing evidence and the discovery of fossils such as Lucy it became apparent that australopithecines were early humans and not just apes. Several *Australopithecus* specimens have been found and it is believed that the genus continued to evolve in Africa from about 3 to 1.5 million years ago.

A hominid fossil dated at 4.4 million years (due to its position between known rock strata) was found in 1994 and originally named as an *Australopithecus* species. This human ancestor was around a million years older than Lucy! This was later renamed as the genus ***Ardipithecus***.

Compared to Lucy and other australopithecines, *Ardipithecus ramidus*:

- Had a much smaller braincase (350 cm^3 compared with 500 cm^3 in Lucy)
- Displayed less specialised teeth with few male–female differences

Table 10.1 A possible evolution of the human lineage

Hominid types	Species	Average date	Notes
The first hominids	*Ardipthecus ramidus*	4.4 million years ago	May be a common ancestor of both humans and chimps!
The australopithecines	*Australopithecus* and *Paranthropus*	3.6 million years ago	A true bipedal gait with larger brains
The first people	*Homo habilis* and *Homo rudolfensis*	1.8 million years ago	Small hominid, probably a gatherer scavenging on carcasses using simple stone tools
Tall and upright people	*Home erectus* and *Homo ergaster*	0.6 million years ago	The first hominid that perhaps looked and behaved like us
'Archaic' people	*Homo neanderthalensis* and *Homo heidelbergensis*	0.3 million years ago	Powerfully built and skilled humans. They were meat-eating hunters surviving in Europe until around 30 000 years ago
Modern people	*Homo sapiens*	0.2 million years ago	Modern man, fully bipedal with characteristic body shape and ability to control his or her immediate environment

Adapted from Tudge (2000).

- ❖ Had a pelvis and hallux (big toe) that suggested it could have walked upright some of the time
- ❖ Had extremely thin tooth enamel compared with other hominids

Paranthropus boisie is a more robust, upright human ancestor (it is sometimes known as the robust australopithecine) found in the wooded grasslands of the Olduvai Gorge in East Africa. Feeding on tough leaves it had a large ape-like skull with strong, muscular jaws. *Paranthropus* lived around 1.8 million years ago; it was a social animal with a flatter human face and existed for around a million years cohabiting with big cats, hyenas and another hominid species – *Homo habilis*.

Humans are set apart from other primates by their possession of a large brain and bipedal gait. Lucy was decidedly bipedal but despite the increasing size of some of the other australopithecines (up to 1.75 metres in height), their brain capacity never exceeded 550 cm^3; a very ape-like characteristic. The leap towards larger brains and increased behavioural and social sophistication came with the origin of a new human genus, *Homo*.

Of the four main groups or clades of human ancestor (*Ardipithecus*, *Australopithecus*, *Paranthropus*, *Homo*) only the final genus (*Homo*) is what might be considered 'modern'. The Hominid family tree consists of multiple lineages with the traditional interpretation of australopithecines leading to early *Homo* then to later *Homo* now seen as too simplistic. However, for convenience, we might summarise the evolution of humans and their immediate ancestors as shown in Table 10.1.

Modern Humans

The genus *Homo* contains what we now think of as modern people – large brained, bipedal, sexually dimorphic and with complex family and social structures. The earliest of these, *Homo habilis*, lived around 1.4–2.5 million years ago in East Africa. It was a relatively small hominid (only 1.3 metres tall) with a brain capacity of 630–700 cm^3 and most probably tool-using. Discovered by Louis Leakey in 1964, its description within the genus *Homo* was at first disputed with its small stature and similarity to the australopithecines prompting several authors to suggest it should reside within that previous taxon. But Bernard Wood suggested that far from belonging to a formerly recorded group, the 'habilines' (he also suggested another species *Homo rudolfensis* found at Lake Rudolf – now Lake Turkana) were sufficiently distinct. They were early tool-users and perhaps were even beginning to develop speech.

The discovery of 'Peking Man' in and around 1920 was a sensation. In 1921 a Swedish anthropologist, Johann Andersson, and an Austrian palaeontologist, Otto Zdansky, were excavating at a small village near Beijing (Peking) in China. They came across two hominid teeth. Over the next few years several bones including mandibles and cranial caps were discovered. There are now 13 sites across China where remains have been found comprising some 45 individuals. The discovery is significant because, as individuals lived communally in caves, evidence of hunting, fire (cooking) and tool use have been uncovered.

Originally named as *Sinanthropus pekinensis*, *Homo erectus* (as it was renamed) arose around 1.9 million years ago in Africa spreading to China (Peking man), Java (Java Man) and central Europe. With a height of 1.6 metres and a brain size of 830–1100 cm^3 *Homo erectus* ('upright man') lived very successfully in semi-permanent settlements. It is probable that *Homo rudolfensis* rather than *Homo habilis* gave rise to *Homo erectus*. Again, there appears to be more than one species at this time (for instance, there is also *Homo ergaster* or 'working man'), and it is probable that the '*erectus'* groups were the first near-humans to move out of Africa around 1.5 million years ago.

'Erectus' group fossils (*Homo erectus* and *Homo ergaster* primarily) are important as they represent the earliest known Hominids with recognisable human body proportions. Fossils suggest an expanded braincase with evidence of complex social interaction, such as looking after older and weaker individuals. The flatter crowns of molar teeth (found by Otto Zdansky) are much more like human molars than those of apes. They walked upright on land not brachiating in trees (shorter arms and longer legs testify to that), and the occurrence of hand axes, hammer stones and other stone tools nearby (but not arrow heads) also suggest a much more sophisticated tool use.

Human-like fossil remains found in the Neander valley in Germany in 1856 proved decisive in demonstrating an ancient human population in Europe around 400 000–30 000 years ago. Powerfully built, meat-eating hunters, the Neanderthals (*Homo neanderthalensis*) stretched from Wales in the West to the Urals in the East, from Germany to Gibraltar. These 'archaic' humans had large brains (like modern-day

humans) receding cheek bones and a prominent eyebrow ridge. They are thought by some to be a 'sister' species to modern humans; they are certainly very closely related, indeed the ranges of *Homo neanderthalensis* and *Homo sapiens* (modern man) overlapped for around 10 000 years.

Homo heidelbergensis is an earlier human ancestor living in Africa and Europe between 600 000 and 300 000 years ago. The first fossil find was a jaw discovered near Heidelberg Germany in 1907. They had a brain size like modern humans but looked quite different with protruding eyebrow ridges, a sloping skull and little sign of a chin. But these proto-humans skilfully butchered animals using simple stone tools, and they are thought by some to be the direct ancestors of modern humans, *Homo sapiens*.

Truly modern humans, *Homo sapiens* ('wise man'), arose between 200 000 and 300 000 years ago in Africa. They had flatter domed skulls, high foreheads and small teeth and jaws. Analysis of Neanderthal and modern human DNA suggests that they shared a common ancestor (possibly *Homo heidelbergensis*) around 400 000 years ago. The Recent African Origin Model (or the 'Out of Africa' hypothesis) postulates a single origin of *Homo sapiens* in Africa 200 000–100 000 years ago. This notion is corroborated by mitochondrial DNA along with anthropological analysis of fossil specimens. However, sequencing of Neanderthal and modern human genomes suggests a mixing (an admixture) of around 4%. Perhaps both humans and Neanderthals had a common ancestor in *Homo erectus* or *Homo heidelbergensis*?

Several models have been put forward to explain the origins of *Homo sapiens*:

- ***Recent African Origin Model***: studies of mitochondrial DNA in the 1980s suggest that the modern human genome was derived from a (single?) African ancestor around 200 000 years ago. Thereafter modern humans left Africa around 60 000 years ago replacing the 'archaic' human populations in Europe and elsewhere.
- ***Multiregional Model***: suggests that there was no single point of origin and that modern humans evolved in parallel in different parts of the globe. Interbreeding between these groups allowed the spread of desirable physical and behavioural features.
- ***Assimilation Model***: promotes Africa as a central point of origin but suggests that *Homo sapiens* gradually interbred with other 'archaic' human populations, like the Neanderthals, eventually superseding them.
- **Serial Founder Effect Model**: where modern human populations expand and diverge within Africa before migrating to Eurasia and the rest of the world.

Evidence from the Human Genome

The genome sequence of Clint, a male chimpanzee, was published in 2005. When Clint's DNA was compared to that of human DNA the following observations were made:

- There is a 96% alignment between the DNA of chimpanzees and humans
- The non-aligned regions consist mainly of insertions and deletions

- ❖ Divergence in chimp/human DNA appears to be greatest nearer the telomeres (near the tip) of the chromosome and least in the (X and Y) sex chromosomes.
- ❖ Of the 13 and a half orthologous proteins (descended from a single ancestor) produced by chimps and humans, 29% have identical sequences (See Cheng et al., 2005)

So, what makes us human? Comparative genomics informs us that humans and chimps have very similar genes and express almost identical proteins. The answer therefore lies within the *dynamics* of gene regulation and gene expression. The use of speech and language is confined to humans and therefore we ought to be able to identify this aspect within the respective genomes of chimps and human beings. Members of the 'KE' family within the UK have a severe motor and language processing disorder caused by a mutation in the FOXP2 gene. This gene is identical (save for two mutations) when compared with other primate sequences. However, the lack of speech and language in the KE family is caused by a mutation in this gene. But the missing factor is not simply a structural protein; it is a transcription factor that will alter the expression and sequencing of a host of subsequent genes. Likewise, higher mental functions are more prevalent in humans. Studies of psychological conditions including autism, schizophrenia and ADH (attention deficit disorder) all show evidence for a genetic component; perhaps research such as this may lead us to a better understanding of chimp and human conditions.

Genomic analysis has also been used to plot human migration patterns. Human mitochondrial DNA is passed down from the mother to her children through the cytoplasm in the ovum. Any paternal mDNA is selectively eliminated and so mitochondrial DNA is not subject to recombination and alters only through mutation. The mutation rate of mDNA is one mutation per 25 000 years (nuclear DNA mutates around 10 times more slowly due to its protective histones and repair mechanisms), and so a timescale for human divergence is afforded to geneticists.

Different mDNA sequences are associated with different human populations (African, Siberian, European, etc.) and groups of related sequences are called **haplogroups**. Beginning with haplogroup L1 in Africa, which is believed to be the oldest surviving **haplotype**, the dispersion of human populations can be estimated. Using this technique, following work by Peter Forster in 2004, we can see:

1. An expansion of the human population in Africa some 70 000 years ago.
2. The human population then moves out of Africa spreading along the coast of the Indian Ocean, reaching Australia around 30 000 years later.
3. Ten thousand years after that populations spread northwards (due to the warmer weather into India, the Mediterranean and Northern Europe).
4. Following the Ice Age (20 000 years ago) humans were forced south and spread into the Americas.

Corroboration of this (Out of Africa) model comes from an analysis of sounds used in more than 500 languages around the world. Languages in Africa, particularly Southwestern Africa, are more diverse and possess more sounds (phonemes) than

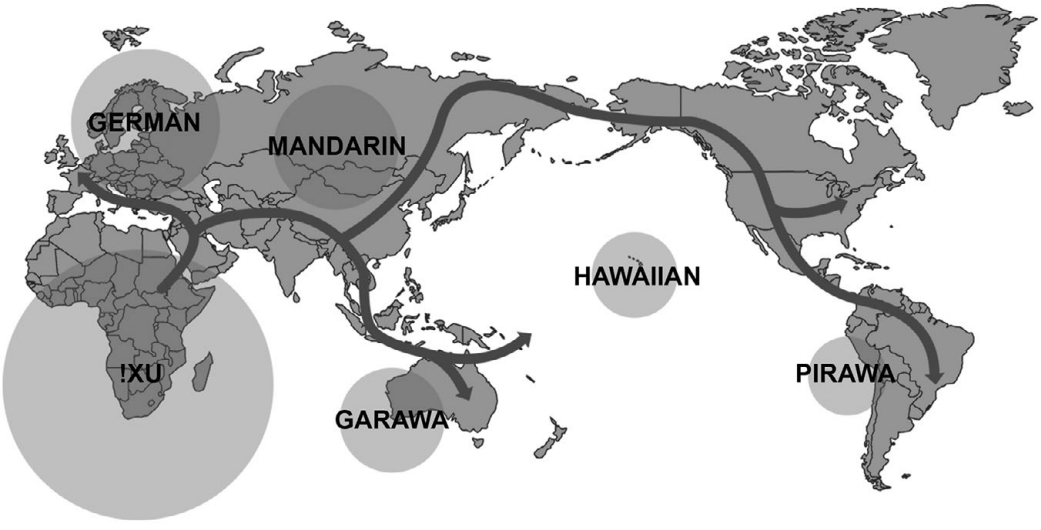


Figure 10.6 Patterns of language development following movement out of Africa.

other, more distant, languages. This pattern holds both regionally within the African subcontinent and globally (see Figure 10.6).

This model (the **Serial Founder Effect Model**) where modern human populations expand and diverge within Africa before migrating to Eurasia and the rest of the world is currently favoured by many geneticists.

Interestingly, different species of human beings overlapped both in space and time. *Homo habilis* and *Paranthropus boisei* inhabited the high African savannah at the same time. Similarly, *Homo erectus* and *Homo heidelbergensis* can be found in Western Europe together, and perhaps the story most familiar to us, modern man and Neanderthal man. Did these species coexist in non-overlapping ecological niches or did they interbreed? For the earlier hominids we are probably looking at the coexistence of two closely related primate species (like what is seen in South America today), but in the more recent hominids we see that Neanderthal man may have contributed DNA (4%) to modern humans possibly through interbreeding.

