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Front cover: Collage of images showing different facets of Evolutionary Biology: Charles Darwin as a young man, Devonian fish from the Gogo Formation, *Macnamaraspis kaprios* Long 1995 (Western Australia's Fossil Emblem), prokaryotes (*Streptococcus*), and a stylised drawing of DNA.


How to reference this Special Issue

HONORARY EDITOR'S FOREWORD

The year 2009 is an important milestone year for Evolutionary Biology, marking the 200th anniversary of the birth of Charles Darwin, the 150th anniversary of the publication of Darwin's *On the Origin of Species*, and the 200th anniversary of the publication of Jean-Baptiste Lamarck's *Philosophie Zoologique*. The Royal Society of Western Australia celebrated these important milestones with a one-day Symposium on Evolutionary Biology, convened by Vic Semeniuk (The Royal Society of Western Australia) and Keith Oliver (Murdoch University), and held on the 17th October 2009 at the University of Western Australia.

This interesting multidisciplinary Symposium covered a wide range of subjects in the field of Evolutionary Biology, from classic palaeontology to modern concepts in evolution, including evolutionary microbiology, neoLamarckism, transposable elements as facilitators of evolution, to exploration of the predecessors and contemporaries of Darwin, and the life and times of Darwin himself. Professor Ken McNamara, from Cambridge University, and a former President of The Royal Society of Western Australia gave the Keynote Address.

This Special Issue is a collation of all the presentations and posters at the Symposium, and additional invited material. All the papers in this Special Issue have undergone the normal peer review process, but have been tailored to appeal to a general scientific community rather than a specialised audience, and are a stand alone collection of papers covering the key issues associated with Evolutionary Biology and the history of investigations into evolution. The Royal Society of Western Australia hopes that the information herein will lead to a heightened awareness and appreciation of Evolutionary Biology and its multidisciplinary nature.

Kathy Meney
Honorary Editor
The Royal Society of Western Australia.
PREFACE

Darwin, the Beagle Voyage, Evolution and 'Luck'

2009 was, of course, the 200th anniversary of Charles Darwin's birth, and the 150th of the publication of On the Origin of Species. It was also the 215th anniversary of his grandfather Erasmus Darwin's Zoonomia or the Laws of Organic Life, the 200th anniversary of the publication of Jean-Baptiste Lamarck's Philosophie Zoologique and the 165th of Robert Chambers' Vestiges of the Natural History of Creation. Evolutionary ideas were obviously 'in the air' in the decades before November 1859. But it is On the Origin that we especially commemorate. Yet it might not have been so.

In his Autobiography, written late in life, Darwin wrote:

The voyage of the Beagle has been by far the most important event in my life, and has determined my whole career; yet it depended on so small a circumstance as my uncle offering to drive me thirty miles to Shrewsbury, which few uncles would have done, and on such a trifle as the shape of my nose.

Had not Darwin, to the great annoyance of his dominating doctor father, taken against a career in medicine in Edinburgh he might not have been sent to Cambridge with the vague thought that he might become a Church of England parson. Had he not spent those not-very-distinguished years at Cambridge, he might not have met Adam Sedgwick, who taught him most of the geology he knew in a couple of weeks in the field in North Wales in the summer of 1831, and John Stevens Henslow, who enthused him with field studies, particularly in botany, and was instrumental in obtaining for him the Beagle invitation. Henslow it was who provided guidance in specimen preservation methods, and received many of the specimens he sent back to Cambridge.

Dr Robert Darwin was against the Beagle enterprise, thinking it was 'a waste of time'. The young Charles wrote to decline the offer. But Josiah Wedgwood, Charles' uncle (Robert's brother-in-law) persuaded Dr Darwin to change his mind. In his interview with Captain FitzRoy in London, one of the things that influenced the commander of the Beagle was the shape of the young naturalist's head (and obviously nose). The Captain was a believer in his own ability to interpret the bumps on the skull and the contours of a face as a guide to the character of an individual.

On the voyage, the Beagle was nearly wrecked in a storm south of Cape Horn. Darwin experienced an earthquake in South America, came close to a firefight, encountered bandits in the Pampas, and ferocious wild bulls in the Falklands. He was bitten by an insect that is the vector of a disease that might have caused his death before he was forty. He seems to have eaten poisonous fish in the Cocos Islands. He climbed high in the Andes and wandered over wave-thrashed coral reefs. Yet he survived.

Darwin was fortunate in the range of environments he encountered – tropical rain forest and semi-arid scrub, temperate woodland of various types, high altitude environments, big cities (for their day) and tiny villages. But he had even greater good fortune in the number (approaching 40) of islands he visited: tropical, 'desert' and Sub-Antarctic; coral, volcanic and continental; in the Atlantic, Pacific and Indian Oceans. They varied in size from the island continent of Australia to tiny St Paul's in the tropical Atlantic. Darwin liked islands and understood their importance. But Darwin also, perhaps, had 'good luck' in the order in which he saw his islands. The first upon which he set foot was St Jago in the Cape Verde group; semi-arid, and sparse in its vegetation cover, its geology was clear to view and relatively straightforward in character. Its study provided a preparation for the complexities of the Andes, the Falklands and Chiloe that followed. Moreover, in South America he found evidence of changes in sea level. Crossing the Pacific he had glimpses (perhaps from the masthead) of coral atolls. A few days later in Tahiti he was able to investigate coral reefs in detail, and see a barrier reef island (Eimeo, now Moorea) from afar. Then, probably on the crossing to Port Jackson, he prepared the first draft of his 'theory of coral reefs'. After visiting New Zealand and Australia, he was able to survey the coral atoll of Cocos in great detail, confirming the correctness of his ideas. A call at Mauritius a couple of weeks later filled in a few gaps. A case could be made for saying the theory that fringing reefs, barrier reefs and atolls are members of a continuous series, resulting from a rise in sea-level (or
island subsidence) was the result not only of Darwin seeing the right islands, but seeing them in the right order! As this theory was Darwin's first flirtation with the notion of 'gradualism' that permeated much of his subsequent work this is of some consequence.

Darwin's good fortune extended into his personal life. During his late teens and early twenties he was passionately in love with a petite, sexy, vivacious, dark-haired young lass called Fanny Owen, the daughter of a Shropshire squirarchy family. There is good evidence that his feelings were at least to some extent reciprocated. But she went and married someone else while he was on the Beagle. It was probably just as well (for Darwin) that she did. She seems to have been rather vain, a bit selfish, and delighted in fine clothes, parties and dances. Her conversation seems to have concentrated on society, who was courting whom, marriages and possible marriages. She read trivial novellas. She would have been bored by Charles' scientific friends. So he married his cousin, Emma Wedgwood, who was the antithesis of Fanny. Stable and motherly she cared for Darwin and their children devotedly and nursed him through his illnesses, real and imagined. She entertained his friends and supported his scientific work, even when she was uneasy about some of its implications. They were very well suited, and had a very happy marriage. Darwin was much better off with Emma than he would have been with 'La belle Fanny'.

Darwin's development of evolutionary ideas, and the publication of On the Origin, thus depended on a striking series of coincidences. Chance and randomness play an important part in the notion of evolution through natural selection. So too with Darwin's life. The modern developments in evolutionary theory, the progress of which is outlined in this issue, depend ultimately for their inspiration on the individual oddities and the personal whims of many people, the chance coincidences of wind and tide, and host of other apparently random events.

In these pages we recall, in the essays of Kevin Thiele, Stefan Revets, and Ted Steele the antecedents of Darwin's evolution, of some of which he certainly was aware before the Beagle's sailing. Joy Unno in her paper provides a critique and review of the terms and perspectives embedded in the definition and description of some fundamental concepts in biological evolution, issues she believes underlie the difficulty that many people have comprehending evolution since humans are not genetically endowed with the cognitive mechanisms to directly perceive biological evolutionary events and must deal with them in a culturally derived intellectual manner. Penelope Clifford, in her essay, explores the history of the times of Charles Darwin looking at the early years and the times of England, then Darwin's data-gathering years, the writing of the On the Origin of Species, and the fallout that followed the publication of his book. I provide a brief account of the significance of the few weeks that Darwin spent in Australia in 1836. Ken McNamara and Kate Trinajstic emphasise the role of fossils in providing evidence, and Vic Semeniuk and Ken McNamara explore and develop the various stratigraphic frameworks that underpin evolution studies using palaeontology. They argue that the fossil record still holds promise, more than have been explored to date, if correctly used, to shed light on evolutionary lineages. These studies recall the dozens of fossils that the young naturalist collected, ranging from brachiopods from East Falkland, to mammal bones from the South American coast. Ted Steele, Keith Oliver and Kemanthi Nandasena apply evolutionary ideas in new ways. These scholars, and philosopher Alan Tapper emphasise the ways in which Darwinian ideas have been modified, developed and appraised since his day. Kate Bryant and Mike Calver emphasise the importance of Darwinian ideas as integrating concepts.

Stefan Revets returns, to, quite rightly, raise our awareness of Alfred Russel Wallace, who developed similar ideas independently of Darwin. The ideas of the two of them were first presented to the scientific world in a joint paper to the Linnean Society hastily cobbled together by Lyell and Hooker in June 1858. The 'bolt from the blue' as Darwin called Wallace's paper and letter, encouraged Darwin to focus his thoughts, and to publish a 'digest' of his complete theory in On the Origin. His full massive work on Natural Selection was almost unpublishable, and did not see the light of day until the 1970s. If it has not been for Wallace's communication Darwin's ideas would not have been published until much later and in a very different way from the very accessible form in which they appeared. We salute Wallace, we salute Lamarck, we acknowledge the way in which all their ideas have been developed over the decades, but we remember particularly the accessibility, inclusiveness and integrative elegance of On the Origin of Species through Natural Selection.

Patrick Armstrong
Nedlands, February 2010
No man is an island: Evolution before Darwin and Wallace

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Abstract
Darwin and Wallace did not publish their Theory of Evolution in an intellectual or conceptual vacuum. The confrontation between a static and dynamic view of the world harks back to the beginning of speculative thought. The nature of the organic world played a role in these early debates and, once Biology came into existence, would become a focal point of attention.

I propose a sketch of the thoughts and ideas on organismic change from the earliest Greek "Phusikoi" through the ages up to Darwin and Wallace's time. Charting the evolution of Evolution as a concept should help and illuminate the climate and context in which Darwin and Wallace proposed their important theory.

Keywords: evolution, history of ideas; Darwin; Wallace

Introduction
The concept of organismic evolution proposed by Darwin and Wallace did not appear in a vacuum. To understand the intellectual climate in which their theory was proposed, we need to see how it evolved.

To cover 2 millennia of thought, theories and philosophies would be a titanic task and to do so within the confines of a short paper is impossible. What is possible is to try and see if we can, by means of some eclectic and hopefully judicious highlights and roadsigns, not only chart but also understand how we moved from myth to scientific theory.

Before we begin, I want to point out that there are a few things we have to be aware of and which we should keep in mind. Most of the concepts we take for granted today are mental pictures that came slowly and fitfully into being (for example, biology as a concept was first proposed in 1802 by Lamarck). As we come across yet another confused and confusing attempt to explain what we would now call a concept, more often than not that person was contributing to the fashioning of the building blocks we use almost unconsciously today. Let us also not forget that the tools we use to think with did not always exist: there was a time before logic. And lastly, a lot of the information, of the basic data to think about, was not known.

Let us now begin, at the beginning ...
is why they think that the sea is becoming smaller as it dries out, and that in the end it will at some time all be dry (Aristotle, Meteorologica 333b6-11, A 27).

A truly remarkable fragment relates the thoughts and ideas of Anaximander’s contemporary, Xenophanes (570–490 BC), coupling observation with reasoning:

Xenophanes thinks that a mixing of the earth with the sea is occurring, and that in time it is being dissolved by the moist. He says he has the following proofs: shells are found in the middle of the land and in the mountains, and he says that near Syracuse in the stone quarries there have been found impressions of fish and of seals, and on Paros an impression of laurel in the depth of the rock, and in Malta prints of all sea creatures. And he says that all this happened some time ago when everything was covered in mud, and that the impressions dried in the mud (Hippolytus, 21 A 33).

Empedocles (490–435 BC) wrote a substantial poem Concerning Nature, which dealt with the natural world and its production. Barnes (1979) described the zoogony of Empedocles as strange and disputed (see 31 B57-62, Aetius A72); but points out that Empedocles surely held both that the earliest living creatures were very different from those with which we are familiar, and also that many of those earlier creatures were, for various reasons, incapable of surviving and perpetuating themselves. The Aristotelian doctrine of the immutability of species later gained a stranglehold on men’s minds; and it is only just that we should honour Anaximander and Empedocles for their insight.

Heracleitus (540–485 BC) is and has been regarded by most as a hermetic, oracular philosopher. These two fragments illustrate his oracular tendency, but also portray his anti-static world view rather well.

Heracleitus says that everything moves and nothing rests (Cratylus 402A, A6);

Cold things grow warm, warm grows cold; wet grows dry; parched grows moist (B 126, 42 M).

Discussion

These writings seem alien, strange, and far removed from what we would nowadays consider to be rational, scientific discussion. We should remember though just how little of the original texts have survived to the present day. A scrap of papyrus here and there, some fragments cited by someone else centuries later, and then much more often than not, distorted to suit the purposes of the writer.

Classical scholars have spent a multitude of pages on these scraps, trying to get a better grasp at the intent of its authors. We therefore know that it is certainly not right to see in Anaximander a pre-Darwinian selectionist. However, there is an embryonic thought that says that the development of living creatures was determined by the nature of their environment. And that is a very different answer to the question of how did living creatures first come into being and propagate, particularly when compared with the usual answer of immutably fixed ones at their creation by a deity. For that, we owe gratitude to the Ionian Anaximander and Empedocles, the first natural philosophers.

Plato and Aristotle

By the time of Plato and Aristotle, things have changed a lot. The explorations by the Ionians, their questions and attempts to answer them was driven by their wish for a better understanding of how the world worked. The methods they developed, a proto-logic and proto-rhetoric came under severe attack by the Eleatic School. Parmenides and Zeno exposed fundamental problems in the Ionian logic, which threatened the entire endevour of philosophical enquiry. The sophists would take this even further and subvert the endevour to develop sophistry, for their own gain as well as that of their patrons.

Plato, followed by Aristotle, went into battle against this sophistry in an attempt to rescue rational thought. Their valiant efforts were ultimately successful, but there were quite a lot of casualties. There is a vast corpus of literature on the works of Plato and of Aristotle and, unlike that of the Pre-Socratics, well known. I shall therefore limit myself and just touch upon some of their results with direct relevance to this paper.

Plato (428–355 BC) developed Idealism, the theory of the forms. His simile of the cave in The Republic describes very effectively the idea that, say, that horse there is just a reflection of the ideal Horse, and that it is that ideal Horse which really exists.