There is much discussion as to which of two scenarios took place following the decline of Neanderthal populations and expansion of *Homo sapiens*. The two main theories are:

- ***Replacement*** of the Neanderthal by modern man (perhaps a form of genocide or, more likely, due to climate change)
- ***Assimilation*** of Neanderthals into the *sapiens*' population through interbreeding (but recent, 2010, analyses of Neanderthal DNA show a 99.5% correspondence with that of modern humans, refuting the idea of interbreeding)

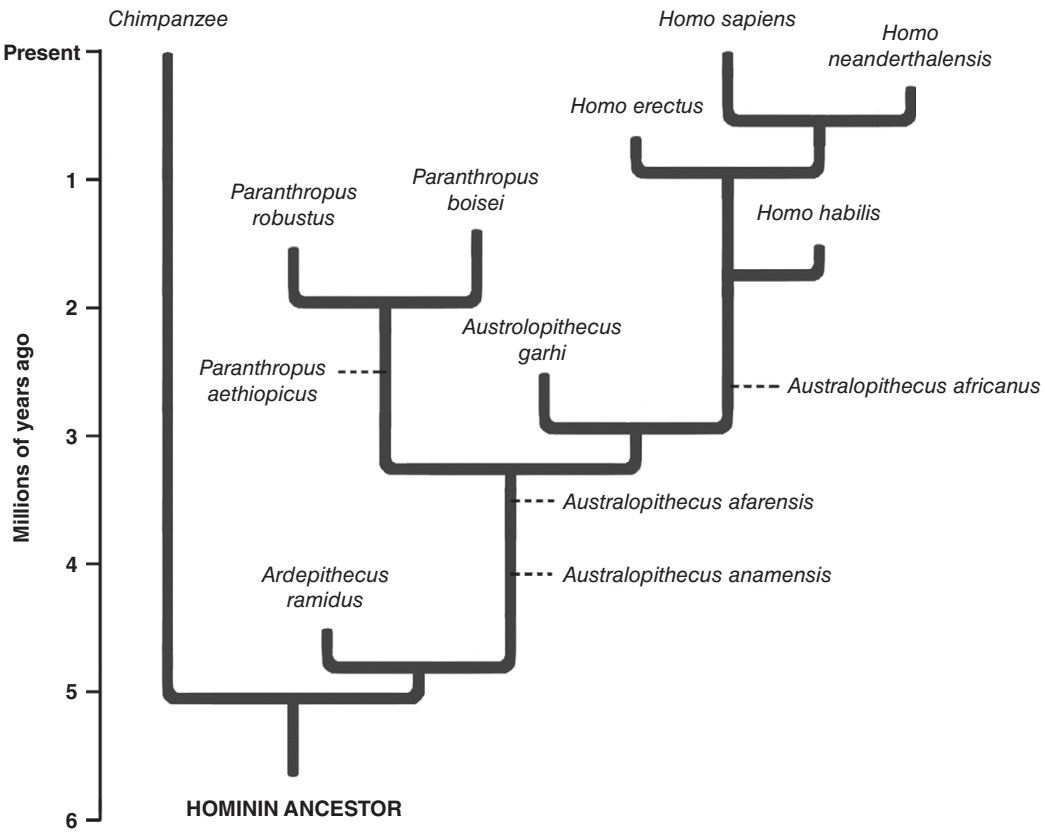


Figure 10.7 A proposed human lineage.

A proposed human evolution (over the past four million years or so) from *Australopithecus* to genus *Homo* is charted in Figure 10.7. The suggested evolutionary history is taken from fossil (or morphological) data and shows the four main clades: Ardipithecus, Australopithecus, the Paranthropus group and the *Homo* group.

Human Success

Homo sapiens, a relatively weak, hairless ape, seems an unlikely candidate to be one of the planet's dominant species. He (or she) has no sharp claws, big teeth or specialist skills. But evolution has provided *Homo sapiens* with features allowing this species to succeed to an unprecedented extent. Major characteristics of human evolution include:

- Large brains
- Walking and running on two legs

Table 10.2 Brain and body sizes of early hominids

	Body mass (kg)				
Species	**Male**	**Female**	**Brain weight (g)**	**Body mass dimorphism quotient (male/female mass)**	**Encephalisation quotient (a function of brain mass and body mass)**
Australopithecus afarensis	45	29	434	1.56	2.4
Paranthropus boisei	49	34	514	1.44	2.7
Homo habilis	37	32	601	1.16	3.6
Homo erectus	66	56	1 019	1.18	4.0
Homo heidelbergensis	77	56	1 156	1.37	4.2
Late *Homo neanderthalensis*	77	66	1 362	1.17	4.7
Homo sapiens	58	49	1 350	1.18	5.8

Adapted from McHenry (1992).

- ❖ Remodelling of the face (particularly the jaw and dentition)
- ❖ Reduced sexual dimorphism
- ❖ Key changes to family and social structure
- ❖ The evolution of language and culture

Humans have big brains. For instance, if the cerebral cortex (one of the 'higher' parts of the brain) were squashed flat, that of humans would occupy four A4 sheets of paper, a chimp's would cover one sheet, a monkey's a postcard and a rat's cerebral cortex would cover the area of a stamp!

Table 10.2 considers the body weight and brain mass of several early Hominids. Brain size has clearly increased over the past three and a half million years with a dramatic shift seen both in Neanderthal man and (especially) in modern man. A strong case can be made here for a genetic change allowing the development of language and culture. Males are larger than females, but the difference decreases markedly after the more robust australopithecines. Following puberty boys tend to grow faster and for longer than girls. But this difference may be exaggerated. Charles Darwin identified sexual selection as a reason for sexual dimorphism (differences between the sexes). In primates those living in groups with a dominant male (such as the silverback gorilla) tend to have males very much larger than females. This is seen in *Australopithecus afarensis* where it is believed that this species, like the modern apes, was **polygynous** (mating pattern where a male breeds with more than one female in a breeding season). In primates that are generally monogamous and live in pairs (such as gibbons and

tamarins) the size difference is nowhere near as accentuated. The reduction in size between human males and females appears then to correlate with closer pair bonding and general cooperative (and less competitive) behaviours.

The human brain is a relatively small organ, but at just under 1.5 kg it demands 20% of the body's metabolic energy. So why did this (energetically) expensive organ suddenly begin to grow bigger around 2.5 million years ago?

The ancestry of the mammalian/human brain probably starts around 65 million years ago following the disappearance of the dinosaurs. Until that point mammals were small shrew-like creatures feeding on insects attempting to compete with their more successful (and larger) reptilian neighbours. Computed tomography (CT) scans of the early mammals such as *Morganucodon* reveal that it was not so much an increase in brain size but *changes in brain regional anatomy* that contributed to their survival. Increases are seen in the size of the olfactory bulb (allowing a more acute sense of smell) together with increases in the neocortex part of the brain that maps tactile stimulation. These results fit in with the idea of mammals as small nocturnal creatures darting through the undergrowth at night avoiding the more visual dinosaur hunters. Following the demise of the dinosaurs our mammalian/primate ancestors probably took to the trees looking for food; and this is paralleled by an increase in the visual part of the neocortex. Living in groups proved a challenge for early primates. Robin Dunbar at Oxford has shown a strong correlation between the size (and interaction rate) of primate groups and the size of the frontal neocortex.

Increasing brain size (and corresponding increases in brain processing power) is seen in the primates ranging from lemurs to chimpanzee. But in the great apes, the gorillas, orang-utan and chimpanzee, the brains appear to have changed little. So, to restate our earlier question, why did this organ suddenly begin to grow bigger around 2.5 million years ago with the advent of 'the first people', *Homo habilis* and *Homo rudolfensis*? Traditionally it was thought that bipedalism somehow encouraged larger brains. But earlier hominids were bipedal beforehand without the corresponding brain/body ratios. More recent thinking describes a situation where changes in the jaw, particularly a reduction of the bite muscles, allows cranial expansion that was otherwise constraining brain growth. Allied to this, researchers note a more energy-rich meat diet together with evidence of stone tools for butchering and the cooking of food (allowing proto-humans to obtain more nutrients from their food). This together with a reduced gut provides more energy for this small but high-energy-consuming organ. Researchers at the University of St Andrews in the UK suggest that this complementarity between cultural and genetic change could provide a positive feedback leading to a 'runaway evolution' of specific traits.

Large, complex brains are undoubtedly linked with the success of modern humans. They allow a high degree of sensory processing in both the capture of a wide variety of foods and motor skills necessary for the dexterity of human limbs and digits. Humans are also social animals and a larger brain will aid the learned responses necessary to navigate the demands of large family and tribal groups. Learning and the development of language skills are also conditional on this level of complexity. Lastly, a large brain may aid mate selection. If females chose males based on their

cultural abilities as well as their hunting prowess, then mating success will also increase selection pressure for this trait.

Homo sapiens left Africa, for a second time, around 70 000 years ago. This time, armed with bigger brains and sharper cognitive abilities, they ensured the elimination of Neanderthal man and all other *Homo* species. In an unprecedented period of change 70 000–30 000 years ago, modern man settled throughout Europe, Asia and even Australia. They developed a sophisticated language and even the beginnings of an artistic predisposition – for instance, the Stadel cave carvings (e.g. the 'lion man') in Germany, which are estimated to be around 32 000 years old.

Additional features contributing to human evolutionary success include:

Bipedalism: Changes to trunk and hind limb morphology were a necessary genetic/developmental adaptation before hominids could walk upright. Early evolutionists such as Lamarck, Darwin and Haeckel predicted that bipedalism preceded the expansion of the brain. And this does, in fact, appear to be the case. In a computer-assisted simulation *Sahelanthropus* shows a foramen magnum below the cranium (therefore the neck is held upright) while *Australopithecus afarensis* shows pelvic, leg and foot morphology indicative of bipedalism. Interestingly, *Homo habilis* has a pelvic structure more suited to an upright gait than modern humans. This, in part, is due to our wider pelvis and the need to give birth to larger brained offspring. An evolutionary compromise perhaps?

There appear therefore to be two grade shifts in the evolution of the primate lower body (an **evolutionary grade** is a taxon or species group united by morphological or physiological similarity). The first of these, in the early hominids, is the transition from a quadrupedal, arboreal gait to a more bipedal one as evidenced by the australopithecines. The second evolutionary change was the development of wider, more human-like hips and longer legs in the genus *Homo*. These features combined with deeper and stronger hip joints permitted efficient striding, allowing early humans to travel further distances. Of particular importance is the Achilles tendon, which acts as a spring during running. This structure is absent in the great apes and provides modern humans with a 40% saving in metabolic energy during endurance running.

Hairless body: The consensus appears to be that lack of fur confers an advantage in a metabolically active animal in order to dissipate heat. The presence of sweat glands will similarly aid this process, while the hair on the head in humans helps to prevent solar overheating (protecting the metabolically active brain). In other mammals (elephant, mole rat, walrus) fur is absent again for thermoregulatory reasons (the elephant with a small surface area/volume ratio tends to overheat, the aquatic walrus swims better without dense fur and underground mammals are less subject to temperature fluctuation). A sexual selection argument has also been put forward; individuals are more attracted to hairless partners. This may result from the attractiveness of bare skin (healthy body, fewer parasites harboured), but this seems unlikely even though the shaving of beards and general removal of body hair is still a preoccupation of many *Homo sapiens*!

Language: Speech is an integral part of human culture. Modern man, it appears, is not the only hominid able to communicate in this way. When examining the bones of

Figure 10.8 Replica skull of *Paranthropus aethiopicus* showing large sagittal crest. Photo courtesy of Nrkpan, Wikimedia Commons

Neanderthals, holes are seen where nerves supplying the tongue, diaphragm and rib cage would have been suggesting that they too had an ability to speak. Neanderthals also share the human variant of the FOXP2 gene important in generating the finely controlled motor memories needed for speech. Most primates possess a large sac near the voice box to create a large booming sound. But fossilised remains indicate that this organ was lost by *Homo heidelbergensis* when this hominid reached Europe around 600 000 years ago.

Diet: Australopithecines such as Lucy have a conical shaped rib cage, narrower at the top and broadening out at the base. This feature is like that seen in great apes such as gorillas who have a primarily herbivorous diet. The large base to the thorax accommodates the additional intestines needed for plant digestion. *Homo erectus*, on the other hand, has a more barrel-shaped thorax. Along with the development of stone tools and possible use of fire, this suggests an omnivorous, though predominantly meat, diet; one rich in fats and therefore calories to supply the demands both of the back and leg muscles and the brain.

Other features of the skull also indicate a switch from tough plant food to meat eating. A large sagittal crest on the crown of ape (and early hominid) skulls indicates large jaw muscles necessary for chewing tough food material (see Figure 10.8). It has also been suggested that the large eyebrow ridges were an adaptation to re-direct the stresses of these very large jaw muscles. The switch to a more omnivorous diet is also seen in the smaller molar teeth of later hominids.

Human Cultural Evolution

Homo sapiens and our immediate ancestors rapidly developed a wide range of activities that freed them from many of the rigours of everyday life. Cooperative behaviour and stone tools aided hunting, development of fire helped with cooking and

Table 10.3 A comparison of biological and cultural evolution

	Biological evolution	**Cultural evolution**
Replicator	Gene (DNA molecule)	Meme (ideas & beliefs)
Mechanism of inheritance	Biological reproduction	Imitation and social learning
Transmission	Vertical	Vertical and Horizontal
Diffusion patterns	Preservational	Motivational, cognitive and preservational
Rate of evolution	Slow	Fast – variable
Error rate	Low	Variable
Appearance	All life forms	Only those with complex learned behaviours

domestication of animals and plants led to settled agricultural societies. Production of clothing finally allowed early man to be independent of the environment and finally language, art and an aesthetic sensibility helped *Homo sapiens* become what we now think of as truly human.

In exploring the possibilities of other kinds of evolution Richard Dawkins, an Oxford evolutionary biologist, considered cultural evolution – changing fashion, songs, hairstyles, myths, etc. that can be transmitted both within and between generations. He coined the term **meme** in his book *The Selfish Gene* (1976) to describe such a unit of **cultural evolution;** to contrast with gene, a unit of genetic or biological evolution (see Table 10.3 for a comparison). A meme, Dawkins argues, exists in a **meme pool** where it has survival value ('resulting from its great psychological appeal') and can be transmitted both vertically (**vertical transmission**: from parents to offspring) and horizontally (**horizontal transmission**: between peers within the same generation). Dawkins also suggests that memes, like genes, are replicators and able (through imitation) to produce copies in different individuals and change over time. That is memes 'power' cultural evolution in the same way that genes control biological evolution.

But memes are ideas or concepts; they are the *products* of an organism's physical body, its genotype and phenotype. A distinction needs to be made therefore between the idea and the conditions needed to create and transmit this idea. A central nervous system, for example, is necessary to transmit and receive such 'memetic' information. The ability to propagate a cultural trait can be seen as a product of natural selection and an adaptationist view of gene/culture coevolution has been championed by several authors.

However, there are several criticisms of the meme concept:

- ❖ It has little explanatory power, merely describing an old idea in a new way
- ❖ The underlying psychological mechanisms are not well understood
- ❖ There are difficulties with an operational definition (is the whole movie a meme or simply a scene from the movie?)
- ❖ Memes have a non-digital nature therefore difficult to quantify

- There is a general lack of fidelity (think of the child's game 'Chinese whispers' where a statement is corrupted the more it is retold)

The idea of memes has proved popular, but its true impact is as yet undecided.

Parallels have been drawn between cultural and biological evolution with Charles Darwin himself demonstrating resemblances between the evolution of human languages and the evolution of animal and plant types. Both show homologies as the result of common descent, both change over time, both have replicators (genes and memes) and both can go extinct. Social learning (particularly imitation) provides a rapid transfer of information. An example is provided by a colony of macaque monkeys on Koshima Island in Japan who were regularly supplied with sweet potatoes. Unfortunately, these were often covered with sand. One day in 1953 a female monkey called Imo was noticed taking sand-covered potatoes to a stream and washing them. This innovative behaviour then spread within the immediate group and further afield suggesting a form of imitative social learning. Although there are alternative explanations (young monkeys have a predisposition to play with objects in water/the uptake seems too slow for trial and error learning), these Japanese macaques demonstrated a cultural change that was both adaptive and had a degree of permanence.

Are We Still Evolving?

It is said that cells are the libraries of the body. And nowhere is this truer than the 30 trillion or so cells of *Homo sapiens*. For within these microscopic structures is a repository of information concerning both our past, our present and maybe even our future?

Recent evidence suggests that humans are continuing to change. We are becoming taller and more obese. So, are we still evolving?

Regarding human height, our genetic (particularly polygenic) inheritance has led to a marked variation in body stature. The smallest humans are probably that of the Mbuti tribe in the Congo (1.37 m), while the Dutch (1.84 m) are thought to be the tallest. Similarly, our feet are very variable with barefoot peoples having a broader foot and more even pressure distribution than shoe-wearing individuals. Both body height and foot shape are the result of **gene/environment interactions**. In the case of human height, genetic factors account for 80% of the variation and environmental factors (diet, etc.) account for the remaining 20%.

But from studies in Finland, it seems clear that humans have the *potential* to evolve. In the Finnish study human reproductive fitness (surviving offspring) was measured from church records and the conclusion is that there is sufficient variation on which selection could operate (Courtiol et al., 2012). Another US study of Mormon families demonstrated that the number of marriages per individual (Mormons are polygamous) again strongly influences male fitness. Thus, human reproductive potential (fitness) is variable and subject to a variety of selection pressures. Selection through resistance to disease or preference for increased parenting skills could therefore still operate in these societies.

Other changes in human anatomy have been well documented:

- An average fall in bone strength of 20% between 2 million and 500 000 years ago, particularly in the arms
- A 50% increase in cranial bone thickness in women over the last 100 years; thought to correlate with raised oestrogen levels
- Increasing incidence of spina bifida occulta (a milder and often unnoticed form of spina bifida) over the past 1500 years
- The median artery in the arm is found in the embryo but generally disappears around the eighth week of pregnancy; an increasing number of adults now possess this artery (10% in the early 1900s to 30% at the end of the century)

Charles Darwin made only brief reference to human evolution in his penultimate paragraph of *Origin of Species*: 'In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation that of the necessary acquirement of each mental power and capacity by gradation. *Light will be thrown on the origin of man and his history*' (my italics). He was understandably nervous about dealing with human evolution in *Origin of Species*, but the evolution of man, problematic though it was, was to be covered by Darwin in three subsequent books: *The Descent of Man*, *Selection in Relation to Se*x and *The Expression of Emotions*. In the event only two books were published:

- *The Descent of Man, and Selection in Relation to Sex* (Charles Darwin, 1871). The two original books are here conflated and represented by Parts I and II. The Descent of Man (Part I) was a natural consequence of the argument for evolution put forward in *Origin*, while Sexual Selection (Part II) was an important theory necessary to understand descent in man and other animals.
- *The Expression of Emotions in Man and Animals* (Charles Darwin, 1872). Emotions and their expression are treated as the product of evolution, a very modern approach recognised by both psychologists and ethologists in the 1960s.

In answer to the question posed at the beginning of this section, 'are we still evolving?', human anatomies and physiologies are indeed continuing to change. And with a genome of around 3 billion nucleotides, variation continues at the molecular level as well.

Natural selection (the differential reproduction of genetic variants) also continues. Differential mortality (especially postnatal mortality) is declining while fertility stays roughly the same (an apparent decline in fertility in industrialised Western countries may be offset by an increased opportunity for selection in smaller families). But selection pressures are still operating despite improved diet and health care.

Part of the *process* of change is that of adaptation. Humans are distinctive in that they exhibit not only *biological adaptation* but also *cultural adaptation*. They do not just adapt to environments by means of natural selection on populations, they also alter the environment to suit their own genomes! And cultural inheritance linked with the speed of cultural adaptation makes this final phenomenon of supreme significance in future human evolution.

11 Trends and Patterns in Evolution

The work of Richard Fortey and others at the Natural History Museum, London has described changes in morphology of the *Trilobita* (an extinct but successful marine arthropod) from the oceans of the Cambrian to their extinction in the Permian around 300 million years later. Trilobites show great diversity in form. In general, trilobites had a flattened and tri-lobed (that is three-part) segmented body. They are often regarded as a **stem group** with a versatile body plan; they have radiated from a common ancestor to form present arthropod groups such as the chelicerates and crustaceans. From studying more than 4000 known species of trilobite clear *patterns* are detected within the different lineages:

- ❖ Loss of surface features (an adaptation to a burrowing lifestyle)
- ❖ Increasing spinosity (a defensive feature?)
- ❖ Reduction in body size (an adaptation to available marine microhabitats)
- ❖ Loss of eyes (an adaptation to dark benthic environments)
- ❖ Streamlined body shape and development of large eyes (an adaptation to a free-swimming, pelagic environment)
- ❖ Pitted fringes (an adaptation to filter feeding)

Trends in trilobite evolution therefore include:

- ❖ Loss of eyes (an adaptation for life on the murky seabeds) but also development of large eyes in free-swimming pelagic species
- ❖ Effacement (or loss of surface features, perhaps an adaptation to burrowing)
- ❖ Miniaturisation (to occupy the many microhabitats)
- ❖ Increasing spinosity (partly for defence and partly to assist movement on a muddy substrate)
- ❖ A thin exoskeleton (for life in low-oxygen conditions)

Such *trends* as these come about through normal genetic processes combined with habitat change, an increase in atmospheric oxygen, development of nutrient-rich soils or muds or the appearance of large predators. Small-scale processes are sometimes referred to as microevolution, while the long-term, larger scale implications for planetary life can be described as a macroevolution.

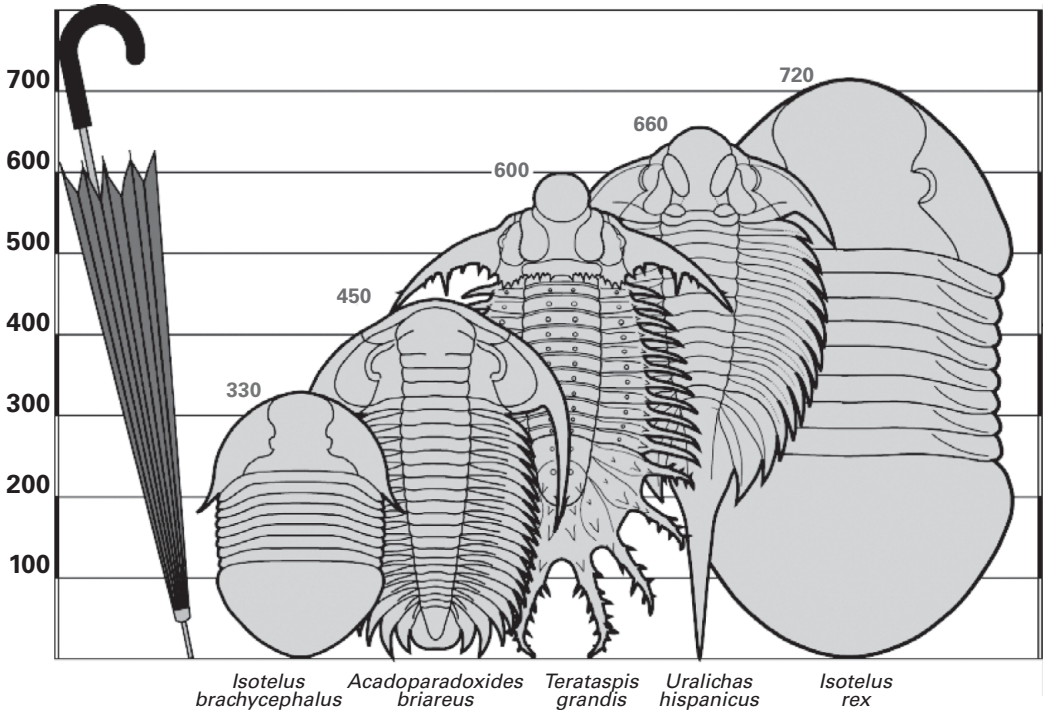


Figure 11.1 A size comparison of fossil trilobites.

Rates of Evolution

The modern synthesis at the beginning of the twentieth century proposed the principle of **gradualism** to describe the process of evolution. Evolutionary change, it was proposed, is slow and incremental. Changes from toes to hooves in horses, sepals to petals in plants or simple eyes to compound eyes in vertebrates is achieved by natural selection, little by little over long periods of time.

It is often thought that large-scale (macro) evolutionary processes follow on naturally from small-scale (micro) activities. In the accepted Darwinian view, evolution proceeds through a series of small genetic changes gradually leading to a change in the phenotype and the eventual formation of new species. However, when we look at living organisms, there is a paradox. One argument suggests that evidence of gradual change is rarely seen. Different species of bird, mammal or tree are very individual. There may be no intermediates or gradation between types. Can gradualism therefore help explain current taxonomies with their gaps and discontinuities between major taxa?

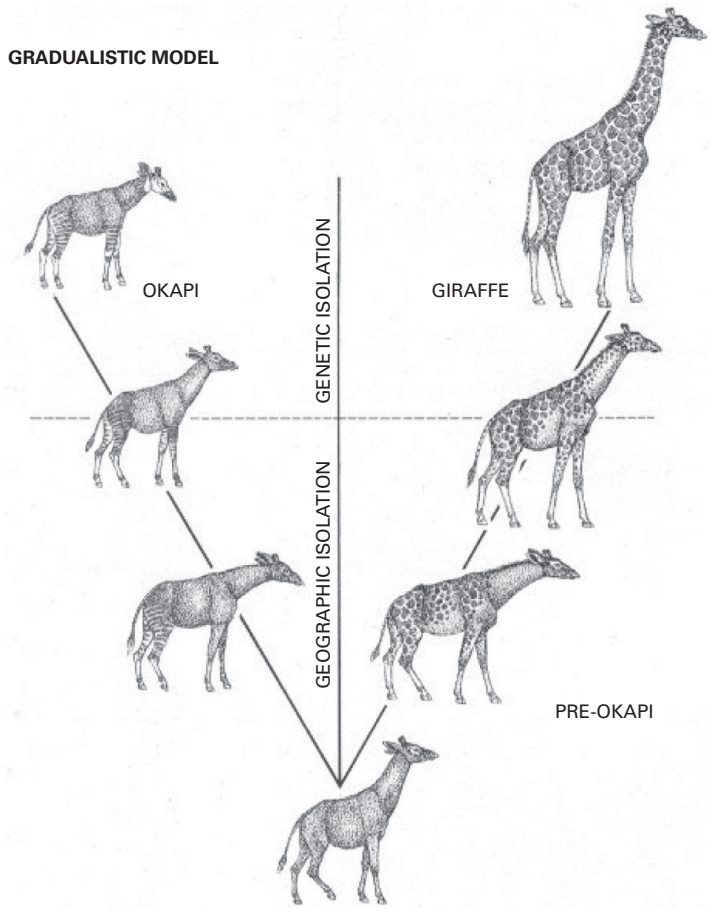


Figure 11.2 Gradual evolutionary change in the giraffe. In the giraffe, it is proposed that a natural variation in morphology accompanied by selection either for feeding (tops of tall trees) or fighting (there is a pronounced sexual dimorphism between males and females) led to a gradual evolution in height and in neck length. Recent research within an extinct species suggests that the C3 cervical neck vertebra elongated in two stages, first the front portion and then the back portion.

Gradualism is certainly seen in nature. Antibiotic resistance in bacteria, heavy metal tolerance in plants and warfarin resistance in rats are all examples of gradual evolution-in-action. A transition both in genotype and phenotype is seen between generations leading ultimately to new forms of organism (see Figure 11.2). Gradual evolutionary change is also seen in the process of artificial selection, for example, the human domestication of animals and plants. Charles Darwin dealt with the morphological changes caused by domestication of pigeons, and recent studies have shown that measurable changes need about 30 generations after domestication before they appear. The fossil record also records further examples of gradual evolutionary change, for example in the evolution of the horse, the giraffe or brachiopod molluscs.

One question that has not been adequately answered yet is that concerning a 'constant rate gradualism'. Several authorities (such as Richard Dawkins) propose that 'gradualism' is an umbrella term covering a range of gradualist approaches.

Several additional theories have been proposed to explain patterns of major evolutionary change, these include *non-Darwinian* mechanisms such as:

- Orthogenesis (innate tendencies within lineages to evolve in a specific way; evolution is severed from the process of natural selection)
- Autogenesis (new features emerge through internal drives rather than natural selection)
- Lamarckian mechanisms (the inheritance of acquired characters, divorcing DNA from participating in the formation of the phenotype)

But these non-Darwinian mechanisms are generally not recognised by evolutionary biologists (though some elements are making a reappearance). This chapter will examine competing theories through an examination of evolutionary rates and developmental change.

Measuring Rates of Evolutionary Change

Animal and plant 'survivors', sometimes also called 'living fossils' (individual species almost unchanged throughout evolutionary time) are a testament to the temporal tenacity of species supremely well adapted to their environment. They are also fortunate not to befall biological or geological catastrophe. In his book *Survivors* (2011), Richard Fortey eloquently describes encounters with such animals and plants. These include horseshoe crabs, velvet worms, extremophile bacteria and *Huperzia* (a Lycopod plant originating in the Silurian some 440 million years ago). The reasons for their survival seem to be a mixture of relative insignificance and good luck. Indeed, as Fortey states, 'The inescapable truth is that luck for old timers will eventually run out. It always does.' (Fortey: p. 301).

Long-term, evolutionary survivorship can also be the result of a stabilising selection (see Chapter 4) where natural selection sculpts the gene pool in such a way that extremes are eliminated and the 'average' is promoted. Sluggish rates of evolution tend to be the result of such a stabilising selection, preserving the status quo regarding the gene pool.