Aristotle (384–322 BC) modified Plato’s views and developed what came to be known as Essentialism. There is a stream in modern times, of philosophers who argue that Aristotle’s philosophy is not as rigidly essentialist as it is usually portrayed (notably Balme, Grene, Lennox).

Neither Plato nor Aristotle were particularly exercised by questions about biological diversity and its genesis. The systems they developed could be used, and were used, to cover the organismic world, but that was not their primary intent.

Their philosophical systems certainly lead to a fixist, if not creationist view of what we would call the organismic diversity. If this seems somewhat unfair compared to the generous treatment of the Pre-Socratics, please bear in mind that we have most of the corpus of these two philosophers, and the hundreds and hundreds of pages are consequently very eloquent as to the intent of their authors.

Theophrastus (371–287 BC) was first a fellow pupil of Aristotle at Plato’s Academy, and became a life-long friend, eventually taking over the Lyceum after Aristotle’s death. He wrote in effect the first botanical works. In these, not a trace of evolutionary thinking can be detected, even as he makes Aristotle’s ideas practical, a constant concern of his. He also wrote a substantial doxography, covering a great many of the Pre-Socratics, which was to give us a little bit more from that well.

It may be worth taking a closer look at Lucretius (99–55 AD). He is often mentioned as a precursor of Darwin, and he used to attract a substantial amount of ire from
the creationism-inclined (Oxford University banned Lucretius’ book for many years as being too dangerous for students), that is, until Darwin became a much more attractive target. In his De rerum natura, Lucretius tried to show that all life, (animal as well as human), and all of human culture and society were the products of the interaction between chance and necessity over time, owing nothing to God.

Lucretius follows the ideas of Empedocles and Democritus through Epicurus. He stands firmly on the side of the anti-teleological atomists, and against Plato (particularly against the Timaeus), Aristotle and the Stoics (all teleologists to varying degrees).

His zoogony appears to lean heavily on Empedocles, but the trail is seriously muddied by Plato’s subversion of presocratic orthodoxy (in which a trend can be detected which views cosmogony, zoogony and anthropogony as part of the same process). Plato tried to isolate cosmogony, while Lucretius attempted to bring cosmogony back into the anti-teleological fold. Lucretius incorporated, in particular, Empedocles’s views that the creation of life was random and undirected and that the number of species was reduced by the extinction of the less adapted forms, giving a nicely non-teleological process to explain the presence of (well adapted) species.

Lucretius is clearly anti-creationist but it is more difficult to portray him as an evolutionist. True, he put forward anti-teleological and mechanistic processes to explain the origin of species, but he does not allow for evolution of one species from another. Ironically, extinction plays a crucial role in his anti-creationism (whereas Cuvier will later use it to support his creationist views). The contribution of Lucretius shows that tension and debates between various factions, indeed, diversity of ideas, was still very much a reality at that time.

Discussion

That is to say, the end of the classical period. By now, the Roman Empire is listing heavily and we know that its end is not far off. Before we move on, let us see what has been achieved.

Biology does not exist as such, neither do concepts of biological species. The ideas of creation, diversity, change and evolution have been more or less articulated, but these are still unclear and often conflated. Nevertheless, a fixist and an evolutionist view of the world have been proposed and are being entertained under a variety of forms. That is about to change, and dramatically so.

The Catholic Church

Pepin and Pope Stephen III make a pact in 754, consolidated fully by Pepin’s son Charlemagne, in 774. Charlemagne is crowned Holy Roman Emperor in Rome on Christmas Day, 800 (a title that ended finally with Napoleon), and the alliance between Catholic Church and State is forged. The church-fathers recuperate the teaching of Aristotle, and orthodoxy is brutally enforced. Philosophy, science, any form of more or less free enquiry stops and the Dark Ages begin. For almost a millenium, intellectual darkness reigns.

The Renaissance

The quatrocento sees the rise of a well-to-do merchant class in the city states of northern Italy. They begin to display their wealth by commissioning artists. The Greek world is held up as an example to emulate, and little by little, ancient texts are brought back. Explorations and expeditions are undertaken, all at least officially ad majorem glorian dei. Marco Polo, Columbus, Magellan, and Vasco da Gama sail well beyond the European World. It seems the world isn’t flat, after all. The expeditions bring back all manner of wonderful things and tales of difference. More and more questions are being asked. Galileo turns his telescope to the heavens and runs foul of the Church. Copernicus publishes his 

which is promptly put on the Index. Thomas More and Erasmus promote Humanism. More is executed for his pains and Erasmus is marginalised. Descartes publishes his Discours des Méthodes. The strongest of the Church is being challenged, particularly in France, where les philosophes éclairés began to flourish.

A very important figure in the Enlightened Movement is Georges-Louis Leclerc, Comte de Buffon (1707–1788). Through and through Cartesian, he is a-religious, to all intents and purposes free from traditional thought, highly intelligent and original. His Histoire Naturelle aimed no less at capturing the history of human knowledge of nature. By giving an account of natural history, to which he added new thoughts of a speculative nature, he wished to provoke reactions and so stimulate further research. He entertained ideas of evolution, which posed few problems to him as he held strong nominalist views on species.

On pourra dire également que le singe est de la famille de l’homme, que c’est un homme dégénéré, que l’homme et le singe ont eu une origine commune comme le cheval et l’âne, que chaque famille, tant dans les animaux que dans les végétaux, n’a qu’une seule souche, et même que tous les animaux sont venus d’un seul animal, qui, dans la succession des temps, a produit, en se perfectionnant et en dégénérant, toutes les races des autres animaux. (Histoire Naturelle, vol. 4, p. 382)

With such views he got into trouble with the Church and was forced to reaffirm his belief in special creation. This he did, with elegant subtle irony:

Mais non, il est certain, par la révélation, que tous les animaux ont également participé à la grâce de la création, que les deux premiers de chaque espèce et de toutes les espèces sont sortis tout formés des mains du Créateur (id, p. 383)

Buffon inspired and influenced both Erasmus Darwin and Jean Baptiste Lamarck, which explains to a considerable extent why both these men independently arrived at similar ideas. Charles Darwin’s suspicions and opinion of Lamarck appear therefore wholly unjustified.
The French Revolution

The French Revolution had a major impact on Europe in many different domains. Many mistakes were made, and the horrors of La Terreur are well known. However, quite a number of positive changes came about too. One of these was a loosening of the grip of the Church. The increase in secularisation proved a boon for intellectual inquiry. Scientific activity in particular flourished. However, making the transition from the Ancient Regime to the new order was not at all straightforward and many an honest intellectual ended up on the scaffold. Even if one escaped the guillotine, life was very different and rarely easy.

Jean-Baptiste Pierre-Antoine de Lamarck (1744–1829) lived through these turbulent times, going from Comte de Lamarck to Citoyen Lamarck. It is not well known that it was he who coined the concept of Biology, to a large degree because his eventual Transformationism would be held up to ridicule, especially against Darwin and Wallace’s theory.

Lamarck is a complex and interesting figure, and his thoughts and ideas evolved considerably over time. To do this man justice requires a discussion all of its own.

Madeleine Barthelemy-Madaule in her Lamarck, ou le mythe du précurseur gives an excellent analysis of Lamarck’s contribution to the evolution of evolutionary theory. She shows that his transformationist views were seriously misrepresented (largely due to Cuvier’s unpleasant role) and since then misunderstood. Charles Darwin, for one, was scathing. Ironically, he adopted Lamarck’s ideas in the very pages of On the Origin of Species.

The next step

The Renaissance and the subsequent humanism and enlightenment returned a situation we have encountered before, in Ancient Greece: fixist and evolutionist views, richer and more varied, are once again in the air.

In December, 1831, a young man steps on board a ship, H.M.S Beagle, to join Captain FitzRoy – his name is Charles Darwin.
Alfred Russel Wallace, co-author of the Darwin-Wallace Theory of Evolution

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Abstract

The intellectual effort, insight and courage to formulate a theory of evolution driven by natural selection was as great for Wallace as it was for Darwin. The neglect, to the point of oblivion, in the last decades of Wallace as Darwin's equal is not acceptable. To help and attempt to redress the balance, a sympathetic sketch of Wallace is called for. Through his publications, correspondence and life history, we gain a picture of Wallace which should encourage us to extend to him the credit to which he is very much due.

Keywords: evolutionary theory; Wallace; Darwin

Introduction

Alfred Russel Wallace is an intriguing figure. With the explosive growth of a Darwin Industry, Wallace has receded to the point where today all too few are aware of his important place in the development of the theory of evolution through natural selection.

It is hardly possible to talk about Wallace and not bring Darwin into the discussion. Of course, it is more often the case that Wallace is mentioned, in passing or even not at all, in the multitude of works on Darwin and evolutionary theory.

In order to get a better idea of who the man Wallace was, it is enlightening to look into the circumstances of his family and to how he grew up.

Biography

Alfred Russel Wallace was born to Thomas Vere Wallace and Mary Ann Greenell at Usk, Monmouthshire, on 8 January 1823, the eighth of nine children, and the third of four boys.

Thomas Vere Wallace, hailed from Hanworth in Middelsex, and was the only son of an inn-keeper. After his schooling, he was articled to a firm of solicitors in London, and from where he became an attorney-at-law in 1792. He never practised as he came into some property which provided him with a modest but good income. It allowed him to live a quiet life, without any systematic occupation. He just enjoyed himself within his means, as a fairly well-to-do middle-class gentleman.

In 1807, he married Mary Ann Greenell and soon the family began to grow. They eventually had nine children, and father Wallace had to try to improve his income. As he was not very business minded, nor very energetic, these attempts were at first unsuccessful and ultimately disastrous. It meant that the family had to move repeatedly to more affordable accommodation, first out of Marylebone, then out of Southwark, then out of Usk, and on to Hertford. At Usk, where the last two children were born (Alfred and Herbert), he managed to keep just one servant, cultivating the land himself and providing his family with fruit and vegetables, teaching the children himself. It seems that life there was rather a happy one.

By 1835, he was swindled out of what property he had left, making life very difficult indeed for the family. They had to make do on the small marriage settlement of his wife, and what income he could make by taking on pupils and by acting as librarian to a subscription library. One of Alfred's older sisters set up a small boarding school for young ladies in Hoddleston, which helped as well. At any rate, those of the children who reached their majority had nothing to start them on in life with exception of a very ordinary education, and had to fend for themselves.

Alfred's eldest brother, William, was articled to a firm of surveyors, then spent time with an architect and moved on to work for a large building company involved in the construction of King's College. He managed to get a good professional education and one from which Alfred was soon to profit.

Alfred remembered his childhood at Usk and Hertford as a very happy one, and was largely unaware of the lack of money in the house. In his youth he had ample opportunity to play along the river and in the surrounding woods and fields. He thoroughly enjoyed helping out his elder brothers with making the things there was no money for. The Boy's Own Book was a most valuable guide to them. It taught him self reliance and ability to improvise, something that would stand him in very good stead later in life.

In 1807, he married Mary Ann Greenell and soon the family began to grow. They eventually had nine children, and father Wallace had to try to improve his income. As he was not very business minded, nor very energetic, these attempts were at first unsuccessful and ultimately disastrous. It meant that the family had to move repeatedly to more affordable accommodation, first out of Marylebone, then out of Southwark, then out of Usk, and on to Hertford. At Usk, where the last two children were born (Alfred and Herbert), he managed to keep just one servant, cultivating the land himself and providing his family with fruit and vegetables, teaching the children himself. It seems that life there was rather a happy one.

By 1835, he was swindled out of what property he had left, making life very difficult indeed for the family. They had to make do on the small marriage settlement of his wife, and what income he could make by taking on pupils and by acting as librarian to a subscription library. One of Alfred's older sisters set up a small boarding school for young ladies in Hoddleston, which helped as well. At any rate, those of the children who reached their majority had nothing to start them on in life with exception of a very ordinary education, and had to fend for themselves.

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When Alfred was 5, the family moved to Hertford where he attended the local grammar school. He "suffered" Latin grammar and geography as two most painful subjects. In his last year at school, he acted as assistant which served instead of paying the fee. He disliked this special position and it reinforced his shyness even further.
Books were a major influence on Alfred. His father belonged to a book club and a constant stream of books came through the house. Later on, when his father took up the position of librarian, Alfred would spend time in the library and read.

When the finances of the family collapsed, Alfred had to leave his schooling (at the age of not yet 14), and was sent to live with an older brother, John, in London, before moving in with his eldest brother, William, and training as a surveyor.

While in London, he began to frequent the Hall of Science, a sort of club or institute set up for advanced thinkers amongst workmen, particularly for followers of Robert Owen and his socialist movement. Here too, Alfred learned a great deal that shaped him as a man. His views on politics and religion developed quickly and thoroughly.

From the summer of 1837, he joined his brother William on his surveys and acquired a variety of skills. He eagerly began to learn trigonometry, got excited by precision measurements and enjoyed learning the use of the sextant and the slide-rule. It awakened in him the thirst for knowledge and he obtained books to help him along. Tramping all over the land, he also observed Nature and began to appreciate the natural diversity. It also exposed him to the diversity of his fellow man, and the shy, observant Alfred again learned a great deal.

When there was a gap in work, Alfred was often left to his own devices, and he would spend the time practising nautical astronomy but engaged in more and more rambling among the moors and mountains. In 1841, he obtained his first booklet on plants, which included descriptions of the more common British plants. This proved to be a revelation to Alfred, and he would spend more and more of his spare time trying to identify the plants he sought out on his rambles. Eventually, he bought, at quite some cost Lindley's *Elements of Botany*. Although it was not what he had hoped for initially, it gave him a much better grasp of systematic botany. He had obtained his first booklet on plants, which included descriptions of the more common British plants. This proved to be a revelation to Alfred, and he would spend more and more of his spare time trying to identify the plants he sought out on his rambles. Eventually, he bought, at quite some cost Lindley's *Elements of Botany*. Although it was not what he had hoped for initially, it gave him a much better grasp of systematic botany. He managed to borrow Loudon's *Encyclopedia of Plants* which contained all British Plants. Alfred would spend many hours copying out descriptions so he could use these to help him identify the plants he found. He found it helpful to construct his own herbarium as well, even if William did not really approve. But:

Neither nor I could foresee that it would have any effect on my future life, and I myself only looked upon it as an intensely interesting occupation for time that would be otherwise wasted. Even when we were busy I had Sundays perfectly free, and used then to take long walks over the mountains with my collecting box, which I brought home full of treasures. I first named the species as nearly as I could do so, and then laid them out to be pressed and dried. At such times I experienced the joy which every discovery of a new form of life gives to the lover of nature, almost equal to those raptures which I afterwards felt at every capture of new butterflies on the Amazon, or at the constant stream of new species of birds, beetles, and butterflies in Borneo, the Moluccas, and the Arau Islands.