Rapid evolutionary change, on the other hand, appears to be correlated with periods of intense adaptive radiation, colonisation within new environmental niches or powerful directional selection. Rapid biological change is common in (human-mediated) artificial selection of traits. The multiple varieties of domestic dog or an edible plant such as the brassicas illustrate the potential for biological change. The wild cabbage, *Brassica oleracea*, is native to southern and western Europe growing mainly on coastal cliffs. Probably brought to the UK by Roman soldiers (the plant was commonly found in their gardens) this leafy vegetable has been significantly altered both in taste (generally much milder) and in form ('leafier'). Selective breeding has resulted

in present-day broccolis, cabbages, cauliflowers and brussels sprouts over around a few hundred generations.

A more spectacular example perhaps of rapid biological change is the Siberian silver fox. In soviet Russia Dr Dmitry Belyaev was looking at the rapid inheritance of domestic traits hoping to gain insight into the domestication of the domestic dog from its ancestor the wolf. Belyaev had founded the Institute of Cytology and Genetics in Novosibirsk in 1959 and selected the Siberian silver fox as his model to explore the process of domestication. He hoped to select for docility or tameness using the inherent variation in this animal. At first, he divided the animals into three groups only breeding from those who showed relatively little fear of humans (by offering food and stroking the pups). After only six generations, he had to create a fourth category for the 'elite' or super-tame animals. After only 10 generations, 18% of fox cubs belonged to this elite group, and after 30 generations, 35% were found to be super-tame. An added interest from this long-term study (over 40 years) is that not only did the fox behaviour change, but their morphology changed too. Changes in coat colour, floppy ears (instead of the fox-like pointed ears) and tails held up (instead of the downward bush of foxes) led to the remarkable conclusion that the foxes were looking more like dogs! These animals were not turning into dogs of course, but it does look like that domestication of behaviour also carries with it physical change. We know this now to be an example of **pleiotropy** (the effects of a gene on more than one phenotypic trait)

There are several methods for measuring the rate or speed of evolutionary change. Perhaps the most obvious is simply dating the rocks in which fossil evidence is found. Alternatively, the 'coalescence method' uses the fixed rate of molecular change, the so-called molecular clock. Firstly, the age of the common ancestor is determined using palaeontological methods, and, secondly, the divergence between their respective DNAs is measured. So, if there is let's say a 2% difference in the DNA between species A and B and it is calculated that the common ancestor first lived 10 million years ago, then the rate of evolution is 2% over 10 million years or 0.2% per million years. Another measure of evolutionary rate is a unit called the **darwin**. Proposed by Haldane in the late 1940s, the darwin uses the natural logarithm of the character change. Thus, rapidly evolving types such as house sparrows introduced into North America change their skeletal dimensions at a rate of around 200 darwins, while studies of horse molar teeth yield values of 40 millidarwins.

The term **assisted (or human-assisted) evolution** refers to a variety of strategies and interventions that enable an accelerating rate of natural evolution. This may be contrasted with selective breeding where organisms are deliberately encouraged to breed with those of a desired genotype. One example of assisted evolution is the use of thermally resistant corals to repopulate coral reefs in tropical seas in order to counteract the effects of climate change and coral bleaching. By actively selecting heat-resistant corals and use of 'nurseries' to grow them, it is hoped to assist the natural gene flow and the spread of heat-resistant corals across the reef (Dixon et al., 2015).

In many fossil lineages there appear to exist long periods of inactivity or stasis punctuated by periods of rapid evolutionary change. This phenomenon describes the

typical 'evolutionary tree' with ancestral types remaining for millions of years in the fossil record and then branching to form new types. We can account for periods of stasis and the sudden appearance of new forms by looking at types of speciation. We have seen that two basic modes of speciation are used to describe interrupted gene flow among populations: allopatric speciation (allos = other, patria = homeland) where geographical isolation disrupts gene flow between individuals and sympatric speciation (sym = together, patria = homeland) where individuals remain together but other factors such as non-random mating may cause speciation to occur. By applying the allopatric model of speciation, we might envision a splinter population extending its geographical range and suddenly appearing in the fossil record either alongside the ancestral species or sometime later. Thereafter a period of stasis ensues as the new form exploits its new home free from adverse selection pressures.

Stephen Jay Gould, Harvard Professor, was 'deeply troubled by the Darwinian convention that attributed all non-gradualist appearances to imperfections of the geological record' (*The Structure of Evolutionary Theory*, Gould, 2002: p. 38). The anticipated evolutionary sequence, he argued, rarely materialised in the phylogenetic record looking either at past or present-day forms. And so, Gould, together with colleague Niles Eldredge, devised the theory of **punctuated equilibrium** (see Figure 11.3). They argued that coadapted gene pools resist genetic change and that the shift from one adaptational form to another is stimulated by the destabilising effect of small population size. The genetic effects of small population size (the **founder effect**) are of course well known. A small population derived from a larger group may well possess alleles with frequencies that differ markedly from the parental stock. This is purely a chance event, but its effects can be very dramatic, shifting the gene pool in one or more directions. For example, new human populations can differ markedly from ancestral groups. The Afrikaan peoples of South Africa and the French in Canada have genetic disorders in frequencies very different from those of the original, European, population. In a similar manner, if a catastrophe occurs that wipes out most of a population, then the survivors will possess a gene pool that is not necessarily representative of the original. Such a **genetic bottleneck** (where the population declines and then re-establishes itself) was seen in the UK in the 1960s with the decline in the kingfisher population and in the 1970s with a decline in ladybird numbers. Indeed, it has been estimated that in one day in July during that decade more than 23 million seven-spot ladybirds were washed up on the south coast of England!

Punctuated equilibrium, therefore, represents an alternative to the traditional gradualist approach. Gould and Eldredge argued that the fossil record does indeed support the hypothesis of small, isolated populations forming new species relatively rapidly (in geological terms) because of strong selection and rapid change. Once formed, and once large enough, a sort of evolutionary inertia will set in resulting in very little evolutionary change – a prolonged period of **stasis**.

There have been arguments both for and against punctuated equilibrium. Gradualists have reported that stasis is merely an illusion; that change is still happening but not in ways that can be detected in the fossil record. Population geneticists argue that the founder effect is ineffective in shifting gene pools to such a degree and that the

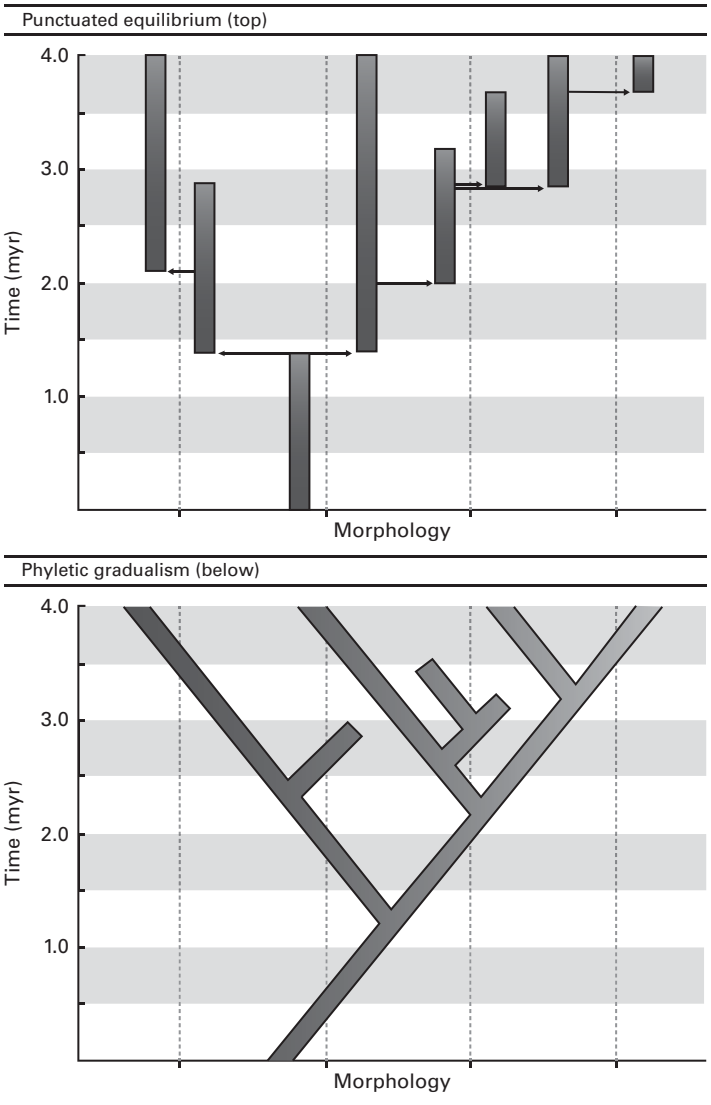


Figure 11.3 A comparison of gradualism and punctuated equilibrium in a hypothetical population.

resultant gene flow is not sufficient to counteract selection. Stasis though does seem to be a fact in both fossil and living forms. Having evolved a new morphology or biochemistry, organisms will stick with this genetically determined phenotype despite obvious environmental change. Stabilising selection can explain stasis but only if the environment remains constant. In a changing environment Richard Lewontin (1929–present) has postulated that organisms possess the ability to change their microhabitats thereby buffering themselves from changes around them.

Data can be used to support both positions.

Punctuated equilibrium, it must be stressed, does not suggest that natural selection is ineffective nor that other evolutionary processes may be operating at the same time. The hypothesis simply suggests that evolution can occur in short bursts.

Extinction and Patterns of Mass Extinction

Extinction occurs when a group or species disappears, and no living relatives remain. The current diversity of life therefore reflects the many periods of extinction and speciation in the Earth's history. At some time in the fossil record a taxonomic group proliferates – this period is referred to as a ***radiation*** (for example an increase in the different kinds of mammals 50 million years ago). At other times taxonomic diversity decreases as a period of extinction begins. We must be careful, however, not to label forms as extinct simply because a palaeontologist takes a view that a lineage has changed sufficiently to be called a new species and the old forms no longer exist. The term **pseudoextinction** is used to describe the process where a lineage evolves, and the new forms are described as a separate (new) species even though a continuous breeding line still exists. In other words, species one merges into species two, the point of separation representing the pseudoextinction of species one.

The knowledge that organisms become extinct is quite a recent event in human history. Early eighteenth- and nineteenth-century naturalists had difficulty reconciling the fossil evidence with their own, often religious, convictions on the nature of Life, and several theories were proposed to explain away extinction and the subsequent absence of fossil forms:

- Extinct animals and plants are the result of some great catastrophe like the biblical flood
- Species are not extinct but merely 'hidden' in some inaccessible location
- Although organisms may change in outward appearance they retain their 'essence' and are in fact one and the same species
- Removal of animal and plant forms from the planet is solely the result of human activity
- Fossils are simply 'pictures' in rocks introduced deliberately, maybe even capriciously, by a supernatural being (not the result of extinction!)

Lamarck denied that true extinction (that is a termination of lineage) could occur. Rather, he argued that change of outward appearance took an inevitable ordered and logical sequence. Organisms, it was thought, did not evolve to match the changing environment. Evolution was therefore an alternative to extinction; life existed as one great continuum. Charles Darwin of course embraced extinction as a component of natural selection. But Darwin himself faced a conundrum. On the one hand, natural selection favours extreme variants, but if we take this to its logical conclusion, each species might exist only as one individual! He answered this problem with two declarations, firstly that the environment itself would restrain diversification by imposing ecological limits (numbers of available niches, etc.), and secondly small

populations, he argued, are more prone to extinction and this would thus serve to regulate diversification.

Georges Cuvier (1769–1832) was a French comparative anatomist studying both living and fossil forms. He provided definitive evidence for extinctions of species; for instance, he described the giant sloth, *Megatherium*, from Paraguay classifying this large mammal and arguing that, along with fossil elephants, such megafauna no longer existed. To Cuvier there were only two alternatives to extinction, migration (unlikely as there was no evidence) or the transmutation of forms (he disagreed with this Lamarckian proposition). The abrupt disappearance of fauna was also observed in Cuvier's exploration of the strata of the Paris basin (one of the first attempts at biostratigraphy). Although rejecting the modification (or evolution) of species, Cuvier's early work his *Essay on the Theory of the Earth* published in 1813 established two important points (Cuvier, 1829):

- That Aristotle's Great Chain of Being (the linear sequence of animals and plants) was highly improbable as it did not fit with his observed schemes of classification.
- Extinction and speciation were real events though not in the Darwinian sense; Cuvier believed that great catastrophes (floods, etc.) affected the past Earth removing some species and allowing in others (though he did not say where these came from).

There is a difficulty in studying the reasons for individual species extinctions. Evidence may be reasonably obvious such as flooding or an advancing ice sheet, but despite the prevalence of extinction little is known about its causes. What we do know is that population extinction will occur if mortality (death rate) exceeds natality (birth rate). Factors affecting the probability of extinction include the following:

- *population size* (small populations are more vulnerable)
- *longevity* (short-lived individuals have less time to recover)
- *fecundity* (or the fertility of an organism; recovery is very slow in populations that have a low intrinsic rate of increase, the young are produced at lengthy intervals, they take a long time to develop, etc.)
- *body size* (longevity appears to be directly proportional and fecundity inversely proportional to body size)
- *environment* (a fluctuating environment promotes extinction)

Given the difficulties with individual species, biologists have found it more profitable to study large-scale (or mass) extinctions.

Quite different from the continuing and steady extinction of individual species (the **background extinction rate** averages something like 2.5 species per year) is the mass extinction of a significant part of the Earth's biota. **Mass extinctions** are generally due to physical causes operating on a global scale. Plate tectonics, igneous (volcanic) activity and failures of ocean and atmospheric circulations have all been put forward as possible causes. Even extraterrestrial impacts (comets, meteorites, etc.) have been implicated.

As a rule, mass extinctions are global calamities of (relatively) brief duration. The most famous of these is probably the ***K-T event*** 65 million years ago. So called

because it occurs on the Cretaceous/Triassic boundary ('die Kreidezeit', or 'chalk era' translates as 'Cretaceous' in German). This event wiped out the dinosaurs, ammonites and many of the flowering plants. Around the world, rock strata from this period show a thin layer of sediment rich in a rare element, iridium (rare in the Earth's crust but common in asteroids), suggesting asteroid impact. Theories of an extraterrestrial cause of extinctions have been around for hundreds of years, but it was Walter Alvarez, son of Nobel-prize-winning Luis Alvarez (1940 – present), who provided a sufficient evidence base. In 1980 Walter Alvarez, his father and chemists Frank Asaro and Helen Michel put forward a theory published in the journal *Science*. Essentially, they (i) gathered evidence of an asteroid impact at this time, (ii) established the coincidence of the demise of many marine and terrestrial organisms (the removal of over 75% of large organisms over 25 kg) and (iii) put forward a theory including large impact/dust cloud/'nuclear winter'. The **impact hypothesis** was further strengthened in 1990 by the discovery of the massive (180 km wide) Chicxulub crater in New Mexico.

Five prominent mass extinctions have been recognised:

1. ***The Ordovician Extinction***: Found at the end of the Ordovician period and closely associated with major climatic change. Correlates with the beginning of an Ice Age. As most life was in the sea, it was marine creatures such as trilobites, brachiopods and graptolites that were drastically reduced in number.
2. ***The Late Devonian Mass Extinction***: A major worldwide extinction of life in the shallow seas and coral reefs. Iridium anomalies and 'shocked' quartz crystals indicate an extraterrestrial impact. It is thought that three-quarters of all life on Earth may have died out (probably through a series of extinctions).
3. ***The Permian Mass Extinction***: At the end of the Permian, the largest of all mass extinctions. Relatively rapid extinction episodes, particularly severe in the oceans (it is estimated 57% of all marine families and 95% of all marine species became extinct). Extinctions coincide with massive volcanic activity.
4. ***The Triassic–Jurassic Extinction***: Comprises two or three phases of extinction found at the Triassic/Jurassic boundary. A volcanic episode with basaltic floods reflects major tectonic plate activity. With a possible asteroid impact and climate change there is a large turnover of animal groups both on land and in the sea.
5. ***The Cretaceous (K-T) Extinction***: Extermination of the dinosaurs, ammonites and other groups are characteristic of this period. Possibly caused by an asteroid impact at the end of the Cretaceous (Chicxulub crater found in the Yucatan Peninsula in Central America) generating huge dust clouds and climate change. Opponents contend that continental drift and increased vulcanicity caused the observed changes.

Joseph Sepkowski Jr. (1948–1999) was a US palaeontologist who modelled changing biodiversity in marine faunas. Using factor analysis, he identified three great evolutionary faunas (Cambrian, Palaeozoic and Modern) characterised by both increase in biodiversity and mass extinction.

Figure 11.4 illustrates the 'Big 5' mass extinction events during Earth's geological period in which abundant life has existed (that is the Phanerozoic).

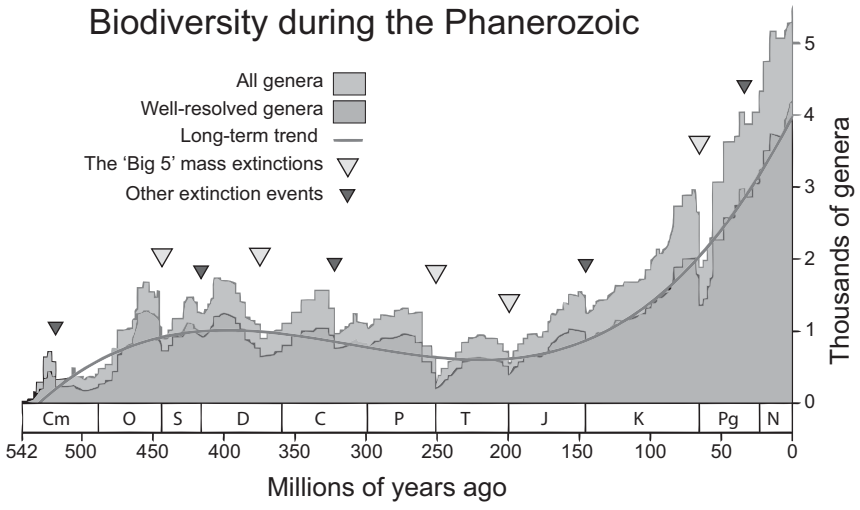


Figure 11.4 The Five Mass Extinctions as evidenced by reduction in biodiversity. Total numbers of genera are used to illustrate diversity (taken from Sepkowski's catalogue; cited by Rohde and Muller in letters to Nature, March 2005: Rohde and Muller, 2005). For genera to be 'well resolved' only those organisms with several occurrences and clear dating are used. The Big 5 extinctions correspond to the Ordovician, Late Devonian, Permian, Triassic–Jurassic and Cretaceous. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

Smaller mass extinctions are also recognised in the fossil record. For example, during the Pliocene period C3 grasses in North America were replaced by C4 grasses. C4 plants have a different kind of photosynthetic physiology allowing them to better survive arid conditions. A crucial factor for the evolution of the horse was the fact that C4 grasses contain more silica. The implication of this was that only those horse species with the longest teeth survived; the others became extinct.

With the present-day loss of biodiversity (some estimates put this at dozens of species becoming extinct every day – one thousand times the background rate) then maybe we are experiencing a sixth mass extinction; this time of **anthropogenic** (that is human) origin? Humanity's main impact is in landscape degradation. Some 'generalist' species will adapt and survive but many of the 'specialists', finding their habitat disappearing, will themselves disappear. At the recent (August 2016) International Geological Congress in Cape Town, a request was placed that we now designate the epoch that we are living in as the **Anthropocene**. Because of humanity's overwhelming impact on the planet (radioactive dispersal, plastic pollution and the prevalence of sheep and chickens!), it is suggested that we curtail the current epoch, the Holocene, and introduce this new, human-centric one. The increasing rate of species extinction over the past 220 years is illustrated in Figure 11.5.

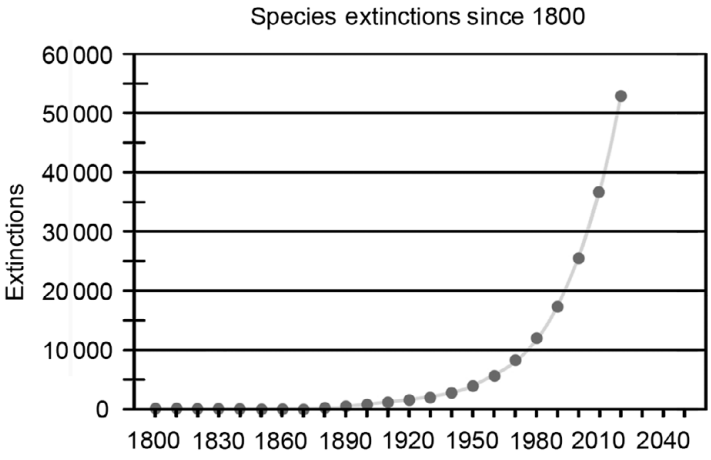


Figure 11.5 The ever-increasing rate of species extinction.

Heterochrony and Life History Strategies

In the nineteenth century Ernst Haeckel, a German biologist, proposed his 'Theory of Recapitulation', which stated that the evolutionary history of an organism could be discerned from its embryological development. The embryo was said to provide a window into how systems develop. Basic vertebrate evolution with tail, gills and tripartite brain can all apparently be seen in a study of human embryos (see Figure 2.4). A direct parallel is therefore drawn between **ontogeny** (development of an individual from zygote to maturity) and **phylogeny** (the evolutionary history of an organism). Modern biologists no longer adhere to Haeckel's Biogenetic Law that 'ontogeny recapitulates phylogeny'; nevertheless, a study of embryos can provide many clues about the ancestral condition and about homologies between related groups.

To Charles Darwin and modern biologists, the resemblance of species' embryos to one another is simply a matter of their having a ***common ancestor*** (plus the fact that embryo development is less likely to be affected by natural selection). Notwithstanding this, ideas of recapitulation persisted well into the 1930s.

The term **heterochrony** refers to an evolutionary change in the rate or timing of developmental events. Often this is seen in the growth rate of bodily structures. Much of evolution occurs this way, for example the dramatic increase in size of antlers of deer species culminating in the unfeasibly large antlers of the now extinct Irish elk. The shorter toes and greater webbing of the tree salamander compared with its ground-dwelling cousin probably arose from a heterochronic mutation affecting the regulatory gene controlling growth. By switching off the growth gene sooner, smaller feet were produced – a distinct advantage for an arboreal way of life.

Similarly, in ancient, mammal-like reptiles (the synapsids) relatively minor developmental shifts have led to significant morphological change. This sort of ***genetic amplification*** typifies macroevolution. The synapsids were the first **amniotes** (tetrapod vertebrates such as reptiles, birds and mammals) to colonise terrestrial habitats widely. During the late Carboniferous and for most of the Permian, they were the most abundant land vertebrate. Skeletal changes in these mammal-like ancestors resulted in a wide radiation of form running from animals such as the *pelycosaurs* (sail-backed, primitive synapsids) to the most advanced, mammal-like forms, the *therapsids*. Heterochronic, evolutionary change in the synapsids include:

- Increasing the size of the temporal fenestra (providing a larger and more powerful jaw)
- The lower temporal bar extending to form the zygomatic arch (indicates larger chewing muscles)
- The dentary or lower jaw is elongated so as to accommodate more teeth
- The dentition changed from homodont (teeth all the same) to heterodont (differentiated teeth)
- Development of a secondary palate allowing for breathing and chewing at the same time
- Limbs placed under the body (an upright posture or gait) provided a higher level of activity
- A calcaneum or heel provides greater leverage for fast starts
- An opposable big toe assisted with balance
- The loss of lower (lumbar) ribs suggesting the development of a diaphragm
- A shorter tail suggesting an upright posture

Heterochrony can affect both **somatic** (body tissue) and **germ** (reproductive cell) lines. If reproductive body development is speeded up, then sexually mature individuals are seen in juvenile bodies. This type of heterochrony is called **paedomorphosis**. Alternatively, acceleration of ordinary (non-reproductive) body development is termed **peramorphosis**. Paedomorphosis (or underdevelopment) is observed in the axolotl, a salamander that becomes sexually mature while retaining tadpole characteristics. This type of paedomorphosis is called **neoteny**. Peramorphosis (overdevelopment) is seen in a human condition called Cockayne syndrome where children are prematurely aged. Peramorphosis is also seen in the giant elk, mentioned earlier, where an extended period of growth developed antlers 12–13 feet across. Sexual selection provided the initial stimulus for such antler development, but a changing climate made the energy costs unfeasible – therefore this animal (technically a deer), ranging across much of Europe and Asia, became extinct at the end of the last Ice Age around 10 000 years ago.

In short, heterochrony affects development of body parts by altering the rates of growth or the duration of growth. Many of the changes we see in animals and plants reflect basic structures growing at different rates. In horse evolution the central digit grows faster than those either side (an adaptation to running at speed), while in salamanders (*Bolitoglossa*) tree-dwelling species have a foot much smaller and more

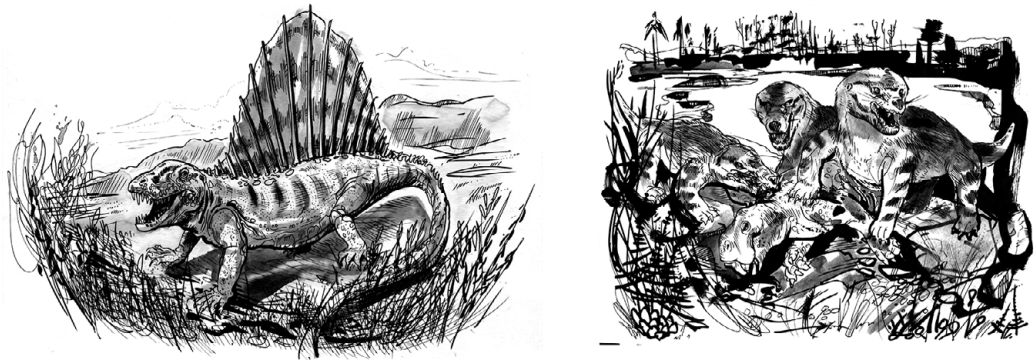


Figure 11.6 *Dimetrodon*, a sail-backed pelycosaurian, a primitive synapsid (left), and cynodont 'dog teeth' therapsid (right).

webbed than those species living on the ground (providing adhesive structures, an adaptation to clinging to smooth branches).

The evolution of life history strategies can also be directly related to the timing of developmental processes. For instance, why do some trees (such as the redwood, *Sequoia sempervirens*) produce over six million seeds in one year (with trees 250 years old possessing maximum seed viability); and how is optimum clutch size in birds reached? The consequences of these decisions, both in the ecology and evolution of organisms, is the province of **life history evolution**.

There is a diversity of life histories, the goal of which is to maximise survival and reproduction. Optimisation theory requires us to look at resource investment and explore how life histories are shaped by both nature (genes) and nurture (the environment). A Darwinian perspective might state that fitness is maximised if organisms reproduce as soon as they are born and continue to produce as many offspring as possible. But this scenario would lead to what Law (1979) calls 'Darwinian demons', organisms that would be so successful they would 'out-reproduce' all others. But of course, this does not happen. Resources are finite, and trade-offs occur. For instance, early reproduction in *Drosophila* has been shown to lead to a shorter lifespan; they are said to be genetically negatively coupled, and energy devoted say to food gathering (in small mammals) or courtship (in larger, more aggressive mammals) will lead to reduced fecundity. So, given the various constraints and trade-offs, life history evolution does not lead to maximisation; rather to a more realistic *optimisation* of available opportunities.

For example, the number of eggs laid by birds and the size of birds' eggs can be thought of as evolutionary compromises. Do you put all your efforts into one or two very large eggs (with presumably a better chance of survival) or many smaller eggs? And, given available resources, do you produce a clutch size as large as possible? The answer to both questions lies in a concept sometimes referred to as **phenotypic plasticity** where life history variation is influenced heavily by the environment. In a changeable environment it may be better to 'spread the cost' and produce smaller eggs, perhaps even more than one brood. Similarly, too large a clutch size may

compromise future breeding and so moderation (not maximisation) of egg number is required. This maxim may well be described as *optimisation not maximisation*.

These two tactics, the conservative ('let's not overdo things') and the maximum effort approach, have been described as 'r' and 'K' strategies. Popular in the 1970s and 1980s 'r' selection refers to those organisms investing in large numbers of offspring with little parental care (for example most fish, some mammals such as mice and many flowering plants), while 'K' strategists, such as primates, orchids and arctic terns, produce fewer offspring, larger body size and longer lifespans. The 'r' strategists follow their maximum *reproductive* capacity, while the K strategists possess a population fluctuating around their carrying capacity or *Kapazitätsgrenze* (capacity limit); hence the terms 'r' and 'K'. This approach is both practical and appealing but there are difficulties in obtaining experimental evidence (results, such as those with *Drosophila*, were contradictory). Disagreement between researchers (for instance in how to define **r/K selection**) eventually led to a decrease in its use. Alternative paradigms such as life history theory (which do not just simply rely on reproductive strategies) now dominate the argument.

Are Trends in Evolution Progressive?