In the autumn of 1843, Alfred began to write. One of the earliest manuscripts was a sketch for a popular lecture on botany. He wrote it, partly because of the difficulties he himself experienced in getting information but largely because of a lecture he had attended. What a local botanist had given was such a meagre, uninteresting and so utterly unlike what a lecture ought to be that Alfred felt that he should try and do better. The botanist had enumerated the whole series of the Linnaean Classes and Orders, giving the characters and naming a few representatives. He had upheld the Linnaean system as the most useful, while the natural system was treated as useless for beginners and only suited for experienced botanists. This incensed the young Alfred:

All this was so entirely opposed to views I had already formed, that I devoted a large portion of my lecture to the question of classification in general, showed that any classification, however artificial, was better than none, and that Linnaeus made a great advance when he substituted generic and specific names for the short Latin descriptions of species before used, and by classifying all known plants by means of a few well-marked and easily observed characters. I then showed how and why this classification was only occasionally, and as it were accidentally, a natural one; that in a vast number of cases it grouped together plants which were essentially unlike each other; and that for all purposes, except the naming of species, it was both useless and inconvenient. I then showed what the natural system of classification really was, what it aimed at, and the much greater interest it gave to the study of botany. I explained the principles on which the various natural orders were founded, and showed how often they gave us a clue to the properties of large groups of species, and enabled us to detect real affinities under very diverse external forms.

In 1843, his father dies at the age of 72, and barely a year later, just after turning 21, his brother William tells him there is not enough work and that he will have to fend for himself.

Alfred finds a position as junior school assistant with the Rev. Abraham Hill, headmaster of the Collegiate School at Leicester. He takes the junior classes in English, reading, writing and arithmetic as well teaching a few boys some surveying and drawing. He settles is well and has the time to improve himself further, mainly in Algebra, Differential Calculus (although he gets "stuck" on Integral Calculus), and he works on Latin as well. He profited from the very good town library and enjoyed reading books such as von Humboldt's *Personal Narrative of Travels in South America*, Prescott's *History of the conquests of Mexico and Peru*, as well as Malthus' *Principles of Population*. This book he greatly admired for its masterly summary of facts and logical induction to conclusions.

It was at Leicester where Alfred was introduced to mesmerism. He was rather impressed, tried it himself and succeeded. With the permission of the headmaster,
he ran a series of experiments which convinced him of the reality of the phenomenon.

It was also at Leicester, in all likelihood in the library, that Alfred first met Henry Walter Bates, an enthusiastic entomologist. The two young men got on straight away, and Bates opened Wallace’s eyes to the diversity of insect life. Soon they would be spending their spare time collecting together.

In February 1846, Alfred received news that William had died. As he had died intestate, Alfred discovered that William had had a small local business, which he proposed to continue. He obtained his release from the School of the Rev. Hill, and moved to Neath. It took him and his brother John a while to wind up William’s affairs (quite a bit of money was due to him), and then Alfred took up surveying again. He diversified a bit into building with John and one of the buildings they designed and oversaw the construction of was a house for the Mechanics’ Institution in Neath. Mr. William Jevons was behind the establishment of the Institute, and invited Alfred to give some lectures at the Institute on elementary physics, mechanics and science in general. He did so, at first reluctantly, but the series ran for two years, and they were popular. Many years later, Alfred received a letter from a workman who attended the meetings and visits to collections that the Malayan Archipelago and other books is the same Mr. Alfred Wallace who taught in the evening classes at the Neath Abbey artificers:

I have often had a desire to know, as I benefitted more while in your class—if you are the same Mr. A. Wallace—than I ever was taught at school. I have often wished I knew how to thank you for the good I and others received from your teaching

(Matthew Jones, Cardiff 1895)

The contact with Bates continued to flourish, not just with letters, but also through joint collecting trips. In the summer of 1847, Bates came up to Neath again, and besides collecting, mounting and exchanging specimens they discussed the books they had read, notably Charles Lyell’s Principles of Geology and Robert Chambers’ Vestiges of the Natural History of Creation. Clearly, Alfred was already engrossed in the question of the origin of species.

He had also gone through Darwin’s Journal and having read von Humboldt’s Personal Narrative a few years earlier and found in them the inspiration to visit the tropics as a collector, something he discussed now with Bates. A few weeks later, coming back from a visit to Paris with his sister, Alfred again wrote to Bates, referring to a day spent in the insect room at the British Museum; he writes:

I begin to feel rather dissatisfied with a mere local collection; little is to be learnt by it. I should like to take some one family to study thoroughly, principally with a view to the theory of the origin of species. By that means I am strongly of opinion that some definite results might be arrived at.

When Alfred and Henry read W. H. Edwards’ A Voyage up the Amazon, they felt that this was the very place for them to go to. The advice they obtained from Edward Doubleday, lepidopterist of the British Museum, confirmed their hopes and intentions. They found an agent in Samuel Stevens, who would remain Alfred’s agent for all his collecting trips.

The two naturalists were all set to sail on 20 April 1848 on the Mischief toPara (now Belen). The story of their adventures is delightfully told in Wallace’s Travels on the Amazon and in his autobiography.

Wallace lost nearly everything on the journey back to London when the ship caught fire and had to be abandoned. All made it safely to shore in the end by October 1852. Wallace had managed to save just a few things in a small tin box. Together with the letters he had written and the drawings he had saved, he began to write up an account of his travels. He could also write some more scientific papers on the specimens he had sent before travelling up the Rio Negro. He received an insurance pay-out which allowed him to continue on for a while at least. His collections and his writings brought him to the attention of Zoological and Entomological Societies and he began to mingle in the scientific circles of the time. Soon after his return, he met Thomas Henry Huxley for the first time, and was very impressed.

He was looking for another opportunity of making a large collection, and picked up from his attendances of meetings and visits to collections that the Malayan Archipelago would offer wonderful riches to the exploring and collecting naturalist. He had made the acquaintance of Roderick Murchison, President of Royal Geographical Society and appealed to him for help. Murchison was very helpful and agreed to use his considerable influence to secure Wallace passage to some Malay port. While this was being negotiated, Wallace spent much of his time examining collections at the British Museum, once again making copious notes and sketches of birds, butterflies and beetles of the Malay Islands. In January 1854, Wallace got word that he could join the Frolic and by February he presented himself at Spithead, Portsmouth. But because of the Crimean War, the plan was abandoned and, through Murchisons representations, Wallace secured a first-class ticket overland to Singapore by the next Peninsular and Oriental Steamer. He arrives in Singapore on 20 April 1854 and travels and collects in the Malay Archipelago until 20 February 1856. The Malay Archipelago and chapters in My Life give ample and engrossing details of the six years he spent there.

He wrote his first contribution to the question of the origin of species in early 1855 during the wet season in Sarawak. There was nothing else to do but read and think, which led to his On the Law Which Has Regulated the Introduction of New Species, published in the Annals and Magazine of Natural History (1855). The law he proposed reads:

Every species has come into existence coincident both in space and time with a pre-existing closely allied species

To Wallace’s surprise, no one seemed to have noticed it. Lyell and Blyth had drawn Darwin’s attention to it and Huxley would later praise “the powerful essay”. Darwin’s copy of the journal is annotated with some comments and largely with approval.
In January 1858, in one of the many letters he wrote to Bates we find that:

I fear my paper on the *Succession of Species* will not appear so clear as it does to you. That paper is, of course, merely the announcement of the theory, not its development. I have prepared the plan and written portions of a work embracing the whole subject, and have endeavoured to prove in detail what I have as yet only indicated. It was the promulgation of Forbes's theory of *polarity* which led me to write and publish, for I was annoyed to see such an ideal absurdity put forth, when such a simple hypothesis will explain all the facts. I have been much gratified by a letter from Darwin, in which he says that he agrees with *almost* every word of my paper. He is now preparing his great work on *Species and Varieties*, for which he has been collecting materials for twenty years. He may save me the trouble of writing more on my hypothesis, by proving that there is no difference in nature between the origin of species and of varieties; or he may give me trouble by arriving at another conclusion; but, at all events, his facts will be given for me to work upon. Your collections and my own will furnish most valuable material to illustrate and prove the universal applicability of the hypothesis. The connection between the succession of affinities and the geographical distribution of a group, worked out species by species, has never yet been shown as we shall be able to show it.

Two months later, the solution for the origin of species dawned on him, recalling Malthus' *Principles of Population* he had read 12 years before. He sends off a manuscript entitled *On the Tendency of Varieties to Depart Indefinitely From the Original Type* with a letter to Darwin. The crisis that this letter wrought has been well documented, as well as its neat resolution in the joint reading of Wallace's and Darwin's writings on natural selection at a special meeting of the Linnean Society on 1 July 1858.

In November 1859, *On the Zoological Geography of the Malay Archipelago*, the paper describing what was later to be known as The Wallace Line, is read before the Linnean Society and Darwin's *On the Origin of Species* is published. On 1 April 1862, Wallace arrives back in Britain.

Thanks to the sales from his substantial collections, he gathered the means with which he hoped would allow him to retire to a quiet life and live as a country gentleman. Of course, he had to deal with the collections first and it occupied him a full three years. During that time he wrote revisions, interpretative works and presented papers at a multitude of professional meetings. He met most of the important English naturalists and many became friends. He had achieved his most cherished dream.

In 1866, he married Annie Mitten (then 18), eldest daughter of William Mitten of Hurstpierpoint (an enthusiastic botanist who inculcated the love of wild flowers and nature's beauty into his daughter). They had three children, Herbert Spencer, William Randolf and Violet. By all accounts, the marriage was a very happy one.

In the first years after his return he was generally regarded as a staunch defender of Darwinism, even considered to be more Darwinian than Darwin himself. However, on the subject of the evolution of man their analysis diverged. From the late 1860s onward, spiritualism began to play a prominent role in Wallace's view of man, and despite his experiments, he failed to convince his fellow evolutionists of his views on spirituality (who were appalled).

That did not stop Wallace from continuing to contribute a wealth of scientific papers and books, diversifying into other fields beyond natural history or biology. He wrote about geodesy, on glacial features, on museum organisation as well as, for the first time, on politics. His best known works are still referred to today: *The Geographical Distribution of Animals* (1876), *Tropical Nature* (1878) and *Island Life* (1880). He began to devote more attention to social issues, including tracts against government aid to science, on the Church of England, on the principles of free trade, on the abolishment of trusts, and on land reform.

Wallace was invited to give a series of lectures in the United States and Canada in 1886 and 1887. This proved to be a highly successful tour, which gave him the opportunity not only to meet a great many people (including President Cleveland), but also to travel and see much of Nature as well. The tour proved important in one more respect: it inspired Wallace to write the highly successful book *Darwinism*.

Honours started to flow, with medals and honorary doctorates aplenty, even if he was rather reluctant to accept them. Around 1900, he had become Britain's best-known naturalist.

Alfred Russel Wallace died at home surrounded by his family on 7th November, 1913, aged 91.

Let me conclude by expressing the hope that you will take the few imperfectly drawn miniatures I have just presented to you as an invitation to find out more about this man. And may I suggest you turn to his own writings, his books, and his autobiography as they are a delight to read. I certainly enjoyed getting to know this remarkable man and I hope you will too.

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The life and times of Charles Darwin

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Abstract

This contribution presents the life and times of Charles Darwin in several major intervals. It begins with an account of his early years with a description of the times in England and the events that led Darwin to join the voyage of H.M.S. Beagle. For Darwin, this was followed by a five-year data-gathering phase during the voyage on the Beagle in which he encountered the world at large—the vast "natural laboratory" that exposed him to the rich diversity of the environment, and life and processes from geology, to coral reefs, to vegetation, from many climatic regions, and from many physiographic settings, all of which were to provide him with data and information from which he was to derive ideas for his book, On the Origin of the Species. The next phase, the post-Beagle years, was the 22-year period of the writing of On the Origin of the Species when his life's work and observations came to fruition. This was followed by the public uproar after publication of his book, when he was faced with antagonism, derision, criticism, and hostility from all sectors of society, as well as support and promotion of his ideas. Darwin's final years saw him in poor health and having to deal with the events following the publication of his book while continuing his investigations into natural selection as the mechanism for evolution. These major natural intervals or periods capture the essence of the main and influential events around Darwin's life and times.

Keywords: Charles Darwin, H.M.S. Beagle, On the Origin of Species; natural selection; evolution

Introduction

Charles Darwin lived during the Victorian Era, a period of great social, scientific, and technological change. The Industrial Revolution of that time brought blessings and hardship: The Great Exhibition, the first century; the Great Famine of 1845 brought starvation to millions in Ireland (the Potato Famine), Scotland and England and the subsequent emigration of over one million Irish people to Canada, the United States of America and other parts of the world, will be examined. The important post-Beagle years will be described, a time following the cataloguing of the specimens Darwin had collected during the voyage, when he moved to London and became an active and respected member of the scientific community, and his subsequent marriage in 1839 and move to Down, Kent in 1842. The publication of On the Origin of Species (Darwin 1859) and the responses of the scientific world, the Church, and the public to this book will be examined, followed by a brief description of Darwin's productive final years.

This paper will trace Darwin's life from his early years at his family's home in Shrewsbury, thence to his university years at Edinburgh and Cambridge where he would read books that would stimulate his interest in the sciences, and he would meet people who would have a lasting influence on the direction and conduct of his scientific enquiry. The fortuitous invitation to take up the post of ship's naturalist and companion to Capt. FitzRoy on the second surveying voyage to South America of H.M.S. Beagle, which would provide Darwin with the opportunity fulfill a long-held desire to visit South America and other parts of the world, will be examined. The important post-Beagle years will be described, a time following the cataloguing of the specimens Darwin had collected during the voyage, when he moved to London and became an active and respected member of the scientific community, and his subsequent marriage in 1839 and move to Down, Kent in 1842. The publication of On the Origin of Species (Darwin 1859) and the responses of the scientific world, the Church, and the public to this book will be examined, followed by a brief description of Darwin's productive final years.

The structure of this contribution, in presenting the life and times of Charles Darwin beginning with an account of his early years, then the Beagle voyage, followed by the post-Beagle years that included the writing of On the Origin of Species and the consequences following publication of his book, and finally, Darwin's last years, needs some explanation. Generally, biographies on Charles Darwin tend to be substantially chronological, following his life and the events therein; this contribution also is chronological, of course, but I have separated the story of Darwin's life into major natural intervals or periods which I think capture the essence of the main and influential events around his life.
and times. In this context, this contribution departs from many other chronological treatments of Darwin’s biography, and others that focus on specific aspects of, or themes in his life and contributions in that it identifies four major time blocks in which the critical events unfolded, and provides a story of Charles Darwin’s life and times from a perspective of these four major periods in his life. The reasons for this approach are outlined below.