'Progress' in evolution is a troublesome concept. Terms such as 'advancement' and 'complexity' are often used with the understanding that, as evolution proceeded, species became more able to exploit their environment and the lineage more 'advanced'. But we need to take especial care, however, when using the terms like 'primitive' and 'advanced'. Are we discussing evolutionary change in terms of 'progress' or 'improvement'? If so, this implies purpose and moves from being a scientific to a philosophical discussion. It is better to think in terms of complexity and derived characters (or synapomorphies).

The idea of progress may be considered a late Middle Ages invention where a study of theological texts gives rise to the idea of a narrative or history of mankind. The discovery of fossils, and the realisation that these were vestiges of the past, led to the view that living things are historical entities too. For those biologists who believed in evolutionary progress (Alfred Russel Wallace, Herbert Spencer, Pierre Teilhard de Chardin and Henri Bergson) progress was seen not only as change but also as improvement. Such a view also coincides with those of prominent philosophers, such as Hegel, Kant and Marx, that a benevolent providence was moving towards a 'perfection' on Earth.

The view that progress equates with improvement though has lost respectability among modern evolutionary biologists (Ruse, 1996). But evolutionary trends remain visible in the fossil record. There is movement from the seas onto land and there appears to be an increase both in diversity and organisational complexity. Francisco Ayala (1934–present) defined this sort of progress as a systematic change leading to improvement or efficiency in a feature, while Stephen J. Gould (1941–2002) suggested restricting the term to the notion of 'directionality'.

Perhaps a sensible compromise between accepting the physical evidence and the risk of teleological interpretation lies with Richard Dawkins. In his book *A Devil's Chaplain* (Dawkins, 2003), Dawkins considers that 'progressive increase in morphological complexity is to be expected' (p. 213) but only if we consider progress to be 'an accumulation of features contributing to adaptation'. For instance, if we discuss 'progress' in the evolution of the vertebrate eye (from simple eye cup to faceted compound eyes, to the vertebrate eye with its lens-and-retina system) we might define progress in very general ways using terms such as 'directional', accumulating and 'improved function'.

We can say that progress is evident in evolutionary biology but only if we specify the term in non-teleological ways (that is ***not*** geared towards an end goal or purpose). Only then can we start to make sense of evolutionary trends.

Biological Evolution As Science

One criticism of evolution, occasionally encountered, is that 'it is only a theory'. The term 'theory' may be confusing or misleading to some. And yes, this term has been used informally to mean conjecture, supposition or hypothesis; but in its *scientific sense* a theory is a set of guiding principles (e.g. psychological theories) or an explanation of natural phenomena supported by both reasoned and empirical evidence (e.g. kinetic theories). In other words:

a theory is a verified body of information.

Whatever the precise definition, a scientific theory is not a guess or a hypothesis. A theory is well established. Would we question the cell theory, the theory of gravity or Einstein's theory of relativity? The theory of evolution is incontrovertible, supported by over a century and a half of detailed research. So why should we accept the presumption that the theory of evolution is different from other theories? Insofar as it is difficult to *prove* anything (other than mathematical theorems), the theory of evolution provides our very best explanation of the processes leading to the inordinate diversity of life on Earth.

So, what makes a good scientific theory? First and foremost, it should be accurate – it should have an impeccable evidence base and fit the observed facts. It should be explanatory (not just describing but explaining the natural world) and it should also be predictive. And, perhaps more unusual but just as important, it should be simple. Science should not 'hide' behind obscurantism and jargon but should explain as simply as possible its main tenets (the term parsimony is often employed here).

In short, good science should embrace the following:

- *Reliability* (of the data sets used) and accuracy of the evidence base
- Use of a logical and rational *argument* developing from clear axioms
- Internal *coherence* (a clear line of argument)

- *Consistency*, both internal (no contradictions) and external (contrasting those with similar theories)
- Empirical *support* (practical observation if possible)
- *Tentative* (not dogmatic) and correctable (if shown to be wrong)
- *Authoritative* support from the scientific establishment (that is peer reviewed and peer approved)

The theory of evolution is a good scientific theory. It has amassed a vast collection of supporting data and has several explanatory mechanisms to support the (observed) data. Although only published around 150 years ago, Darwin's proposal that natural selection provides an acceptable mechanism for change still holds true. That is not to say that evolutionary theory does not have its critics. Belief in a deity and directed progression of life on Earth remains strong as does the view of special creation. But, in general, much of the professional criticism revolves around alternative *mechanisms* such as punctuated equilibrium and epigenetic inheritance.

There has also been confusion when discussing the 'nature of science' and what is popularly referred to as the 'scientific method'. The nature of science differs from the scientific method both in scale and in content:

- The scientific method concerns itself with developing testable hypotheses (the term 'testable hypothesis' is of course a tautology as a hypothesis is defined as being testable) and experimental methods with random sampling and control groups. There is not one but several scientific methods. The physicist will use different methods from the biochemist or the ecologist. In all cases, though the methodologies will be valid to the area under investigation, the methods are systematic and rigorous and the data reliable.
- The nature of science debate is much broader and all-encompassing; limits of science are discussed along with the caveat that scientists acknowledge the difficulty of an absolute truth (and so work within certain confidence limits). Science is acknowledged to be a social enterprise and a scientist is part of a larger community of scientists with concerns about ethics, transparency and sharing.

In summary, the theory of evolution through natural selection is good science:

- It is both consistent and coherent (an internal consistency) and even though there can be disagreement over which precise mechanism is operating at any one time, the basic features of common descent, lineage, selection and adaptation continually hold true. Neither does the theory of evolution contradict any of the other physical and chemical laws (it has therefore an external consistency as well).
- Evolution is both testable and predictive. Experimental evolution (generally with microbial cultures with short generation times) is well established, while predictions regarding gaps in the fossil record have generally been found to be correct.
- Evolution possesses a huge evidence base starting with the 'natural groupings' of Linnaeus, Darwin's voyage of the Beagle and Haeckel's embryological studies.

The wealth of fossil data in the world's museums and laboratories, Wegner's theory of continental drift (explaining biogeographies), Haldane's evolutionary genetics and Hamilton's work on kin selection again contribute. Lewontin's population genetics, Wilson's sociobiology and the theories of Dawkins and Gould can likewise be cited. The list could go on . . .

- ❖ Evolution is parsimonious. It is at heart a beautifully simple theory without unnecessary concepts or obscure and meaningless jargon. It is the most straightforward and reliable guide to the diversity of life on our planet.

12 Questions, Debate and Controversy

One hundred and fifty years ago debate began following publication of Charles Darwin's carefully articulated and well-evidenced theories. In 2011, a survey by Ipsos of 24 countries revealed that 41% of those polled declared that they were evolutionists, 28% creationists and 31% 'don't knows'. However, the concept of **intelligent design** has been put forward by some to introduce a supranatural intelligence (a 'designer') to the natural order and a scientific 'flavour' to the debate. In short, this idea states that the complexity of body parts (such as the cell flagellum) is irreducible and could not have arisen through gradual means. This movement arose from the creationist claims of the 1980s. We still need to argue the case for biological evolution, this topic remains socially divisive even today. Continuing scientific and public debate is the theme of this chapter.

Questions in Evolutionary Biology

Evolutionary theory has witnessed both continuity and change, tradition and innovation. Its story is by no means complete. Ernst Mayr (1904–2005) rather uniquely participated in several evolutionary movements – the early Darwinian paradigm, the Evolutionary (or Modern) synthesis of the 1940s and the genomic paradigm at the turn of the new millennium. In a personal reflection, Mayr states 'new research has one most encouraging message for the active evolutionist: it is that evolutionary biology is an endless frontier and there is still plenty to be discovered' (quoted by Wetherington, 2012: p. 146).

Some questions currently asked by evolutionary biologists include:

- Can we reconcile the mechanisms of microevolution to explain macroevolutionary patterns?
- Does evolution suggest an ethical code?
- Are there issues integrating gene transmission with the rest of biology?
- Is there a correct way to classify?
- Is there an emergent biology?
- Does the concept of the meme better help us understand cultural evolution?

Can We Reconcile the Mechanisms of Microevolution to Explain Macroevolutionary Patterns?

Micro and Macro evolution are terms which are thoroughly interlinked. So much so that several biologists prefer not to use them both for sound academic reasons (macroevolution is considered by many to be a consequence of gradual changes produced during microevolution) and also for reasons of utility (antievolutionists often use the terms as separate entities with specious arguments such as 'I can see how a dog might change into a slightly different dog but I don't see how a dog can turn into a cat'). However, the terms are valuable in asking how we move from small-scale ('micro') processes to the larger scale patterns of diversity we see today ('macro').

In philosophical terms, this is an epistemological question; that is, it looks at the origin and the types of (scientific) knowledge. And it appears that the question hinges on the definition of the higher taxa (phyla, classes, orders, etc.). On the one hand higher taxa are simply seen as an artificial construct, assemblages of distinct populations forming a hierarchical assembly. On the other hand, taxa are believed to be 'real' entities in that they operate as autonomous units of selection (a group selection idea). Although the question as to whether taxonomic hierarchies are 'real' or not has never been fully resolved, it is apparent that most biologists subscribe to the view that the patterns we see in nature are the result of an accumulation of microevolutionary processes.

Does Evolution Suggest an Ethical Code?

Forty years ago, following his treatise on sociobiology, E. O. Wilson stated 'the time has come for ethics to be removed temporarily from the hands of the philosophers and biologicized'. By this he meant that moral philosophers, although questioning human moral conduct, had never really asked questions about the origins of morals. A biological study of human ethics has used an evolutionary framework in looking at behavioural altruism (often explained by kin selection) and selection for group cooperation. These topics would loosely sit under the banner of descriptive evolutionary ethics as attempts are made to describe and explain specific behaviours. A more controversial area, however, lies in the realm of prescriptive evolutionary ethics where a biological focus is used to justify societal norms such as male-dominated groups and free-market economics.

Herbert Spencer (1820–1903) was an English philosopher and popular author producing major works on the 'Principles of Psychology', 'Principles of Education' and 'Ethics and Biology' applying evolutionary principles to human action (where he believed humanity's morals provide a survival value). He popularised the term 'evolution' while also coining the phrase 'survival of the fittest'. As a philosopher of evolution, Spencer had several admirers but unfortunately had a profound misunderstanding of Darwinian evolutionary theory. He believed in Lamarck's inherited, acquired characteristics and thought of evolution as a teleological or purposeful process directed towards the production of more 'evolved' forms (which Charles Darwin never believed in). Spencer's evolution was more embracing and

cosmological than others. He saw evolution as an inevitable progression from homogeneity to heterogeneity (from simple to complex). But by applying what he considered to be evolutionary rules to human societies, Herbert Spencer is probably best remembered as a forerunner of **Social Darwinism**, a radical philosophy suggesting that 'survival of the fittest' justified mankind's class divisions and laissez-faire capitalism together with colonisation and subjection of other peoples.

A final matter when considering evolutionary ethics is the question of natural selection and whether an ethical code in humans is due to natural selection and adaptation or whether it is an **exaptation** (a shift in function during evolution). A moral sensibility allows humans to judge actions as right or wrong. This action is useful if it promotes survivorship (such as in reciprocal altruism) and would presumably be selected for. However, by examining evidence from other primates and human ancestors, the focus of natural selection (and therefore adaptation) is the development of a bigger brain and advanced intellectual capacities. A 'moral compass' or 'moral code' has been suggested in very young children. However, there does not appear to be a 'natural' or 'incipient' moral code. It is likely therefore that ethical considerations are an exaptation – it arose because of possessing big, clever brains. This view of course is not universally shared, but whatever its origins, an ethical code is an integral part of our humanity.

Are There Issues Integrating Gene Transmission with the Rest of Biology?

In some quarters it is thought that there may be a difficulty in integrating evolution with the rest of biology. One issue of concern to some biologists is that of transmission; how do changes in population gene frequencies act as agents for the formation of new species, and do genes simply carry the information to make a new phenotype (the classic textbook account)?

In looking at genetic transmission, the argument is that genes do not carry *absolute* information; rather this information is *predictive*. The concept of information needs redefining. A cross-generational flow of information is perhaps best described through gene lineages trying to secure the resources needed for replication (Dawkins, 1982). Perhaps we may be overstating the case for gene-based inheritance. For instance, cytoplasmic components of inheritance, symbiotic microbes, the conditioning effects of mother's milk and behavioural imprinting can all modify gene expression.

Understanding gene regulation and gene expression has been instrumental in our understanding of embryo development and the links between genotype and phenotype. No longer do biologists recognise our genome as a template or mould for an organism but rather a script that may be interpreted in different ways. The information transmitted between generations is provisional.

Is There a Correct Way to Classify?

Classification (ordering and placing objects into groups) is almost part of the human condition and plays a role in every science from Cosmology (the classification of stars), Chemistry (the Periodic table) and Geology (rock and soil types) to Biology.

The main function of a classification is, by place value, to convey information to the reader, but dispute often exists around the best way to classify. Taxonomy, following the efforts of Carolus Linnaeus (see Chapter 7), operates a system of nested groups (groups within groups) and a hierarchical (higher and lower rank) system. The Periodic Table on the other hand is non-hierarchical (information is positional and not ranked), but both convey detailed information and by knowing the position in the classification, accurate predictions can be made.

Charles Darwin suggested a natural, branching classification that reflected the history of the groups being classified. He also revealed in *Origin* that the classification would represent genealogy – and it is this point (determining ancestry and exploring homologies) that some biologists are uncomfortable with. By the 1970s two schools of thought tried to clarify taxonomy by removing the assumptions being made:

- The **cladists** (who argued that the key characteristic is that of branching and phylogeny with clades representing groups of homologies and thus common ancestries) and
- The **pheneticists** (who sought a clearly defined numerical approach independent of evolutionary considerations)

The cladistic approach to taxonomy is now widely accepted though evolutionary taxonomists try to combine elements of both views. It is true that modern taxonomy holds objectivity (and not assumption) as a key consideration. Towards this end there is even talk of adapting or dispensing with the traditional Linnaean scheme. Linnaeus recognised only five ranks (we now employ seven – kingdom to species), but with subphylum, infraclass, cohort, etc. there are now at least 21 ranking categories. There is also confusion over major groups such as the Reptilia. Reptilia is assumed to be a discrete group of animals, but cladists point out that lizards, crocodiles ***and birds*** are monophyletic (possess a single ancestor) and so the reptiles form only branches of a much larger clade.

Therefore, given:

- ❖ the inadequacy of the traditional Linnaean scheme,
- ❖ a difficulty in reconciling plant and animal kingdoms within a single scheme,
- ❖ the effect of molecular data on recent taxonomies,
- ❖ accurately describing what a species is (the species problem) and
- ❖ knowing where to place new fossil species,

then a revision of taxonomic practice is long overdue.

Some suggest simply inserting new categories within the Linnaean scheme; others suggest replacing the Linnaean hierarchy altogether with a more stable system (a 'phylocode' has been suggested rejecting Linnaean ranking completely).

Is There an Emergent Biology?

To bridge the divide between a mechanistic biology and the doctrine of vitalism the philosopher–biologist C. Lloyd Morgan (1852–1936) suggested a middle path where

a new feature can emerge from the antecedent physical properties without being reducible to those properties. These **emergent properties** are unique and not deducible from the components of which they are derived. Examples might include the taste of salt as an emergent property of the sodium and chloride atoms from which it is made or the presence of consciousness emerging from the billions of neurones that go to make up the human brain. Emergent properties in religion include a sense of the sacred in art or a sense of hope in literature. Peter Corning, a US biologist and systems scientist, also introduces a further level by suggesting that the process of emergence is an iterative one; in other words, interactions within biological systems produce synergistic effects which themselves cause further interaction and further complexity. That is, the effects produced themselves become the causes.

In terms of biological evolution, it is suggested that emergent properties both 'shape' and explain features such as the complex social structures of ants and termites, the production of biological communities from individual populations and the complex biochemistry resulting from the molecular biology of the cell. Emergence is not intended to represent some vital principle; merely a natural process where uncommonly complex features are derived from an aggregate of relatively simple components. Emergent properties have been used to suggest the ordered and predictable behaviour of macroscopic objects from their unpredictable atomic parts. In taxonomy it has been suggested (by authors such as Stephen J. Gould) that emergent properties both form and describe the higher taxa. These properties might include specialisation or genetic variability and may be a useful way of looking at macroevolution and units of selection.

John Henry Holland (1929–2015), a US professor of psychology and computer science, was a strong advocate of emergence in adaptive systems – both natural and artificial. His work, for example, has been used in attempting to explain the emergence of life in a prebiotic (and physical) world along with a genetic algorithm for large populations that purport to explain evolutionary dynamics.

Attractive as this position sounds, the notion of emergence and emergent properties lacks explanatory power and several authors (for instance Francisco Ayala) have suggested that this term is simply a shortcut for explaining complex processes for which we have, at present, no satisfactory empirical information.

Does the Concept of the Meme Better Help Us Understand Cultural Evolution?

Cultural evolution was considered in Chapter 10 where a meme was defined as a unit of cultural inheritance. Coined by Richard Dawkins in 1976 the term has come to define an alternative self-replicating unit (equivalent to the gene) which copies information and behaviours to be passed on to the next generation (that is from one *vehicle* to the next). Sometimes described as 'thought contagion', memes operate by transferring information (often through imitation) from one nervous system to another.

Critics describe memes as 'a useless analogy' or a 'meaningless metaphor'; there is also a question regarding their very existence in biology. There are indeed serious questions to be answered; is it possible to divide culture up into discrete units? And

there are genuine problems when using analogies (in this case gene and meme). But the term does have utility; cultural evolution certainly occurs, teenagers follow fashions and adults follow various religious conventions which could also be construed as memes. Given the rapid development of the internet and social networking (and the profusion of memes relating to current affairs), one can envisage the concept also being of value to researchers. Memes therefore have their uses, along with other aspects of social study such as semiotics (the science of signs and signal communication) in describing social imitative phenomena, but unlike genes they are not particularly explanatory. The meme's-eye view is a novel hypothesis but perhaps contributes very little to a deeper understanding of cultural change.

Life's Continuing Existence

The question of life is central to biology, but life itself remains an enigma. Are life forms merely replicating, coded information bodies as suggested by Richard Dawkins or might we be finally looking at a more holistic biology suggested by E. O. Wilson? Also, what about the energetics of biological systems; does life not transgress the second law of thermodynamics by resisting dissolution?

To answer these questions, we must look a little deeper into what it means to be alive. Biology is a relatively young science and 'Big Questions' certainly remain. The assembly and maintenance of ecosystems is still not fully understood, and the nature of consciousness is only now beginning to reveal itself. But there are optimistic signs. There is a confidence in unifying the different levels of biology from ecosystems to the molecular levels of genomics and proteomics. Systems biology is another promising development adopting a more unified approach. But biological *questions* are not so straightforward. For instance, 'why does the grasshopper jump' can be answered in several ways? We can say it is the result of sensory systems and electrical nerve impulses stimulating muscle physiology. Or we can say that the grasshopper jumps because it is somehow programmed to jump in certain conditions (it has evolved this way). There is a sort of epistemological pluralism here and, as Steven Rose says in his book *Lifelines* (Rose, 2005), 'It all depends'.

Another major question is one of probability. Is life improbable or is it inevitable wherever the 'correct' conditions occur? Cosmologists have identified many exoplanets where conditions for life may be favourable; but no evidence of life yet.

One of the major properties of living systems is their ability to obtain and maintain a source of energy. For an organism to grow there needs to be an orderly increase in its chemical components mediated by the two processes of anabolism (building up molecules) and catabolism (breaking down molecules). The energy for life's processes is ultimately derived from the sun and we believe that life is (energetically) very costly. The transition from prokaryote to the more complex eukaryote cell appears to be costlier still. So how did the earliest cells obtain their energy? Probably not through lightning bolts, possibly through chemical reactions but equally possible is the ubiquitous proton concentration difference across cell membranes. An electrical potential difference of only 150 millivolts across cell membranes provides a field strength of many millions of

cell membranes provide a field strength of many tens of millivolts per millimetre across the whole cell. Such a large electrical potential can therefore be used to form the ATP necessary for energy transfer within the cell.

Living cells still adhere to thermal laws such as the second law of thermodynamics. However, cells are open systems that allow transfer of both energy and materials through their membranes and so the energy obtained maintains the non-equilibrium state of the cell until death when normal physical events take over.

Evolution and Religion

Science and religion can be uncomfortable bedfellows; the one promoting pragmatism and an open, empirical approach, the other faith, belief in scripture and revelation. However, it is increasingly difficult to simplify this discussion; for just as there are many different areas of science, there are several major belief systems. Eastern religions such as Hinduism and Buddhism do not separate humanity and nature in the same way as do theistic religions. The existence of sacred texts in Islam and Christianity promotes a literal approach which can often pose problems in science, while Puritanism in seventeenth-century Europe is often seen to promote a rapprochement by providing a culture in which practical science could flourish.

Natural theology was a philosophical doctrine that attempted to demonstrate the existence of a 'Creator' and the Creator's purpose not through revelation but through an observation of nature coupled with human reason. Beginning with Plato in the ancient world and St Thomas Aquinas in the Middle Ages, the philosophy of natural theology was used to reconcile scientific evidence with the works of a Supreme Being. The English naturalist John Ray (1627–1705), the cleric William Paley (1743–1805) and the political economist Thomas Malthus (1766–1834) all discussed the view that nature revealed the works of a Creator. Over the years this approach has been used to support the study of the natural sciences and is instrumental in the creationists' argument from design (for instance William Paley's assertion that just as a watch has a 'maker' so does the human eye).

As was stated earlier, recent polls in the United States showed that most citizens believe human beings have a 'Maker' – 'humans evolved with God guiding' (31%) or 'God created humans in their present form' (42%) – Gallup 2014. A poll reported in a UK newspaper (*The Guardian*, 1 February 2009) also suggested that 'Half of Britons do not believe in evolution'.

But what are the views of the clergy? Surprisingly, they appear more moderate:

> I think creationism is, in a sense, a kind of category mistake, as if the Bible were a theory like other theories. Whatever the biblical account of creation is, it's not a theory alongside theories. It's not as if the writer of Genesis or whatever sat down and said well, how am I going to explain all this … 'In the beginning God created the heavens and the earth … Rowan Williams, Archbishop of Canterbury, *The Guardian* newspaper, 21 March 2006

Creationism is therefore a religious view adhering to an act of divine creation. Life, creationists might argue, is more than a 'cosmic accident', and the naturalistic

view of evolutionary scientists is simply a means of achieving freedom from the 'weight of moral obligation'. And creationists (like evolutionists) have diverse views:

- Gap theorists (the Earth was created formless and then populated; gaps appear due to floods etc. and God's judgement)
- Progressive creationists (God created the first of each 'kind' and thereafter others developed through evolution – that is, microevolution but not macroevolution)
- Theistic evolutionists (scripture tells us God made the world but not how; science explains how)
- Young-Earth creationists (based on a literal interpretation of the biblical book of Genesis – that is, 6 days, 10 000 or fewer years ago)

Creationist thinkers criticise evolution on several levels: the philosophical (implies Life has no purpose), the empirical (no one has observed this) and even the scientific (no evidence for non-living to living or simple to complex). But mainly religious creationists do not like to believe that the universe is capricious (or ignore the ordering due to the Laws of Nature).

It is important that creationist views are addressed. Not to deny faith or to ridicule this behaviour but to emphasise the nature of evidence and theories of best-fit. As was argued both in Chapter 1 and in the earlier chapter, evolution is a true science. Evolutionary change has both a description (explanandum) and an explanation (explanans) giving evolutionary theory parity to that of particle theory, cell theory or the theory of gravity.

In discussing the religion/evolution debate we have already encountered Thomas Henry Huxley (1825–1895). Also known as Darwin's bulldog, Huxley was an Oxford anatomist and staunch supporter of evolution. In a similar way to Charles Darwin, Huxley served an apprenticeship (assistant surgeon) on board a Royal Navy ship bound for the Southern Hemisphere where he collected marine invertebrates and received many awards on his return. Although not an evolutionist from the outset (he attacked Robert Chambers' (1844) early evolutionist book, *Vestiges of the Natural History of Creation*), he subsequently supported Darwin following the publication of *Origin*. Perhaps the most famous confrontation in the religion/evolution controversy took place at a British Association meeting, on Saturday 30 June 1860 at the Oxford University Museum. 'Soapy' Samuel Wilberforce (1805–1873), so called because of his slippery nature, was Lord Bishop of Oxford and a Fellow of the Royal Society. The Huxley–Wilberforce debate was a noisy affair in front of more than a thousand people. Appearances from Captain Fitzroy of HMS Beagle (who with bible in hand implored the audience to believe in God) and Joseph Hooker (Darwin's friend and one of the greatest botanists and palaeobotanists of his age) enlivened proceedings, but by all accounts the Darwinist view prevailed in spite of Wilberforce asking Huxley whether it was through his grandmother's or grandfather's side that he was descended from a monkey!

On the topic of religion though Huxley was ambivalent. He rejected arguments for the existence of God but still did not see himself as a materialist (a view promoted by the German philosopher Buchner that the world was mechanistic made up solely of matter and force) or an atheist. He subscribed to the view that animals were

'automata', but a consciousness also existed as an 'intimate connection'. This pragmatic view was surprisingly popular in the mid-nineteenth century and Huxley, in a book he was writing, welcomed David Hume's (1711–1776) naturalist and sceptical philosophy. Huxley said it gave him more reason for being an **agnostic** – a term he coined himself. Charles Darwin, his religious belief eroding, came to consider himself an agnostic as did Herbert Spencer.

There were several attempts later to reconcile Science and Religion; Rudolph Virchow (1821–1902; German physician and developer of biology's 'Cell Theory') determined that Science should restrict itself to 'facts' while elements of consciousness be left to the Church. But another great evolutionary philosopher Ernst Haeckel (1834–1919) denied all of this; all true science he wrote is 'natural philosophy', mind and body cannot be separated. He also took exception to Huxley's agnosticism calling it a form of obscurantism.

The Science/Religion debate in the mid-to-late-nineteenth century appears to centre on the mind/body problem articulated by Rene Descartes almost two centuries earlier. To some extent this is also mirrored by current, twenty-first century debate into neuroscience and human cognitive ability. The question is how the workings of the brain provide insight into its non-material part; one's consciousness (or as some would prefer to say, the soul). The development of MRI has generated much neurobiological research exploring areas as diverse as moral judgement, religious experience and near-death scenarios (see Preston, 2013, for a discussion of mind/body issues and implications for looking at the future of the 'soul'). This burgeoning field of 'neuroethology' or 'spiritual neuroscience' attempts to explain religious experience and behaviour in neurological ways thereby escalating the debate. Are we looking at mechanistic or vitalistic workings of the human body? Religious scholars are generally critical of the neuroscience approach arguing that religious or any other significant experience is broad-ranging and unlikely to be recognised in localised regions of the brain.

The Western Christian Church and the scientific establishment have had an uneasy relationship. A theocratic world view was dominant in the ancient world – government by clergy, the deity is the ultimate source of authority. But the scientific revolutions of the seventeenth and nineteenth centuries brought into focus religious and scientific differences. Perhaps the most well-known disagreement was the charge brought against Galileo Galilei in 1633. Galileo's acceptance of (Copernicus's) heliocentric view of the solar system (that the planets orbit around the sun, not the other way around) putting him in direct conflict with the Catholic church.

Religious orthodoxy in Europe began to decline at the end of the eighteenth century particularly because of the French Revolution. Biblical accounts of the age of the Earth were being questioned by the new science of Geology, while descriptions of the cosmos were being repudiated by accurate measurement and observation. The expansion of the geological time scale 'not only rocked science but was also a major transformation in European thought … it radically diminished the significance of human life' (Fara, 2009: p. 271). And it is into this world of fluidity and changing ideas that Darwin introduced his concept of natural selection and change with modification.

Many of our current thinkers abstain from the view that science and religion cannot be reconciled. Theologians, philosophers and scientists often strive to put forward a compromise. Consider perhaps Stephen J. Gould (1941–2002) and his belief in the coexistence of both science and religion. He refers to these two belief systems as the 'Magisterium of Nature' and the 'Magisterium of Religion' both of which represent different and distinct fields of enquiry (his view of 'non-overlapping magisteria').

From So Simple a Beginning

Biological evolution describes evolutionary trajectories but operates on several levels

- the reductionist (exploring adaptations to describe their environmental 'fit'),
- the determinist (the 'selfish gene' promoting its own survival),
- the stochastic (patterns in nature produced by random processes) and
- the integrative (a holistic approach emphasising the 'connectedness' of organisms both in time and space).

In the early twentieth century Rudyard Kipling, a Victorian writer, constructed the 'Just So Stories' for children to describe such curiosities as how the leopard got his spots or how the camel got his hump. Conjecture such as this is good fun and raises interesting questions; however, it is not science. And although we can forgive Mr Kipling for his little bit of children's whimsy, we require a more sophisticated world view. But consider Ernst Haeckel, a German zoologist and embryologist whose work was profoundly shaped by reading Darwin's *Origin*. Although a believer in spontaneous generation (probably through his earlier studies of the beautifully crystalline marine planktonic *Radiolaria*) and famous for his biogenetic law ('ontogeny recapitulates phylogeny'), Haeckel nevertheless went on to popularise Darwin's descent through modification and natural selection which he saw as a unified explanation. He was referred to as the 'T H Huxley of the European continent'. Haeckel denied the concept of final causes and the creation arguments of the Church but still possessed an acute aesthetic sense producing beautiful artwork and a strong appreciation of symmetry (see Aescht et al., 1999, *Weltraetsel und Lebenswunder* (*World Puzzles and Wonders of Life*) for a better appreciation of his life and work). Science and wonder can indeed go hand in hand.