The chronicle of the events during the life of Charles Darwin provides a context of why and how he eventually undertook the journey on the Beagle, and perhaps insights into how his writings developed in that it provides a social and political flavour to the events that shaped his thinking and ethos, particularly, for instance, the “revolution” in the Victoria Era where middle-class gentlemen were free to pursue their scientific interests, a factor that is relevant in that Darwin was living and exploring at a time when such activities were socially acceptable. Similarly, the Potato Famine in Ireland in 1845 and the subsequent migration of many people from Ireland helped provide Darwin with a context for an understanding of the struggles of populations to survive, something that would have influenced him in the writing of On the Origins of Species. For societies where life was not a struggle, or for those living in privileged society, there may not have been the arena of “struggle” which would provide important “grist for the mill” in the writing of the On the Origins of Species. In fact, Darwin lived in times where there were hardships, and I am of the opinion that these influenced him in the concept of species and their struggles to survive. Also, the times of Darwin were those when women were being emancipated. He would also have been aware of the works of Malthus at this time, and its implications for Theology and general social criticism, hostility and rejection. His book had major implications for Theology and general social understanding, and of course, Man’s concept of his place in the Universe. While Darwin inadvertently and implicitly challenged established paradigms (and this was not without scientific, social, and theological fallout), many scientists and learned persons accepted his ideas and provided support in scientific circles.

The major milestones in Charles Darwin’s life are summarised in Figure 1.

The early years

Charles Robert Darwin was born at Mount House, Shrewsbury, in Shropshire, England on the 12th February, 1809, the fifth of six children of a local doctor. Darwin was the grandson of the physician, natural scientist, and poet, Erasmus Darwin and thus was born into the upper class of British society (Price 2008). In 1818, the year following the death of his mother, Darwin was sent to Shrewsbury School as a boarding student. Darwin’s interests in natural history and chemistry were developing during these early years, however he did not excel in the strictly classical education afforded by the school, of which Darwin writes: “Nothing could have been worse for the development of my mind than Dr Butler’s school ... as a means of education to me [it] was simply a blank” (Darwin 1887). It was at this time that Darwin’s desire to travel to remote countries was initiated by reading a school-friend’s book on the wonders of the world. Darwin to recalls that “... I believe that it was this book first gave me a wish to travel in remote countries, which was ultimately fulfilled by the voyage of the Beagle” (Darwin 1887).

In 1825, at 16 years of age, Darwin entered the University of Edinburgh to study medicine (Barlow 1958) however, he did not complete his studies, but nonetheless it is an important period in Darwin’s life. He forged a lasting friendship with Professor Robert Grant who taught zoology and it was from Grant that Darwin learned about Lamarck and transmutation (a term coined by Lamarck and later replaced by the term “evolution” (Lamarck 1801). During his sojourn in Edinburgh Darwin read several influential books including his grandfather’s book, Zoonomia: or the Laws of Organic Life (Darwin 1794–96) wherein Erasmus argued that every living organism on the Earth had descended from one common ancestor, Lamarck’s Système des Animaux sans Vertebras (Lamarck 1801), and Paley’s (1802) Natural Theology, or Evidences for the existence and attributes of the Deity collected from the appearances of nature in which Paley explained adaptation as God acting through the laws of Nature. While in Edinburgh Darwin forged a friendship with William MacGillivray, the Curator of the University Museum, from whom Darwin learned about anatomy, botany, and making notes on observations. With his developing interest in natural science, Darwin began to keep field notebooks, and joined an undergraduate science club, the Plinian Natural History Society, where, on 27th March 1827, he presented a talk on two marine invertebrates, Flustra (a bryozoan) and Pontiabella muricata (Skate-leech) (Barrett 1977; Burkhardt 2008; Nicholas & Nicholas 2008).
While his father hoped that Darwin would continue in the family tradition of practicing medicine, Darwin did not complete his medical studies as he was unable to tolerate the sight of blood, nor did he find the classes interesting.

Robert Darwin, aware that his son did not want to become a physician, proposed that he should study theology to become a dergeman (Barlow 1958). To that end, in January 1828, Darwin entered Christ's College, Cambridge where he enrolled in a three-year Bachelor of Arts degree as a precursor to studies in Theology (Price 2008). At Cambridge, as at Edinburgh, Darwin's interests were clearly outside the established academic curriculum. He met Reverend Professor John Henslow, botanist, naturalist, and theologian who encouraged his interest in natural history for which there was no degree offered at that time (Burkhardt 2008). Henslow became Darwin's tutor in geology (Goikie 1909), and his friend and mentor with whom he maintained a constant correspondence for many years. He encouraged Darwin to broaden his study of the natural world, and recommended John Herschel's A Preliminary Discourse on the Study of Natural Philosophy (1831) which, in part, advocated the use of observation and experimentation in scientific research. A letter to Henslow from Darwin reveals that, as early July 1831, Darwin had read von Humboldt's Personal Narrative of Travels to the Equinoctial Regions of the New Continent during the Years 1799-1804 (in 7 volumes) (1814–29), the book that inspired him to travel to the New World (Burkhardt 2008).

It was at Cambridge that Darwin also met geologist, Adam Sedgwick, Woodwardian Professor and Chair of Geology, through whom Darwin became interested in geology (Price 2008). In 1831, Darwin accompanied Sedgwick on a two-week geological field trip to Wales, during which he became conversant with the methods of recognising and interpreting fossils and rock formations, field methods which he would use and later refine during the voyage of H.M.S. Beagle (Barlow 1958). Darwin completes his undergraduate studies after undertaking units in geology, and graduates in 1831.

The voyage of H.M.S. Beagle

The five-year voyage of H.M.S. Beagle was to set Darwin irrevocably on the path to becoming a distinguished naturalist, an experience which, in his autobiography, he acknowledged "... has been by far the most important event in my life and has determined my whole career" (Barlow 1958), and will establish Darwin as an eminent geologist whose observations and theories would support Charles Lyell's uniformitarian theories (Desmond & Moore 1991).

Darwin's journey began on the 30th August 1831, several months before H.M.S. Beagle was due to commence its voyage, when he received a letter from Henslow informing him that Captain FitzRoy R.N. was seeking an unofficial, unpaid naturalist to sail with H.M.S. Beagle on its survey voyage to the south coast of South America, a voyage that was expected to last two years (Burkhardt 2008; Price 2008). Darwin was eager to take up the position, and on Henslow's recommendation, Darwin was invited to travel on H.M.S. Beagle. As Darwin must pay his own way, Darwin needed his father's financial assistance but faced opposition from him. Josiah, Darwin's uncle, interceded and Darwin's father eventually agreed that Darwin could go on the voyage, and further that he would pay all Darwin's costs that would be incurred during the voyage (Price 2008). Having received his father's permission, Darwin left England on board the H.M.S. Beagle, on the 27th December 1831.

A full description of the voyage of H.M.S. Beagle, the subject of numerous books, is not possible here, however a chronology of the voyage is provided in Table 1, followed by comments on several places of call where Darwin embarks on excursions and undertakes field work.

After two weeks of continuous sailing, on 16th January 1832, H.M.S. Beagle arrived at the Cape Verde Islands, an archipelago of volcanic outcrops approximately 400 miles off the coast of West Africa where the Beagle was to remain for twenty-three days (Price 2008). Darwin disembarked at St. Jago, and welcomed the respite from the chronic seasickness which was to afflict him throughout the voyage. He wrote to his father that: "St. Jago has afforded me an exceedingly rich harvest in several branches of Nat: History" (Burkhardt 2008). The Cape Verde Islands also provide Darwin with his first opportunity to explore a volcanic island, and it is here that Darwin conceived the idea to write a book on geology (Moorehead 1969).

Leaving the Cape Verde Islands, the Beagle reached Brazil six weeks later and landed at the ancient town of Bahia where Darwin "... in earnest strolled in the forests of the new world" (Burkhardt 2008). Darwin at last is fulfilling his desire to see the New World which was inspired by his reading of Alexander von Humboldt's Personal Narrative (1814–29).

The next two years are spent surveying the southeastern and southern coastline of South America during which time Darwin spent many weeks ashore. Rio de Janeiro presented Darwin with an opportunity to begin his botanical research and collection of specimens. He took up rented quarters in Botofogo Bay and within days visited a plantation 100 miles from the town, passing through tropical forest which, with its profusion of flora and fauna, was a source of delight to Darwin (Moorehead 1969). Darwin's observations were not restricted to the flora and fauna of South America. In Argentina, he undertook an excursion to the pampas where he observed not only the wildlife but the life-style of the gauchos who spent much of their time in the saddle, and noted, in particular, their hunting skills with the lasso and bolas. It was on the pampas that Darwin observed two species of rhea which, in On the Origin of Species, he would use as an example of two separate species co-existing in the same place while remaining distinct (Darwin 1859). Travelling south, the Beagle landed in Tierra del Fuego, the indigenous inhabitants of which Darwin described in a letter to Henslow on 11th April 1833: "The Fuegians are in a more miserable state of barbarism than I ever expected to see in a human being" (Burkhardt 2008). However, despite his unfavourable observations of the Fuegians, he found the geology "very interesting – the country is non
Charles Darwin: his life and times

Darwin's contribution in his publication, *On the Origin of Species by Means of Natural Selection*, was a major event in the history of science, and the influence of his theory of evolution had far-reaching effects - not only biologically, but also in other arenas of science, as well as socially, and theologically. This contribution examines the life and times of Darwin listing and briefly describing what I consider to be the milestone events in his life. From 1809, the year of his birth, to 1882, the year of his death, I have divided Darwin's life into six phases: 1. his early years dealing with his childhood and college years; 2. the historic voyage of *H.M.S. Beagle* during which he collected much of the data that were to help develop the theory of evolution; 3. the post-*Beagle* years when he published some of the results obtained during the voyage of the *Beagle*, continued further research and publishing, moved into the scientific community, and married; 4. Published *On the Origin of Species by Means of Natural Selection*; 5. the period immediately after publication of the book when there was intense debate and controversy about the theory and its implications, which continue to this day; and 6. His final years wherein he continues research and publishing until his death.

**1809-31 Early Days**

1809  
Born 12th February in Shrewsbury, Shropshire, England; fifth child of a local doctor, and grandson of the physician, natural scientist and poet, Erasmus Darwin who was one of the first writers to suggest that existing species might have evolved from earlier forms of life; shows an early interest in natural history.

1818  
Darwin's mother dies; Darwin sent to Shrewsbury School.

1825  
Attends University of Edinburgh to study medicine; does not complete studies.

1827  
Enter Christ's College, Cambridge to study theology; meets Prof. John Henslow, botanist and naturalist; Darwin extends his knowledge of natural history and spends many hours on the seashore studying barnacles; becomes interested in geology during a visit to Wales; graduates in 1831.

1831  
On Henslow's recommendation, Darwin is invited to travel on *H.M.S. Beagle* on its second surveying voyage as naturalist and companion to Captain Robert FitzRoy.

**1831-36 The Voyage of H.M.S. Beagle**

1831  
27th December: *H.M.S. Beagle* leaves England.

1832  
16th January: Arrives Cape Verde Islands and at St. Jago discovers rock cliffs embedded with seashells.

28th February: Arrives Bahia, Brazil; in the rain forests, Darwin collects exotic insects.

1832-34  
Two years spent surveying the coast of southern South America and the Falkland Islands, the main objective of the expedition; Darwin observes the Indigenous people of Tierra del Fuego.

1835  
16th September to 20th October: Galapagos Islands; first geological description of Galapagos islands; Darwin perceives the significance of the linear arrangement of the volcanoes on the islands; collected many specimens of closely-related finches; Darwin later realises that similar and therefore closely-related species frequently occur in adjacent regions.

The *H.M.S. Beagle* crosses the Pacific Ocean, landing in Tahiti on 15th November and New Zealand on 21st December. Observations of coral islands and volcanic islands provide material for two books.

1836  
12th January: Arrives at Sydney Cove; visits Sydney and the Blue Mountains; travels extensively in Tasmania; stops at King George Sound in W.A.; Darwin describes the geology of Australia as 'magnificent, astounding, and unique' (his formal description of the geology of New South Wales appears as Chapter 4 of *Volcanic Islands*); discovers two new species of brachiopod; makes detailed observations of many species of trees in Australia, attributing their general appearance of 'infertility' to "...a great deficiency of rain and running water"; Darwin is intrigued by Australia's fauna, his observations leading him to make important conclusions about animals in different parts of the world having similar adaptations but obviously belonging to different species (now known as convergent evolution); observes Aboriginal people and remarks on their hunting skills, however, he does not fully appreciate the richness of the hunter-gatherer lifestyle, placing them 'some few degrees higher in civilisation' to the "Feugians" (the Indigenous people of Tierra del Fuego) who he considers barbaric.

2nd October: arrives back in England and is reunited with his family.
1837 The post-Beagle Years

July: Darwin opens his Red Notebook, which reveals his first speculations on the transmutation of species, thus beginning the process that would lead to the theory of natural selection, the first comprehensive outline of which was written in 1842.

1838-42 As editor, Darwin oversees the publication of The Zoology of the Voyage of H.M.S Beagle in five parts: Birds (by John Gould), Fish (by Leonard Jenyns), Fossil Mammalia (by Owen), Mammalia (by G. R. Waterhouse), and Reptiles (by Thomas Bell).

1839 January: Marries his cousin, Emma Wedgwood; first child born at the end of that year; first edition of Journal of Researches is published.

1842-46 The extensive geological observations and notes Darwin made during the voyage on H.M.S Beagle result in the publication of three volumes, one each on coral reefs (1842), volcanic islands (1844), and South America (1846).

1847 March: Moves to London where he sees his future with the scientific elite; becomes involved with the Geological Society of London where, as a supporter of Lyell, is acknowledged as one of the elite group entitled to speak with authority on theoretical issues; ill-health prompts the purchase of, and subsequent move to, the house of Down in Kent.

1858 Daughter, Anne, dies; Darwin’s faith is tested; becomes an agnostic.

1st July: The Down-Wallace paper - On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection - was communicated to the Linnean Society of London by Sir Charles Lyell, J. D. Hooker, and others.

1859 On the Origin of Species by Means of Natural Selection

24th November: On the Origin of Species by Means of Natural Selection is published; five editions follow (1860, 1861, 1866, 1869 and 1872), each edition updated with new information, and answers to questions raised by critics; title modified to The Origin of Species in the sixth edition.

On the Origin of Species provides a plausible mechanism to explain how species can change: natural selection. In providing this mechanism, Darwin succeeds where his grandfather, Erasmus, had failed. Embedded in this comprehensive work is the idea of a species as a population; speciation in which Darwin stresses the importance of isolation; sexual selection; and intercrossing of individuals, amongst others.

Opinion of Science, Church and Public

Darwin’s theory of evolution challenged most biologists who thought of species as fixed and eternal groups, ordained by God. They thought that each species had its essential defining characteristics, facies assumed to be those possessed by the original member of each species. Many biologists failed to see how wings, for example, could have arisen except by a sudden major modification.