It is tempting to imagine Charles Darwin treading the well-worn path around his gardens at Down House pondering the self-same problem, how to describe the complexity of what we see around us. In the final paragraphs of *Origin* he states:

> It is interesting to contemplate an entangled bank clothed with many plants of many kinds, with birds singing in the bushes, with various insects flitting about . . . these elaborately constructed forms so different from each other and dependent on each other in so complex a manner, have all been produced by laws acting around us."

And

> from so simple a beginning endless forms most beautiful and most wonderful have been and are being evolved.

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Recommended Reading

Chapter 1

Attenborough, D. (2013) Galapagos with David Attenborough [DVD]. Sky1. (An excellent visual introduction to the Galapagos archipelago, written and directed by the acclaimed UK naturalist and presenter, David Attenborough. Set in three parts ('Origin', 'Adaptation' and 'Evolution'), the programme explores both the evolution of the islands together with their unique plant and animal communities.)

Bowler, P. (2003) *Evolution, the History of an Idea*, 3rd ed. University of California Press, Berkeley. (A detailed survey of the history of evolutionary thought. Often used as a textbook to teach the 'History of Science' to university undergraduates.)

Bridson, G. (2008) *The History of Natural History*, 2nd ed. The Linnean Society of London, London. (An interesting and comprehensive account of the development of natural history.)

Darwin, C. (1845) *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of HMS Beagle round the World*, 2nd ed. [Later re-titled 'Voyage of the Beagle']. John Murray, London. (The best account of the Beagle voyage is still that of Charles Darwin himself. It has been reprinted many times.)

Grant, P. R. (1999) *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton, NJ. (Originally published in 1986, this new edition has an 'Afterword' bringing each chapter up to date.)

Parent, C. E. and Crespi, B. J. (2009) Ecological opportunity in adaptive radiation of Galápagos endemic land snails. *The American Naturalist*, 174(6), 898–905. (A model example of 'ecological opportunity' leading to phenotypic divergence (adaptive radiation) in endemic land snails.)

Ridley, M. (Ed.) (2004) *Evolution, Oxford Readers*, 2nd ed. Oxford University Press, Oxford. (An anthology of major scientific writing on a variety of evolutionary topics ranging from Darwin's, 1858, unpublished works on species to Palumbi's, 2001, description of 'Humans as the world's greatest evolutionary force'. Each extract comes with its own brief summary.)

Ruse, M. and Travis, J. (eds) (2009) *Evolution: The First Four Billion Years*. Harvard University Press, Cambridge, MA. (A series of essays written by top US and UK academics to celebrate the 200th anniversary of the birth of Charles Darwin. The latter half of the book (pp. 401–934) comprises a very useful 'Alphabetical Guide', a sort of glossary where both scientific terms and important individuals and discoveries are thoughtfully explained, each entry with its own mini-bibliography.)

Stott, R. (2012) *Darwin's Ghosts: In Search of the First Evolutionists*. Bloomsbury, London. (Using the premise that Charles Darwin had overlooked his 'intellectual predecessors', Rebecca Stott looks at a range of individuals who, themselves, had planted the seeds for the development of the theory of evolution by natural selection.)

Sulloway, F. J. (1982) Darwin and his finches: the evolution of a legend. *Journal of the History of Biology*, 15, 1– 53. (The most reliable account of Darwin, the finches and the origin of his evolutionary views.)

Weiner, J. (1994) *The Beak of the Finch: A Story of Evolution in Our Time*. Jonathan Cape, London. (One of the best popular books on evolution which is based on the work of the Grants.)

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Cox, C. B and. Moore, P. D. (2000) *Biogeography: An Ecological and Evolutionary Approach*, 6th ed. Blackwell Science, Oxford. (A standard text on biogeography.)

Coyne, J. A. (2009) *Why Evolution Is True*. Oxford University Press, Oxford. (A very readable introduction to the evidence for evolution providing a mix of both interesting observation and plausible explanation. The book makes a compelling case for evolution and is written with scientific rigour.)

Dawkins, R. (2009) *The Greatest Show on Earth*. Bantam Press, London. (A masterly synthesis of the evidence for evolution written by a passionate evolutionist. The book has comprehensive coverage and is very well illustrated.)

Gallup (2017) Evolution, creation, intelligent design. Gallup News. http://news.gallup.com/poll/21814/Evolution-Creationism-Intelligent-Design.aspx (accessed 29 December 2017). (An interesting look at public opinion reflecting 'the primitive nature of the evolution debate'.)

Hall, B. R. (ed.) (2000) *Homology: The Hierarchical Basis of Comparative Anatomy*. Academic Press, San Diego. (A collection of papers from experts in comparative biology with a focus on the 150th anniversary of Richard Owen's seminal paper. Homology is dealt with at all levels from molecules to behaviour.)

Kemp, T.S. (1999) *Fossils and Evolution*. Oxford University Press, Oxford. (Rather than a survey of the extensive information concerning fossil evidence, this book focuses on 'the ideas, methodology and scope of contemporary palaeobiology'. It is particularly concerned with ideas and the interpretation of fossil evidence.)

Laubichler, M. D. and Maienschein J. (2009) *From Embryology to Evo-Devo* (Dibner Institute Studies in the History of Science & Technology Series). MIT Press, Cambridge MA. (A well-integrated book exploring embryology and evolution from a particular, Evo-Devo, viewpoint. A comprehensive study of embryology and developmental genetics as they apply to evolution.)

MacFadden, B. J. (1994) *Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equidae*. Cambridge University Press, Cambridge, UK. (Synthesises a large body of data from geology, biology and palaeontology to present a thorough overview of horse evolution.)

Chapter 3

Cook, L. M. and Callow, R. S. (1999) *Genetic and Evolutionary Diversity*. Stanley Thornes, Cheltenham. (A short introduction to population genetics and variation; the text explores the possibility of single-locus and multiple-locus genetic studies explaining the evolutionary process. A broad-ranging and well-evidenced summary.)

Edwards, A. W. F. (2008) G. H. Hardy (1908) and Hardy-Weinberg Equilibrium. *Genetics*, 179, 1143–1150. ('Although this is an account of G. H. Hardy's role in establishing the existence of what is now known as "Hardy–Weinberg equilbrium," we start with Weinberg's description of the problem and its solution, which cannot be bettered'.)

Gillespie J. H. (2008) *Population Genetics: A Concise Guide*. (2nd Edition) John Hopkins University Press. (A concise overview and reprint of a popular US primer in this topic.

Genetic drift and natural selection are well covered together with an interesting final chapter on the evolutionary advantages of sexual reproduction.)

Griffiths, A. J. F., Miller, J. H., Suzuki, D. T., Lewontin, R. C. and Gelbart, W. M. (2000) *An Introduction to Genetic Analysis*. W. H. Freeman, New York. (A comprehensive genetics teaching text discussing both genetic variation and genes at the population level. There is much background material, and it is fully illustrated throughout.)

Hartl, D. L. and Jones, E. W. (2009) *Genetics: Analysis of Genes and Genomes*. Jones and Bartlett, Sudbury, MA. (A detailed, standard text on genomics, genetic variation and gene regulation. A balance between observation and theory is maintained with many useful figures and a glossary.)

Henig, R. M. (2000) *A Monk and Two Peas*. Weidenfeld and Nicolson, London. (Beginning with William Bateson's 'rediscovery' of Gregor Mendel's work at the turn of the century, this book relates the story of Mendel from his time at the St Thomas monastery to his death from Bright's disease in 1884. An excellent account of both the man and his work are provided.)

Howard, J. (2001) *Darwin: A Very Short Introduction*. Oxford University Press. Oxford. (A particularly good introduction to Darwin and Darwinism in this excellent 'Very Short Introduction' series.)

Mielke, J. H. and Konisberg, L. W. (2008) *Human Biological Variation*, 2nd ed. Oxford University Press, USA. (An exploration of human diversity using genetic, anthropological and evolutionary models. Blood group polymorphism and DNA markers are covered in detail with a clear description of basic molecular genetics.)

Neal, D. (2004) *Introduction to Population Biology*. Cambridge University Press, Cambridge, UK. (Darwin's theories of natural selection and evolutionary biology are used as underlying themes in the study of population genetics and interactions between species. Problems are provided at the end of each chapter; answers are found at the end of the book. A well written and suitably descriptive introduction to this complex topic.)

Schluter, D. (2000) *The ecology of Adaptive Radiation*. Oxford University Press, Oxford. (The text focuses on the evolution of ecological diversity. Examples are used throughout and an evidence-based approach is employed. Having worked on the Galapagos finches, Dolph Schluter is currently working on sticklebacks and the evolution of differences between species.)

Vinicius, L. (2010) *Modular Evolution*. Cambridge University Press, Cambridge, UK. (Arguing from units of inheritance to origins of species to the development of multicellularity and life cycle evolution; this text emphasises, as stated in its subtitle, 'How natural selection produces biological complexity'.)

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Bell, G. (2008) *Selection: The Mechanism of Evolution*. Oxford University Press, Oxford. (A detailed and up-to-date account of both natural and artificial in a range of different populations.)

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*. John Murray, London. (Every student of evolution should read the *Origin* in the original – the first edition (reprinted many times) is recommended.)

Ford, E. B. (1976) *Ecological Genetics*, 4th ed. Chapman & Hall, London. (The classic account of Ford's and other's work in ecological genetics.)

Gould, S. J. and Lewontin, R. C. (1979) The Spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society B*, 205, 581–598. (Stephen Jay Gould coauthored this account with his friend Richard Lewontin

where they argue that not every morphological structure or piece of behaviour can be accounted for by natural selection historical circumstances and chance must also be taken into account. A classic paper.)

Grant, B. S. and Wiseman, L. L. (2002) Recent history of melanism in American peppered moths. *Journal of Heredity*, 93, 86–90. (An interesting account, drawing on UK studies, mapping the rise and fall in the incidence of melanism in the USA.)

Kimura, M. (1979) The neutral theory of molecular evolution. *Scientific American*, 241, 94–104. (Motoo Kimura's thesis is that at the molecular level most evolutionary change and most of the variability within a species are caused not by selection but by random drift of mutant genes that are selectively equivalent. A study of neutralism.)

Krebs, J. R., Davies, N. B. and West, S. A. (2012) *An Introduction to Behavioural Ecology*, 4th ed. Wiley-Blackwell, Oxford. (Still the standard text on the topic; the text adopts the modern adaptationist programme. This edition is superbly illustrated and reveals much of behavioural evolution.)

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Vinicius, L. (2010) Modular Evolution, How Natural Selection Produces Biological Complexity. Cambridge University Press, Cambridge, UK. (With sections on epistasis, gene expression and the origins of animal phyla, this text looks in detail at information systems and the origins of biological complexity.)

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Tudge, C. (2000) *The Variety of Life*. Oxford University Press, Oxford. (A tour de force – surveying all living creatures plus an introductory chapter on 'The Craft and Science of Classification'.)

Chapter 8

Dawkins, R. (2009) *The Greatest Show on Earth: The Evidence for Evolution*. Bantam Press, London. (A comprehensive account of Life on Earth introducing evolutionary theory to a lay reader. Topics such as 'missing links', 'macroevolution' and 'molecular clocks' are described in a clear and coherent manner.)

Makishima, A. (2017) *Origins of the Earth, Moon and Life: An Interdisciplinary Approach*. Elsevier, Amsterdam. (Beginning with the origin of elements, and thence formation of the early solar system, and the oldest records of life, this interdisciplinary reference affords an overview of Life's potential within our solar system.)

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Chapter 9

Comfort, N. C. (2001) *The Tangled Field*. Harvard University Press, Cambridge, MA. (A fascinating insight into the life and work of Barbara McClintock, in particular her discovery of transposable genes. Although her life has been described as a struggle for acceptance in a male-dominated world, Comfort describes the meticulous experimenter and original thinker.)

Gilbert, W. (1986). *Origin of life: The RNA World*'. *Nature*, 319(6055), 618–618. (A professor at Harvard and co-founder of the company Biogen, Walter Gilbert was perhaps the first person to use the term 'The RNA World'.)

Lesk, A. M. (2007) *Introduction to Genomics*. Oxford University Press, Oxford. (The elements of heredity comprehensively covered at the molecular level. Chapter 3 (Evolution and Genomic Change) is particularly relevant and explores change at various levels.)

Chapter 10

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Roberts, A. (2010) *The Incredible Human Journey*. Bloomsbury, London. (An exploration of palaeoanthropology through the movements of Homo sapiens 'Out of Africa' to 'The New World'.)

Chapter 11

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Trut, L. (1999) Early canid domestication: the farm-fox experiment. *American Scientist*, 87(2), 160–170. (A detailed account of the silver fox domestication experiment by Dr. Lyumeda Trut who currently runs the Institute where Dmitri K. Belyaev began these studies.)

Chapter 12

Brockman, J. (2016) *Life*. Harper Perennial, New York. (A collection of interviews and commissioned essays belonging to the 'Best of Edge' series (Edge.org) exploring life and the modern evolutionary synthesis with biologists such as Dawkins and Mayr and Venter, physicists such as Dyson and Sasselov. A fascinating insight into life and evolution from some of the world's most acclaimed scientists).

Depew, D. J. and Weber, B. H. (1996) *Darwinism Evolving*. MIT Press, Cambridge, MA. (An overview of Darwinian evolutionary **theory** (not evolutionary **biology**). Beginning with Darwinism as a research tradition, the book explores neoclassical biology, genetic Darwinism, molecular biology and the future of Darwinism.)

Mayr, E. (2004) *What Makes Biology Unique?* Cambridge University Press, New York. (As Ernst Mayr says, 'this will be my last survey of controversial concepts in biology'. In support of an empirical approach (rather than the philosophic-logical) the book looks at past, present and future biologies with a particularly interesting account of the Darwinian paradigm and his major theories.)

Wetherington, R. K. (2012) *Readings in the History of Evolutionary Theory*. Oxford University Press, New York. (An excellent review of the broad field of evolutionary biology using primary source readings. An insightful commentary makes this a particularly useful addition to the library of 'Evolution' texts.)

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