However, Darwin had the support of many including Thomas Huxley who engaged in vigorous debates with Darwin’s critics, e.g., Bishop Wilberforce and comparative anatomist, theistic evolutionist and leading opponent of Lamarckism, Richard Owen. Another of Darwin’s supporters, Asa Gray, Professor of Botany at Harvard, was the major champion of Darwinism in America. William Thomson (later Lord Kelvin) indirectly argued against natural selection also, by attacking Lyell’s uniformitarian geology. Darwin had relied on the vast amounts of time allowed by Lyell’s geology because he believed that natural selection was an immensely slow process. The popular press of the time is scoffing and publishes caricatures of Darwin. Darwin’s friendship with Richard FitzRoy, who believes the literal interpretation of the Bible, breaks down, and Darwin’s long friendship with Henslow is also adversely affected ... the debate continues to this day!

The Final Years

1870s Darwin’s health, which has been poor for many years, improves; continues work on botanical projects; studies the small-scale effects that were most directly illuminated by his theory of local adaptation due to natural selection.

1881 Publishes his last major work, a book on earthworms.

1882 19th April: Darwin dies at his home in Down, Kent, and is buried in Westminster Abbey.

Figure 1. Summary of the major milestones in Charles Darwin’s life.
### Table 1
Chronology of the voyage of H.M.S. Beagle with details of Darwin's excursions (after Moorehead 1969)

<table>
<thead>
<tr>
<th>Date/Period</th>
<th>Place of call</th>
</tr>
</thead>
<tbody>
<tr>
<td>27 December 1831</td>
<td>H.M.S. Beagle departs from Plymouth Sound, England</td>
</tr>
<tr>
<td>1832</td>
<td></td>
</tr>
<tr>
<td>18th January to 8th February</td>
<td>Arrives at Cape Verde Islands</td>
</tr>
<tr>
<td>28th February to 18th March</td>
<td>Bahia (now Salvador) in Brazil</td>
</tr>
<tr>
<td>8th to 23rd April</td>
<td>Excursions to various estates inland</td>
</tr>
<tr>
<td>4th April to 5th July</td>
<td>Rio de Janeiro, Brazil</td>
</tr>
<tr>
<td>26th July to 19th August</td>
<td>Montevideo, Uruguay</td>
</tr>
<tr>
<td>6th September to 17th October</td>
<td>Bahia Blanca, Argentina</td>
</tr>
<tr>
<td>2nd to 26th November</td>
<td>Montevideo, Uruguay</td>
</tr>
<tr>
<td>16th December to 26th February 1833</td>
<td>Tierra del Fuego, Argentina</td>
</tr>
<tr>
<td>1833</td>
<td></td>
</tr>
<tr>
<td>1st March to 6th April</td>
<td>Falkland Islands</td>
</tr>
<tr>
<td>28th April to 23rd July</td>
<td>Maldonado, Uruguay</td>
</tr>
<tr>
<td>3rd to 24th August</td>
<td>Mouth of the Rio Negro, Brazil</td>
</tr>
<tr>
<td>11th to 17th August</td>
<td>Excursion from El Carmen to Bahia Blanca</td>
</tr>
<tr>
<td>24th August to 6th October</td>
<td>Surveying the coast of Argentina</td>
</tr>
<tr>
<td>8th to 20th September</td>
<td>Excursion from Bahia Blanca to Buenos Aires</td>
</tr>
<tr>
<td>6th to 19th October</td>
<td>Maldonado, Uruguay</td>
</tr>
<tr>
<td>22nd September to 20th October</td>
<td>Excursion to Santa Fe and along the Parana</td>
</tr>
<tr>
<td>21st October to 6th December</td>
<td>Montevideo, Uruguay</td>
</tr>
<tr>
<td>14th to 28th November</td>
<td>Excursion to Mercedes, Argentina</td>
</tr>
<tr>
<td>23rd December to 7th January 1834</td>
<td>Port Desire, Argentina</td>
</tr>
<tr>
<td>1834</td>
<td></td>
</tr>
<tr>
<td>9th to 19th January</td>
<td>Port Saint Julian, Argentina</td>
</tr>
<tr>
<td>29th January to 7th March</td>
<td>Tierra del Fuego, Argentina</td>
</tr>
<tr>
<td>10th March to 7th April</td>
<td>Falkland Islands</td>
</tr>
<tr>
<td>13th April to 12th May</td>
<td>Santa Cruz river, Argentina</td>
</tr>
<tr>
<td>18th April to 8th May</td>
<td>Excursion up the Santa Cruz river</td>
</tr>
<tr>
<td>28th June to 13th July</td>
<td>Chiloe, Chile</td>
</tr>
<tr>
<td>31st July to 10th November</td>
<td>Valparaiso, Chile</td>
</tr>
<tr>
<td>14th August to 27th September</td>
<td>Excursion into the Andes</td>
</tr>
<tr>
<td>21st November to 4th February 1835</td>
<td>Chiloe and Chonos archipelago</td>
</tr>
<tr>
<td>1835</td>
<td></td>
</tr>
<tr>
<td>8th to 22nd February</td>
<td>Valdivia, Chile</td>
</tr>
<tr>
<td>4th to 7th March</td>
<td>Concepcion, Chile</td>
</tr>
<tr>
<td>11th to 17th March</td>
<td>Valparaiso, Chile</td>
</tr>
<tr>
<td>13th March to 10th April</td>
<td>Excursion from Santiago across the Andes to Mendoza</td>
</tr>
<tr>
<td>27th March to 17th April</td>
<td>In the neighbourhood of Concepcion</td>
</tr>
<tr>
<td>17th April to 27th June</td>
<td>Chilean coast</td>
</tr>
<tr>
<td>27th April to 4th July</td>
<td>Excursion to Coquimbo and Copiapo, Chile</td>
</tr>
<tr>
<td>12th to 15th July</td>
<td>Iquique, Peru</td>
</tr>
<tr>
<td>19th July to 7th September</td>
<td>Callao, Peru</td>
</tr>
<tr>
<td>16th September to 20th October</td>
<td>Galapagos Islands</td>
</tr>
<tr>
<td>15th to 20th November</td>
<td>Tahiti</td>
</tr>
<tr>
<td>21st to 30th December</td>
<td>New Zealand</td>
</tr>
<tr>
<td>1836</td>
<td></td>
</tr>
<tr>
<td>12th to 30th January</td>
<td>Sydney, Australia</td>
</tr>
<tr>
<td>2nd to 17th February</td>
<td>Hobart, Australia</td>
</tr>
<tr>
<td>3rd to 14th March</td>
<td>King George Sound, Australia</td>
</tr>
<tr>
<td>2nd to 12th April</td>
<td>Cocos (Keeling) Islands</td>
</tr>
<tr>
<td>29th April to 9th May</td>
<td>Mauritius</td>
</tr>
<tr>
<td>31st May to 18th June</td>
<td>Cape of Good Hope, South Africa</td>
</tr>
<tr>
<td>7th to 14th July</td>
<td>St Helena</td>
</tr>
<tr>
<td>19th to 23rd July</td>
<td>Ascencion Island</td>
</tr>
<tr>
<td>1st to 6th August</td>
<td>Bahia, Brazil</td>
</tr>
<tr>
<td>12th to 17th August</td>
<td>Pernambuco, Brazil</td>
</tr>
<tr>
<td>2 October 1836</td>
<td>Voyage ends with the Beagle's arrival at Falmouth, England</td>
</tr>
</tbody>
</table>
fossiliferous and a common place succession of granitic rocks & Slates: attempting to make out the relation of cleavage, strata &c. anchored off the coast of Chile near Chiloe Island, (Burkhardt 2008). Before leaving South America, the Beagle sailed up the west coast of South America. While anchored off the coast of Chile near Chiloe Island, Darwin and FitzRoy observed two volcanic eruptions on the mainland, and later, in the town of Concepcion, Darwin saw the devastation caused by an earthquake, the epicenter of which was located near the town (Darwin 1844). Darwin recorded that: "since the great Earthquake ... the Island of S. Maria [a volcanic island off the Chilcan coast] has been elevated 10 feet: Capt. FitzRoy found a bed of Muscles [sic] with putrid fish that many feet above high water mark" (Burkhardt 2008).

After leaving South America, the crossing of the Pacific Ocean began. Arriving in the Galapagos Islands on 16th September, the next thirty-six days were spent sailing between the different islands of the archipelago. Darwin’s first reaction to their volcanic landscape was not positive, however his initial impression was revised as his Journal records: "The natural history of this archipelago [the Galapagos Islands] is very remarkable: as his Journal records: "The natural history of this archipelago is very remarkable: the archipelago [the Galapagos Islands] is very remarkable: Darwin’s first reaction to their volcanic landscape was not positive, however his initial impression was revised as his Journal records: "The natural history of this archipelago [the Galapagos Islands] is very remarkable: as his Journal records: "The natural history of this archipelago [the Galapagos Islands] is very remarkable:

Darwin discovered that the islands were formed in relatively recent times, a process that was still continuing, and made the first geological description of them (Darwin 1844). One of the most important fauna that Darwin observed in the Galapagos Islands were the thirteen species of finch, John Gould’s illustrations of which would show the differences in size and shape of beak which were adaptations to food source (Gould 1841; Darwin 1859). Darwin would later propose that the different species of finch were descendants of a common ancestor, and that closely-related species often occur in adjacent regions (Darwin 1859).

After leaving the Galapagos Islands, H.M.S Beagle visited Tahiti and New Zealand in November and December, 1835, then proceeded to Australia, arriving at Sydney Cove, New South Wales on 12th January, 1836. The other regions visited in Australia were Tasmania where Darwin travelled extensively, and King George Sound in Western Australia. Whilst in Australia, Darwin made detailed observations of many species of trees, attributing their general appearance of "infertility [due to] ... a great deficiency of rain and running water" (Darwin 1839). Darwin was intrigued by Australia’s fauna, his observations leading him to make important conclusions about animals in different parts of the world having similar adaptations but obviously belonging to different species - now known as convergent evolution (Darwin 1839). He described the geology of Australia as "magnificent, astounding, and unique" with his formal description of the geology of New South Wales appearing as Chapter 4 in Geological observations on the volcanic islands visited during the voyage of H.M.S Beagle Darwin (1844). In Tasmania, 4 km south of Hobart, Darwin discovered two species of brachiopod which he termed "Terebratula". These were later identified as new species and named by G. B. Sowerby, Producta brachythaerus and Spirifera subradiata (in appendix to Darwin 1844). Darwin also observed Aboriginal people and remarked on their hunting skills, however he did not fully appreciate the richness of their hunter-gatherer lifestyle, placing them “some degrees higher in civilization ... to the Fugijans” who he considered to be barbaric (Nicholas & Nicholas 2008). H.M.S Beagle left Australian waters on the 14th March, 1836 and, after making landfall several times, arrived back in England on the 2nd October 1836.

The record of Darwin’s voyage on H.M.S. Beagle first appeared as the third volume (Journal and Remarks) of Narrative of the Surveying Voyages of His Majesty’s Ships Adventure and Beagle (FitzRoy 1839), later published in its own right as the Journal of Researches into the Geology and Natural History of the Various Countries Visited by H.M.S. Beagle under the Command of Capt. FitzRoy, R.N. (Darwin 1839), with a second edition published in 1845 (Darwin 1845); in its current form it is known as The Voyage of the Beagle.

The post-Beagle Years

The post-Beagle years begin with Darwin’s return to England in 1836, and end with the presentation of the joint Darwin-Wallace paper read to the Linnean Society in 1858. These two important decades in Darwin’s life started in Cambridge where he spent several months, followed by his move to London, marriage to Emma Wedgwood, and his entry into the scientific community. It was a time when he made influential friends who would later champion his theory of evolution after the publication of On the Origin of Species.

The five-year voyage of the Beagle ended in October 1836. After a brief sojourn with his family in Shrewsbury, Darwin travelled to Cambridge and spent several months cataloguing the specimens from the voyage that had been stored by Henslow. In March 1837 Darwin moved to London where he perceived his future to lie with the scientific elite. It was a time when there was geological debate between two camps, the catastrophists and the uniformitarians, of which Sedgwick was a leading member in the first instance, and Lyell, with whom Darwin was aligned, in the second (Bowler 1990). On Lyell’s nomination, Darwin was accepted as a member of the Geological Society of London where he was welcomed as a geologist who could speak on equal terms with men of science, and a member of a select group entitled to speak with authority on theoretical issues (Bowler 1990). Darwin was elected a Fellow of the Royal Society in January, 1839, and Vice-President of the Geological Society of London in 1845; he also became a member of The Royal Geographical Society, and the Zoological Society of London. At this time Darwin was appointed to a committee to “consider the rules by which the Nomenclature of Zoology may be established on a uniform and permanent basis” (Darwin et al. 1842).

In January 1839, Darwin married his cousin, Emma Wedgwood. Their first child, William, was born at the end of that year. Nine more children are to follow. Darwin’s ill-health prompted the purchase of, and subsequent move to, the house at Down in Kent in 1842.

Over the next few years Darwin wrote prolifically, drawing on material and observations made during the voyage of H.M.S. Beagle. On the invitation of FitzRoy,
Darwin contributed his *Journal and Remarks* 1832–1835 which are published in 1838 as the third volume of *Narrative of the Surveying Voyages of His Majesty's Ships Adventure and Beagle* (FitzRoy 1839), later republished in its own right as the *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle Round the World* (later known under the title: *The Voyage of the Beagle*). In addition, between 1838 and 1843, Darwin, as editor of *The Zoology of the Voyage of H.M.S. Beagle*, supervised its publication in five parts: 1. *Fossil Mammalia* (Owen 1840); 2. *Mammalia* (Waterhouse 1839); 3. *Birds* (Gould 1841); 4. *Fish* (Jeffreys 1842); and 5. *Reptiles* (Bell 1843).

The extensive geological observations and notes that Darwin had made during the voyage provided the basis for three books, the short titles of which are: *The Structure and Distribution of Coral Reefs* (published in 1842); *Geological Observations on the Volcanic Islands Visited During the Voyage of H.M.S. Beagle* (published in 1844); and *Geological Observations on South America* (published in 1846). The years between 1846 and 1854 were devoted to his research on barnacles which resulted in two monographs (each in two volumes): *Living Cirripedia* (Darwin 1851a; Darwin 1854a) and *Fossil Cirripedia* (Darwin 1851b and 1854b).

**Darwin, Wallace, and a theory of evolution**

Alfred Russel Wallace (1823–1913) was a British naturalist and biologist who had travelled extensively in South America and the Malay Archipelago in the late-1840s and 1850s collecting zoological and botanical specimens for sale in Britain. It had been a decade since Darwin returned to England, and a time when Darwin was slowly formulating his theory on evolution. In a letter to Hooker dated 11th January, 1844, Darwin revealed that since his return to England he had been "... engaged in a very presumptuous work ..." and that he was almost convinced that species were not immutable, and that his conclusions were not dissimilar to those of Lamarck; "... though the means of change are wholly so" (Burkhardt 2008).

Both Darwin and Wallace had read Malthus' *An Essay on the Principle of Population* (1798). Darwin's *Autobiography* records that he read Malthus' essay in October 1838 — he comments:

```
I happened to read for amusement Malthus on Population, and being prepared to appreciate the struggle for existence which everywhere goes on, from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result would be the formation of a new species (Barlow 1958)
```

Also in 1838 Darwin recorded in his Notebook (designated "D") his first reference to the principle of population, and that Malthus' concept of the 'struggle for existence' played a major role in leading his thoughts towards natural selection (Bowler 1990). This is borne out in a letter from Darwin to Wallace six months after the publication of *On the Origin of Species*:

```
You are right, that I came to the conclusion that selection was the principle of change from study of domesticated productions; & then reading Malthus I saw at once how to apply this principle (Burkhardt 2008)
```

Wallace also had been formulating a theory of evolution along similar lines to Darwin. In 1855 Wallace published a paper entitled: "On the law which has regulated the introduction of new species" in *Annals and Magazine of Natural History* (Wallace 1855). The law proposed that every species has come into existence coincident both in time and space with a pre-existing, closely allied species. At this time Darwin and Wallace were corresponding regularly; Darwin received a letter from Wallace dated 10th October, 1856, and in his reply (dated 1st May 1857) acknowledged that he had also read Wallace's paper, and "... can plainly see that we have thought much alike & to a certain extent have come to similar conclusions" (Burkhardt 2008). In this same letter Darwin wrote that he was preparing his work for publication but did not think that the book would be published for at least two years (Burkhardt 2008).

Lyell urged Darwin, who had been developing his theory for over twenty years, to write up his theory for publication to establish precedence (Bowler 1990). Darwin received a manuscript from Wallace in June 1858 in which a principle of natural selection was proposed that was almost identical to Darwin's idea, precipitating a crisis in Darwin. On the advice of Lyell and Hooker, a simultaneous publication of Wallace's paper and a short extract of Darwin's own to ensure propriety was arranged (Bowler 1990). Thus, on the 1st July 1858 the Darwin-Wallace paper — *On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection* — was communicated to the Linnean Society of London by Sir Charles Lyell and J. D. Hooker, and published in the *Proceedings of the Linnean Society, Vol. 3 1858*, pp. 45-62. The paper consisted of: 1. a letter of introduction by Charles Lyell and Joseph D. Hooker; 2. an unpublished Work on Species by C. Darwin, Esq. consisting of a portion of a chapter entitled, "On the Variation of Organic Beings in a state of Nature; on the Natural Means of Selection; on the Comparison of Domestic Races and true Species"; 3. an abstract of a letter from C. Darwin, Esq. to Prof. Asa Gray (Boston, U.S.) dated 5th September, 1857; and 4. the manuscript "On the Tendency of Varieties to depart indefinitely from the Original Type" (known as the *Ternate Paper of 1858*) by Alfred Russel Wallace.

### On the Origin of Species by Means of Natural Selection

In Darwin's time, the concept of evolution by descent was not a new concept, dating at least from the classical Greek philosophers. Leakey (1979) states there were no fewer than twenty predecessors who had written on aspects of evolution before Darwin, for example, in the early 18th Century Carolus Linnaeus (1707–1778) postulated limited mutability of species by descent and hybridization, and coined the term "transmutation". Towards the end of the century, Erasmus Darwin (1731–1802), and the French naturalist, Jean Baptiste de
Lamarck (1744–1829) were the main proponents of evolution (transmutation) at a time when the majority of naturalists were concerned with species identification (Leakey 1979; Bowler 1990). Later, Chambers, publishing anonymously in England, proposed a theory which argued for an evolutionary view of life similar to that proposed by Lamarck (Chambers 1844).

On the 24th November, 1858, Darwin’s theory of evolution was published under the title On the Origin of Species by Means of Natural Selection; or the Preservation of Favored Races in the Struggle for Life. Five editions follow (1860, 1861, 1866, 1869, and 1872), each updated with new information, with answers to questions raised by critics. The title is modified to The Origin of Species in the sixth edition.

Modern evolutionary theory derives from Darwin with On the Origin of Species providing a plausible mechanism to explain how species can change, that is, natural selection. In providing this mechanism, Darwin succeeded where his grandfather, Erasmus Darwin, and others had failed (Leakey 1979). Embedded in Darwin’s comprehensive work is the concept of descent by modification which could result in the appearance of new species, the idea of a species as a population; speciation in which Darwin stressed the importance of isolation; sexual selection; and intercrossing of individuals (Leakey 1979).

Opinion of Science, Church and Public

The publication of On the Origin of Species aroused intense interest in all sectors of society, not only in England but also in the United States, and was the focus of heated debate.

Science

Darwin, who was living in Down, though physically removed from the centre of debate, was not insulated from the controversy that raged over his theory; he wrote to Lyell on 10th December 1859 to say that he had heard that “Herschel says my Book is the law of higgledy-pigglety” a comment that Darwin believed was contemptuous, and which, if it was true, was a “great blow and discouragement” (Burlhardt 2008).

However, Darwin had the support of many notable people in science, including botanist, Joseph Hooker, and naturalist, Thomas Huxley (who was later dubbed “Darwin’s bulldog”), who engaged in vigorous debates with Darwin’s critics, namely Bishop Samuel Wilberforce of Oxford (at the 1860 Oxford evolution debate – “the Great Debate”), and comparative anatomist, theistic evolutionist, and leading opponent of Lamarckism, Richard Owen (Leakey 1979; Desmond & Moore 1991). Owen (1860) was responsible for a damaging review of On the Origin of Species in the Edinburgh Review in which he labelled transmutation as nonsense, a comment which drew public castigation from Huxley.

Another of Darwin’s supporters, Asa Gray, Professor of Botany at Harvard University, was the champion of Darwinism in America, and on the Continent, William Haeckel, a German biologist, became a great promoter of Darwin’s theory (Quammen 2008).

The Church

The responses to Darwin’s theory by theologians varied widely. Prof. Adam Sedgwick, a geologist and theologian who followed the natural theology tradition, accepted Darwin’s idea of change over time but disagreed about the mechanism (Clark & Hughes 1890). On the other hand, Charles Kingsley, a country rector and novelist who was described by Huxley as “an excellent Darwinian to begin with”, praised On the Origin of Species and wrote that “… if you be right I must give up much that I have believed” (Desmond & Moore 1991).

Darwin’s friend and mentor, Henslow wrote to Rev. Jenyns (his brother-in-law) and said that “the Book is a marvellous assemblage of facts & observations – & no doubt contains much legitimate inference – but it pushes hypotheses (for it is not real theory) too far”, however Henslow eventually dissented and protested to the papers when he was linked with Darwin’s supporters (Desmond & Moore 1991), no doubt a great disappointment to Darwin.

Across the Atlantic Ocean in America, Charles Hodge, Principal of Princeton Theological Seminary, was affronted by Darwin’s theory of natural selection, arguing that Darwinism was, in essence, atheism, and launched a sustained assault on Darwin’s theory over a number of years (Hodge 1874).

The Public

The popular press was scathing; contemporary cartoon commentary tended to focus on primate evolution, especially after the publication of Darwin’s (1871) book, The Descent of Man (Quammen 2008). Punch relentlessly published many caricatures of Darwin, for example, one in 1861 entitled Monkeyana depicted a grotesque cartoon of an ape sporting a placard on which were the words: “Am I man and a brother?”. Light satire focussed on Darwin was still being published by Punch in 1887, nearly thirty years after publication of On the Origin of Species (Quammen 2008). Not only did Punch lampoon Darwin, in 1881 Professor Huxley, (who was Inspector of Fisheries at the time), a long-time friend of Darwin, featured in Punch’s Fancy Portraits – No 23 where he is unflatteringly shown riding a fish and dubbed with the following caption: “There is more in heaven and earth, O ratio, than is dreamt of in your philosophy – (so perhaps he’ll find it in the rivers)” (Quammen 2008).

The final years

The publication of On the Origin of Species did not mark the end of Darwin’s investigation into natural selection as the mechanism for evolution. In the 1860s Darwin had been studying plant adaptations to attract insect pollinators, in particular orchids and their pollinators, to demonstrate how natural selection worked, that is, in the case of orchids there was a mutual dependence in which both insect and orchid exert selective pressure on the other. His research was published by John Murray on 15th May, 1862 in a book entitled: The Various Contrivances by which British and Foreign Orchids are Fertilized by Insects (Darwin 1862).

In the 1870s Darwin’s health, which had been poor for many years, improves. By this time evolution as descent
with modification had become accepted by most scientists, but few agreed that natural selection had been the main but not the exclusive means of modification (Bowler 2003). Darwin now turned his thoughts to the evolution of humans, a subject to which he only vaguely alluded in *On the Origin of Species. The Descent of Man, and Selection in Relation to Sex*, published in 1871, draws evidence from many sources that illustrated that humans were animals showing continuity of mental and physical attributes, an idea that would not have been well received at the time of publication of *On the Origin of Species* twelve years earlier. Darwin provided evidence to show that humans are all one species, and covered the subjects of sexual dimorphism, cultural racial characteristics, and the evolution of human culture (Darwin 1871).

Darwin published his last major work in 1881: *The Formation of Vegetable Mould, through the Action of Worms, with Observations on Their Habits* (Darwin 1881) about which Darwin commented: "... a subject of but small importance; and I know not whether it will interest any readers, but it has interested me" (Barlow 1958).

Charles Robert Darwin died on the 19th April, 1882 at his home, Down House, in Kent. He was honoured with a State funeral and is buried in the Nave at Westminster Abbey with other luminaries such as Ben Jonson, Isaac Newton, Robert Stevenson, David Livingstone, and Clement Attlee.

**Afterword**

This paper has focussed on the life of Charles Darwin, the *naturalist*, but it should not be forgotten that Darwin began his scientific career as a geologist. Geikie, at the Darwin Centennial Commemoration on 24th June, 1909, paid homage to Darwin when he delivered The Rede Lecture entitled: *Charles Darwin as Geologist* (Geikie 1909). He described Darwin as a man whose earlier years were devoted mainly to geological problems, and it was:

... from the side of geology that he was led into those evolution studies which have given him so just a title to our admiration and gratitude, and have placed him so high among the immortals (Geikie 1909)  

This is fitting praise for a man who has contributed so much to the understanding of the world in which we live.

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Charles Darwin in Australia

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It is well-known that Darwin did not particularly like Australia, and negative images shine through the writings — notes, diaries and letters — that he compiled while he was here. He visited three different parts of Australia. 12th-30th January 1836 (an extremely hot January) had seen him at Port Jackson in New South Wales, and then riding inland to the Blue Mountains and Bathurst. After 'a six days passage .. the latter part of which were very cold and squally' the ship arrived at Hobart Town, where he spent 7th-17th February. Then, after a passage during which he suffered 'no little misery' from the 'strong westerly swell' the Beagle spent a week at King George's Sound (6th-14th March). Charles Darwin thus spent a total of some 36 days or part-days in the Australian colonies (Barlow 1934; Nicholas & Nicholas 1989; Armstrong 2004).

Amongst his first impressions approaching New South Wales in the ship was that the land 'was covered by thin scrubby trees that bespoke useless sterility'. On 20th January he reached Bathurst which he thought 'not very inviting': 'a hideous little red brick church' stood by itself. On his return ride towards Sydney he stayed for one night at a farm run by two newly arrived Englishmen: 'the total want of comfort was not very attractive'. Darwin did not like the reliance of the colony on convict labour, he thought the people were money-grubbing, and remarked that 'children learn the vilest expressions'. Maybe he had a point (Barlow 1934).

His comments on the tiny settlement of King George's Sound on the Southwest of the continent were particularly acerbic. 'He who thinks like me will never wish to walk again in so uninviting a country'. Negative words and phrases abound: 'bare hills', 'sandy, very poor soils', 'stunted trees', 'uncomfortable appearance', 'coarse grass'. And on departing:

Since leaving England I do not think we have visited any one place so very dull & uninteresting as K. George’s Sound. Farewell Australia, you are a rising infant & returned full of admiration at the whole scene. It is a most magnificent testimony to the power of the British nation: here in a less promising county scores of years have effected many times more than centuries in South America. My first feeling was to congratulate myself I was born an Englishman. ... the streets are regular, broad, clean and kept in excellent order ... shops are well furnished (Diary 12 January 1836)

And so it goes on. He comments on the rapid expansion of the suburbs of Sydney, comparing this to the development of London and Birmingham. The transport infrastucture is particularly admired, for example the 'many large ships' in Sydney Cove, and the surrounding warehouses. The roads were excellent and made on the Macadam principle, he remarks. He approved of the early development of steamships, which he noted in both Port Jackson and Hobart Town. He admired the expansion and prosperity of the wool industry; while he stayed on a sheep property, he talked at some length to the superintendent. In Tasmania particularly, he comments favourably on the development of agriculture: 'bright yellow fields of corn', 'potato crops appeared luxuriant', 'good supplies of water', 'scenery magnificent', 'cultivated fields look well', 'gardens abounded with luxuriant vegetables and fruit trees'. He much preferred Tasmania to New South Wales (or King George’s Sound).

It is where he is evaluating the economic development of the Australian colonies that he is most positive. The Darwin family were Whigs, his father, as well as being a doctor, was an entrepreneur; there were family connections with the manufacturing Wedgwoods (Darwin married Emma Wedgwood not long after his return). Whigs believed in progress, trade and industry and the power of science and technology, so the reaction is perhaps not surprising. The landscape was unfamiliar and alien, and it is here that his remarks are most initial downbeat assessment of the countryside of New South Wales comes something of a eulogy:

In the evening I walked through the town & returned full of admiration at the whole scene. It is a most magnificent testimony to the power of the British nation: here in a less promising county scores of years have effected many times more than centuries in South America. My first feeling was to congratulate myself I was born an Englishman. ... the streets are regular, broad, clean and kept in excellent order ... shops are well furnished (Diary 12 January 1836).

I have used the 1934 edition of Darwin’s Journal (Charles Darwin’s Diary of the Voyage of HMS Beagle, edited by Darwin’s granddaughter, Nora Barlow, Cambridge University Press). There are other editions. References here are to Diary. The book now known as The Voyage of the Beagle, is an edited version of this, with the style improved. I used a modern reprint of the 1845 edition.

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negative, particularly during those bakingly hot days in inland New South Wales. But where Darwin looks ahead he is positive: 'Australia you are a rising infant and ... will reign a great princess in the south'; Australia must ultimately depend upon being the centre of commerce for the southern hemisphere, he foresaw. He was often remarkably prescient; he heard that there was 'excellent land' some 30 miles inland from King George's Sound, and he foresaw that in the very near future 'the land will be under cultivation', and the settlement that became Albany would become 'the seaport of this inland district'. Whiggery came with a firm belief in progress and the future.

It is sometimes maintained that by the time he reached Australia Darwin was tired, and fed up with the sea, ships and the sea-sickness to which he was very prone. This may well be so, but his powers of scientific observation and recording remained on a high level. He collected dozens, perhaps hundreds, of insects and shells, and a number of vertebrates (reptiles, birds, fish and amphibians). In Tasmania he found also some flatworms or planaria, which he encountered in the some rotting wood, with which the forested country inland from Hobart abounded. Darwin did a number of experiments with these, testing their irritability. For example he described their reaction to light (they 'disliked' it and immediately crawled beneath fragments of wood). He also bisected one individual, and observed the organism's ability to regenerate from a fragment. But over a month later, as the Bngle entered the tropics 'they gradually sickened and died' The creatures perished 'through neglect' before the work could be completed. Amongst the shells he collected as he clambered over the rocks along the shoreline of the Derwent Estuary were barnacles, the group of which Darwin made a special study in his later life - a study that in no way, established his reputation as a scientist.

His interest in geology was maintained. He wrote an extremely detailed memorandum on the geology of the Hobart region of Tasmania, identifying many rock-types accurately and reconstructing the geological history perceptively; unfortunately it was not published until the 1970s (Banks 1971). He also had some perceptive remarks on the deep valleys in the Blue Mountains, but he was wrong in believing that the sea had had a part in their erosion (Armstrong 1993). He had something of a preoccupation with sea-level change at the time, having just developed his theory of coral reefs. Some of his remarks on the geology of King George's Sound were more accurate, and he compared the rounded granite domes with some of the landscapes of South America, deducing that they were of similar material and had had a similar origin (Armstrong 1985).

He also attended an Aboriginal corroboree at King George's Sound, and has an excellent description of the dances he witnessed. In keeping with his age, Darwin often shows great interest in the weird, extraordinary and (to him) bizarre:

As soon as it grew dark, small fires were lighted, and the men commenced ... painting themselves white in spots and lines, ... large fires were kept blazing, round which the women and children were collected as spectators; the Cockatoo and King George's Men formed two distinct parties, and generally danced in answer to each other. The dancing consisted in their running either sideways or in Indian file into an open space, and stamping on the ground with great force as they marched together. Their heavy footsteps were accompanied by a kind of grunt, by beating their spears together, and by ... extending their arms and wriggling their bodies. It was a most rude and barbarous scene, and to our ideas without any sort of meaning; but we observed that the black women and children watched it with the greatest pleasure. Perhaps these dances originally represented actions, such as wars and victories; there was one called the Emu dance, in which each man extended his arm in a bent manner, like the neck of that bird. In another dance, one man imitated the movements of a kangaroo grazing in the woods, whilst a second crawled up, and pretended to speak him. ...[T]he air resounded with their wild cries. ... the group of nearly naked figures, viewed in the light of the blazing fires, all moving in hideous harmony, formed a perfect display of a festival amongst the lowest barbarians. In Tierra del Fuego, we have beheld many curious scenes in savage life, but never, I think, one where the natives were in such high spirits and so perfectly at their ease. (Voyage of the Bngle Chapter 19)

Darwin sees other peoples through the lens of his own background and education. Here again are the negative phrases: 'rude and barbarous', 'without any sort of meaning', 'hideous', 'lowest barbarians', 'savage'. But there is detailed observation, a comparative approach, and at least an attempt at interpretation. He also encountered indigenous people in New South Wales, suggesting that their numbers were declining. By the time of his Hobart visit the indigenous Tasmanian people had already been nearly exterminated and relocated, but he made extensive enquiries about them.

Darwin collected few plants in Australia, but his observation was excellent.

The extreme uniformity in the character of the Vegetation, is the most remarkable feature in the landscape of all parts of New S. Wales. Everywhere we have open woodland, the ground being partially covered with a most thin pasture. The trees nearly all belong to one peculiar family: the foliage is scanty & of a rather peculiar light green tint; it is not periodically shed: the surface of the leaves are placed in a vertical, instead of as in Europe a nearly
horizontal position: This fact & their scantiness makes the woods light & shadowless; although under the scorching sun of summer, this is loss of comfort, it is of importance to the farmer, as it allows grass to grow where it otherwise could not (Diary 12 January 1836).

Anyone familiar with the Australian bush immediately feels that Darwin has captured the essential nature of Australian eucalypt woodland extremely well. He noted that the trees stood ‘tolerably straight’ and ‘well apart’. He described the way in which the bark was annually shed, often hung in long shreds swinging in the wind, giving the landscape an ‘untidy’ and ‘desolate appearance’, and one of ‘arid sterility’: ‘I cannot imagine a more complete contrast in every respect than the forest of ... Chiloe [an island off the coast of southern Chile], with the woods of Australia’, he wrote.

He recorded:

The Grey hounds pursued a Kangaroo Rat [probably Potarous tridactylus, a potatroo] into a hollow tree out of which we dragged it; it is an animal as big as a rabbit, but with the figure of a Kangaroo.

Darwin noticed that the almost ubiquitous effects of fire and he saw large flocks of white cockatoos (probably sulphur crested, Cacatua galerita), and ‘a few most beautiful parrots’ (perhaps crimson rosella, Platycercus elegans, eastern rosella, Platycercus eximius and king parrot Alisterus scapularis), there were crows ‘like our Jackdaws’, and ‘another bird something like a magpie (Cymnorhina tildien’) (see also Nicholas & Nicholas, 1989). He saw casuarinas, thinking it odd that they were called oaks (she-oaks) as they did not resemble English oaks at all! In the pleasant evening he took a stroll along a chain of ponds, where he had the good fortune to see several individuals of the ‘famous platypus’ or Ornithorhyncus anatinus. In the same dairy entry he recorded:

...I had been lying on a sunny bank & was reflecting on the strange character of the animals of this country compared to the rest of the World. An unbeliever in everything beyond his own reason might exclaim, ‘Surely two distinct Creators must have been at work; their object is the same & certainly the end in each case is complete’ (Diary 18 January, 1836).

But he then spotted an antlion, capturing its prey and he continued:

Without doubt the predaceous Larva belongs to the same genus but to a different species from the European kind. Now what would the Disbeliever say to this? Would any two workmen ever hit on so beautiful, so simple, & yet so artificial a contrivance? It cannot be thought so. The one hand has surely worked throughout the universe. A Geologist perhaps would suggest that the periods of Creation have been distinct & remote the one from the other; that the Creator rested from his labor.

The ‘sunny bank’ was possibly that of Cox’s River, between Blackheath and Bathurst. Darwin had travelled for several days through an open forest of eucalypts, acacias and casurinas, often burnt. He had had been hunting for emu and kangaroo, and seen flocks of cockatoos and parrots. He had encountered groups of hunting Aborigines. He was very conscious of travelling through a very different environment from any that he had seen before.

But there was more to it than that. A few hours before he encountered the antlion, he had held in his hand a somewhat rabbit-like kangaroo-rat; he had had seen several platypus playing in a chain of ponds that represented the dry summer remnants of a river; they ‘might easily have been mistaken for many water rats’, although when his companion shot one he could see that they were quite different – ‘a most extraordinary animal’. There were birds ‘something like the [European] magpie but although black and white, were very different in structure. The Australian trees were completely different from the oaks of the East Anglian and Shropshire countryside (but they were nevertheless trees). And the antlion (the larval form of an insect related to the lacewings, family Myrmeleontidae) was remarkably similar to that from Europe, in its appearance and its behaviour, and yet also subtly different.

Darwin was noticing an environment that was different, with different organisms, isolated from the rest of the world and yet there were creatures that, even if they belonged to different species, genera or families, resembled those with which he was familiar. Of the ‘two distinct Creators’, one of Australia, one of the rest of the world, he mused, ‘their object has been the same and certainly in each case the end is complete’ Today we might argue that the platypus and the water rat, the Australian magpie and its European analogue, the two species of antlion, the marsupial carnivores and their placental mammal equivalents, filled similar ecological niches, and had been subjected to similar selection or adaptation pressures. Darwin was not able to go as far at the time, but he was on his way. He was not an evolutionist when he lay on the grassy bank in New South Wales that hot summer day in early 1836, but he was already beginning to think ecologically, in terms of whole environments, and to wonder about the manner in which individual organisms related to their surroundings. The she-oaks and gum-trees with their vertical leaves, the climate, the occurrence of fire, the soils, the Aborigines, the parrots and cockatoos, the emus, kangaroos and the kangaroo-rat were components of an integrated system.

Towards the end of the voyage Charles wrote in his journal:

The habit of comparison leads to generalisation.

By comparing environments one could bring out themes, trends and ideas. And Darwin was constantly comparing. He compared the Australian bush with the forests of South America, and with English woodlands. He compared the 40 or so islands HMS Beagle had visited. Before Australia the Beagle had called at Cape Verde, St Paul’s and the Falklands in the Atlantic. The islands of Tierra del Fuego and Chiloé (off southern Chile) are of continental rocks and formed a contrast to the corals and
volcanic lavas of many of the islands he visited. Crossing the Pacific, the Beagle touched at four islands of the Galapagos, and at Tahiti; several other islets were observed from afar, before spending a few days at the Bay of Islands, New Zealand. After Australia the little ship proceeded to Cocos (Keeling) Islands and Mauritius and after a brief sojourn at Cape Town, visited Ascension Island, St Helena and the Cape Verde Islands (again) on the homeward run.

Constantly in his notes we see some comparative notes added to observations made when he had seen a similar phenomenon elsewhere. The volcanic rocks of the Galapagos Islands were compared with those of Ascension and St Helena. The customs and appearance of the Tahitians were compared with those of the Maoris, and the Fuegians with the Australian Aboriginal people. Possibly similar comparisons were going on, unconsciously perhaps, when he compared Australian landscapes and societies with those of England. Where there were similarities to things with which he was familiar (in the landscape of Tasmania, in the thrusting economic development of New South Wales) he approved. Where it differed (in the convict society, and in the harsh dry hot interior) he was less impressed.

In the popular imagination, the Galapagos Islands are sometimes seen as the 'high point' of the voyage. But a detailed scrutiny of Darwin's notes shows that he did not particularly like that archipelago, and there was no 'Eureka' moment there. They were important, but not all important. In fact, the young naturalist spent much more time on East Falkland than in the Galapagos Islands. He collected more specimens there, and covered more pages with notes. The visit was prior to that to the Galapagos Islands, but it is possible that he noted that the foxes from East Falkland and West Falkland were different (long before he saw the birds or tortoises of the Pacific island group). Or one could argue that the visits to coral islands – Tahiti, the Cocos (Keeling) Islands and Mauritius – the locales in which he developed his theory of coral reefs, were particularly significant. Or St Jago in the Cape Verde Islands where he first resolved to write a book about his discoveries. Or Australia, where to some extent 'it came together'.

But the argument is barren. It was all of them. It was his comparative approach that served him so well in evaluating the totality of some of the environments he encountered, and was ultimately one of the keys to his success.

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The Importance of Developmental Repatterning in the Evolution of Trilobites

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Abstract

Historically, in his *On the Origin of Species*, Charles Darwin is remembered for, among other things, remarking on how poor the fossil record was and being concerned that it would not support his view of modification by natural selection. He is much less well remembered, though, for arguing for the importance of developmental change in inducing both intra- and interspecific variation. In this paper I explore how, using trilobites, the fossil record can be shown to reflect not only the patterns, but also the processes of evolution, in particular the important role of developmental repatterning (by heterochrony) in evolution. Examples are discussed from Early Cambrian oryctocephalid trilobites from China, and Late Devonian trilobites from Western Australia. Both show evolutionary trends fuelled by heterochrony. Although the targets of selection show significant differences between the Cambrian and Devonian, reflecting, perhaps, changes in the nature of the selection pressure, both demonstrate the importance of heterochrony in convergent evolution.

Keywords: development, evolution, heterochrony, trilobites, Cambrian, Devonian.

Introduction

"Geology assuredly does not reveal any such finely-graduated organic chain; and this, perhaps, is the most obvious objection which can be urged against this theory. The explanation lies...in the extreme imperfection of the fossil record." (Darwin 1859, p. 280).

Of all the doubts expressed by Darwin about the validity of his theory of the origin of species by natural selection, it was the fossil record that seems to have given him the most sleepless nights. At such a nascent age in the development of geology as a science, it is really not surprising that Darwin's opinion of the extent of palaeontological collections was less than enthusiastic: "...our richest geological museums ...what a paltry display we behold!" (Darwin 1859, p. 287). But with the burgeoning collections made, especially during the latter part of the 19th century, and into the succeeding centuries, not only have many examples of the finest gradations that Darwin expected to see been found in many taxa, but so too many of the so-called "missing links" between higher taxa, such as between fish and tetrapods and between dinosaurs and birds.

With the exploration of evolutionary transitions in the fossil record, from intraspecific to supraspecific levels, not only have there been the patterns of evolution been revealed, but so too have some of the mechanisms responsible for these changes (e.g. McNamara 1990). Foremost among this research has been the extent to which developmental change has played a primary role in evolution. Despite being an unfashionable discipline in the late 1970s and early 1980s, a number of studies of the fossil record demonstrated that many of the phenotypic changes that occurred in many lineages could be explained by changes to developmental regulation - developmental repatterning (Arthur in press) (see McNamara 1997 for a review). The model used to interpret developmental changes in these palaeontological studies has been heterochrony. This is defined as changes to the rate and timing of developmental events, relative to the same events in the ancestor (Alberch et al. 1979; McKinney & McNamara 1991). Since these early works, much has been written on the role of heterochrony in evolution. To some, it is a major player in evolution (McKinney & McNamara 1991; McNamara 1995, 1997). Others have ascribed a more limited role Zelditch (2001) arguing that other processes, such as, 'heterotopy' (changing position) and 'heterometry' (changing number) are as important. This paper is not the appropriate vehicle to discuss the merits of these concepts, apart from making the point that changing position (heterotopy), changing number (heterometry) both derive from changes to the timing and rate of developmental change. Thus it could be argued that they are mere subsets of heterochrony.

It is clear even from such a brief discussion as this that the study of developmental repatterning in evolution has been forever beset by questions of semantics. One of the delights of reading Darwin's *On the Origin of Species* is the fact that he eschewed semantics. However, one consequence of this has been that many of his insights have often been under appreciated. Such is the case with his views on the role of development and embryology in evolution. Because so much of his book centres on the role of natural selection, and thus the extrinsic factors...
driving evolutionary change, his thoughts on the intrinsic factors that contributed to the intraspecific phenotypic variation upon which natural selection works, have been rather neglected. Yet, reading the section on development and embryology, tucked away in the latter part of the 'Origin' reveals the importance with which Darwin viewed the role of developmental change in evolution. Moreover, it is then not too difficult to realise that many of the subsequent apparent breakthroughs, by workers such as Ernst Haeckel in the late nineteenth century and Walter Garstang and Gavin de Beer in the 20th century, had been anticipated by Darwin.

With the burgeoning interest in the relationship between developmental repatterning and evolution since the 1990s, often termed 'evolutionary developmental biology', or its less than euphonious epithet 'evo-dev', heterochrony has, to some degree, been reduced to something of a bit-player. While there are still many contemporary studies of heterochrony being carried out, (e.g., de Jong et al. 2009; Shitsukawa et al. 2009; Bertram et al. 2009) there are fewer examining its role in the fossil record. Is this because the importance of heterochrony is self evident? Or is it due to the problem of discribing timing data to fossil material, making evaluation of heterochronic processes difficult? Or is just a casualty of changing scientific fashions? Here I wish to reiterate the importance of heterochrony in palaeontological studies and stress its usefulness as a model to explain phenotypic changes that have occurred in extinct organisms, using trilobites as the example.

Heterochrony encompasses both 'increase' and 'decrease' in the extent of developmental change between ancestors and descendants, depending on whether the descendant adult has gone through 'more' or 'less' developmental change than the ancestor (McKinney & McNamara 1991; McNamara 1993, 1997). If it has passed through more change it is known as peramorphosis (analogous to Haeckel's 'recapitulation'). Using the nomenclature of Alberch et al. (1979), this can occur by an increase in rate of development (acceleration); or by a delay in the offset of pre-adult growth (hypmorphosis) or by an earlier onset of growth of a particular trait (predisplacement). Correspondingly, if the descendant adult has passed through less developmental change than its ancestor, this is called paedomorphosis. This can occur by a reduction in the rate of growth (nerey or deceleration); earlier offset of growth (progenesis) or a delay in the onset of growth of a trait (posidispacement).

While the heritage of peramorphosis (under the guise of 'recapitulation') is generally traced back to the late 19th century and the work of Haeckel in the 1860s, and paedomorphosis to the work of Garstang in the 1920s, Darwin (1872, p. 395) had appreciated that both types of developmental repatterning played an important role in evolution by natural selection: "...it is highly probable that with many animals the embryonic or larval stages show us, more or less completely, the condition of the progenitor of the whole group in its adult state."

On paedomorphosis acting intraspecifically, Darwin (1872, p. 395) observed: "With some animals the successive variations may have supervened at a very early period of life, or the steps may have been inherited at an earlier age than that at which they first occurred. In either of these cases, the young or embryo will closely resemble the mature parent form..."

Whereas interspecifically (Darwin 1861, p. 393 ) he noted: "...some animals are capable of reproducing at a very early age, before they have acquired their perfect characters; and if this power became thoroughly well developed in a species, it seems probable that the adult stage of development would sooner or later be lost; and in this case, especially if the larva differed much from the mature form, the character of the species would be greatly changed and degraded."

In this paper I review heterochrony in trilobites separated by 150 million years: one of the earliest metazoa, Early Cambrian oryctocephalid corynexochid trilobites, and some of the last of their clades: Late Devonian trilobites comprising the last corynexochids, as well as the last harpetids, the last odontopleurids, phacopids and proetids. In addition to describing heterochronic repatterning in these groups, I will argue for the importance of heterochrony in generating evolutionary trends, and attempt to interpret the functional significance of some of the morphological changes engendered by heterochrony.

**Trilobite Ontogenetic Development**

Amongst arthropods, trilobites have a unique developmental system. The axis of the exoskeleton of adult trilobites is divided into the cephalon, thorax, and pygidium. The degree of segmentation expressed in these three regions is variable. It is most striking in the thorax, where the segments were articulated. The posterior of the cephalon and anterior of the pygidium each articulated with the anterior-most and posterior-most thoracic segments, respectively. Segmentation is also strongly expressed in the pygidium. However, the pygidial segments did not articulate as they were fused to one another. However, thoracic and pygidial segments had a common developmental origin. New post-cephalic segments were generated during ontogeny. The number of segments generated and their allocation to the thorax or pygidium varied ontogenetically and between taxa. As Hughes (2007) has pointed out, the post-cephalic region was either homonomous, where post-cephalic segments differed only in relative size or articulation pattern, or heteronomous, where the post-cephalic region possessed more than one type of segment.

As with other arthropods, trilobite development occurred through a series of instars, each produced by a moulting event. All trilobites may show a hemiianamorphic pattern of development (Hughes et al. 2006) where the instars are typified initially by the sequential appearance of additional post-cephalic segments, followed by a sequence of instars with a fixed number of segments. This is known as the epimorphic phase (Hughes et al. 2006). New segments were formed adjacent to the anterior of the last segment of the post-cephalic region (Stubblefield 1926). Trilobite development is divided into three phases: the protaspider, meraspider and holaspider stages. The protaspider stage is characterized by the formation of facial sutures. The meraspider stage is marked by the separation of the cephalon and the post-cephalic region. During this period segments were
sequentially added at the front of the meraspid pygidium. The onset of the holaspid stage is characterised by the cessation of addition of segments to the thorax. During the meraspid period of segment addition, the number of segments in the pygidium could either decrease, stay fixed, or increase.

**Heterochrony in Early Cambrian Oryctocephalid Trilobites from China**

One of the striking features of the oryctocephalid trilobites that occur in the Early Cambrian Balang Formation in eastern Guizhou Province, southwest China, is the occurrence of convergent evolution in two clades of trilobites: species of *Arthricocephalus* (McNamara et al. 2003) and in the Dogunaspis-Balangia clade (McNamara et al. 2006). Moreover, the same morphological changes, that arise from developmental changes, which are seen here at the specific and generic levels, have their parallels at the suprageneric level within oryctocephalid trilobites (McNamara 1986). Within a sequence of about 100m of shales of the Balang Formation, four species of *Arthricocephalus* occur. The oldest, and longest ranging, is *A. chauveaui*, followed by *A. xinzhaiheensis*, *A. balangensis*, and lastly *A. pulchellus*. What most distinguishes these species is the number of thoracic and pygidial segments. All species possess 13 post-cephalic segments in the holaspid period. Whereas in *A. chauveaui* there are 9 thoracic segments and 4 pygidial segments, in *A. xinzhaiheensis* there are 8 thoracic segments and 5 pygidial segments; in *A. balangensis* 7 thoracic segments and 6 pygidial segments, and lastly, with 6 thoracic segments and 7 pygidial segments, *A. pulchellus* (Figure 1). What is changing between these species is the location of the thoracic/pygidial margin. There is no evolutionary change in the extent of somitogenesis, i.e., the rate of production of segments during ontogeny, but the difference is in the tagmosis, i.e., the apportionment of segments between the thorax and pygidium. Thus each successively evolving species is paedomorphic relative to the presumed ancestor, the sequence of increasingly paedomorphic species forming a paedomorpholine (*sensu* McNamara 1982).

By investigating the ontogenetic development of segmentation in the oldest species, *O. chauveaui*, it is possible to explain the developmental changes that are occurring between the four species. The ontogeny of the species can be subdivided into three phases. The first phase comprises meraspid stages 0–3; the second phase is meraspid stages 3 to 5; the third phase meraspid stages 5 to 9 (McNamara et al. 2006, text-Figure 9). The meraspid stage number relates to the number of thoracic segments present in that meraspid stage. In the first phase, between meraspid stages 0 to 3, 2 segments are added at each moult, but the thorax only increases by one. This means that the pygidium increases rapidly in number of segments, from 4 in meraspid 0 to 7 in meraspid 3. In the second ontogenetic phase somitogenesis ceases even though the trilobite is only partially through its meraspid period of development. The boundary between the thorax and pygidium migrates posteriorly, with the result that as the number of thoracic segments increases, the number of pygidial segments decreases. So by meraspid stage 5 there are 5 thoracic segments, but only 5 pygidial segments. In the final phase of meraspid development there is another growth pattern. Somitogenesis recommences so that at each moult an extra segment is added, the post-cephalic segment number increases from 10 to 13, and as it does so the boundary between the thorax and pygidium migrates posteriorly. So between meraspid stages 5 and 8 the pygidium always has 5 segments. Between the last two meraspid stages, 8 and 9, there is no new segment added, just the posterior movement of the boundary to reduce the pygidial segment number by one, to 4, and increase the thoracic segment number to its adult complement of 9.

The succeeding species, *A. xinzhaiheensis* reveals subtle differences in growth pattern, with one fewer post-cephalic segment at meraspid stage 3, but one more than *A. chauveaui* in meraspid stage 5. The holaspid phase occurs when 8 thoracic segments have been produced, and the pygidium has 5 segments, a condition that is the same as meraspid stage 8 of the earlier, presumed ancestral species, *A. chauveaui*. In this regard *A. xinzhaiheensis* can be regarded as paedomorphic. Only the last three meraspid stages of *A. balangensis* (meraspid stages 5 to 7) are known, and all have 13 post-cephalic segments, suggesting an acceleration in somitogenesis. The older *A. chauveaui* at meraspid stage 5 had only produced 10 post-cephalic segments. However, cessation of somitogenesis occurred at an earlier stage in this descendant species. In the youngest species, *A. pulchellus*, only meraspid stage 6 was reached, before onset of maturity and cessation of production of new segments (Figure 1). In addition to changes in segment number the position of the fulcrum on the thoracic pleura changes from being set close to the distal margin in earlier

![Figure 1. Paedomorphic evolution of species of the oryctocephalid trilobite *Arthricocephalus* from the Early Cambrian of Guizhou Province, China (after McNamara et al. 2003, text-Figure 8).](image-url)
species, progressively moving in towards the axis in later species. This had the effect of increasing the overall convexity of the exoskeleton. Lastly, there were also paedomorphic changes to the cephalon, with a widening of the cephalon in later species; narrowing of fixigenae, deepening of glabellar furrows; and widening of the glabella.

The other oryctocephalid clade that occurs in the Balang Formation consists of two species, *Duyunaspis duyunensis* and *Balangia balangensis*. The heterochronic changes between the older *Duyunaspis* and younger *Balangia* mirror very closely the changes seen in the *Arthricocephalus* clade. When compared with *Balangia*, the holaspis of the older *Duyunaspis* has a greater number of thoracic segments (7) than *Balangia* (4). However, the pygidium of the holaspis of *Balangia* has the greatest number of segments (7), compared with *Duyunaspis* (5) (Figure 2). The holaspis of *Balangia* compares with the mid-meraspids of *Duyunaspis* in retaining a relatively narrow pygidium, the width being about two-thirds the length (McNamara et al. 2006). The holaspis of *Balangia* has free cheeks similar in width to those of a meraspid degree 4 of *Duyunaspis*. Like meraspids of *Duyunaspis*, the eye lobe is relatively longer in the holaspis of *Balangia*, compared with the holaspis of *Duyunaspis*.

The question has to be asked: what is the strong selection pressure on reducing thoracic segment number and increasing pygidial segment number and length in these two oryctocephalid clades? The answer probably lies in the inward movement of the fulcrum. The morphological consequence of this was that through both clades the overall convexity of the trilobites increased. By raising the level of the axis higher off the substrate, unless the trilobites underwent a lengthening of the pygidium, the width of the anterior-most pygidial segment meant that the level of the eyes was raised, so increasing the range of vision (McNamara et al. 2006).

The reduction in number of thoracic segments seen in both oryctocephalid clades did not simply arise from neoteny or progenesis. In the *Duyunaspis-Balangia* clade, as thoracic segment number decreased along the clade, as occurred in *Arthricocephalus*, the number of pygidial segments increased; there was a developmental trade-off (sensu McNamara 1997). Two different mechanisms, somitogenesis and tagmosis, occurred during the ontogenetic development of the postcephalic region, and the rate and timing of change of these mechanisms appears to have varied independently, producing the heterochronic changes in the post-cephalic region in these two clades. Developmentally, it is more appropriate to consider the boundary between the thorax and the pygidium as migrating posteriorly at each moulting event, rather than the anterior-most pygidial segment moving anteriorly into the thorax. The mechanism for these changes is described in detail in McNamara et al. (2003, 2006).

### Heterochrony in Late Devonian Trilobites from Western Australia

For a length of about 350 km Late Devonian sedimentary rocks are present along the south-western margin of the Kimberley Block in the northern Canning Basin in Western Australia. These rocks are the remains of a major reef complex that existed during the late Givetian to Famennian. Within the marginal slope facies, known as the Virgin Hills Formation, trilobites occur. The oldest part of the Virgin Hills Formation to yield trilobites is Frasnian conodont Zone 11 in age (Klapper 2007). They occur commonly through Zones 12 and 13b, and into the overlying Famennian to the *rhomboidea* Zone. The Frasnian-Famennian boundary represents one of the major Phanerozoic mass extinction events and greatly impacted trilobite biodiversity.

Five orders of trilobites are present in the Virgin Hills Formation: Corynexochida (McNamara & Feist 2006); Odontopleurida (Feist & McNamara 2007), Harpetida (McNamara et al. 2009), Phacopida (Feist et al. 2009) and Proetida (McNamara & Feist 2008). The first three orders became extinct globally at the end of the Frasnian Stage, their representatives surviving in the Virgin Hills Formation to the last zone of the stage. Evolutionary changes in all groups, either before or after the Frasnian/Famennian boundary, show varying degrees of heterochrony. Where suitable ontogenetic information is available, the role of developmental repatterning in response to changing environmental conditions can be determined. Of particular interest are variations in eye morphology prior to and after the Frasnian/Famennian boundary in a number of clades within the Corynexochida, Phacopida and Proetida. Although some species are blind, others show evolutionary trends of varying numbers of lenses arising from heterochronic changes.

### Corynexochida

The last surviving family of the Corynexochida is the Scutellulidae. This family is represented in the Frasnian
of the northern Canning Basin region by the last two known species of the order, Telopeltis woodwardi McNamara & Feist 2006, which ranges from Zones 11 to 12, and T. microphthalmus McNamara & Feist 2006, from Zones 13a and 13b. Telopeltis is an unusual scutelluid in possessing a very convex exoskeleton, the pygidium being especially strongly convex. However, there is a reduction in convexity between the two species. A trend of reduced convexity also occurs in other trilobite groups in the Virgin Hills Formation (see below). Moreover, the eye lobe reduces in size in the younger species of Telopeltis (Figure 3). Eye reduction also occurs in other trilobite groups in the Frasnian part of the Virgin Hills Formation.

A strongly vaulted transitory pygidium typifies early ontogenetic growth in many phylogenetically older scutelluids, the adults developing a much flatter pygidium. This suggests that in adults of Telopeltis this character is paedomorphic. A further five paedomorphic features are present in the younger species, T. microphthalmus and eight in T. woodwardi. These include glabellar furrow depth, development of occipital spine, in addition to the reduction in eye size, and higher exoskeletal vaulting (McNamara & Feist 2006, p. 990). The relatively small size of these species compared with phylogenetically earlier scutelluid genera suggests that possibly the paedomorphic features evolved in response to selection for earlier maturation in a stressed environment (McNamara & Feist 2008, p. 270).

**Odontopleurida**

These are rare trilobites in the Virgin Hills Formation of the fauna. Species present in zone 13b of the latest Frasnian are the last representatives of the order Odontopleurida and belong in the family Odontopleuridae. Five species are known from zones 11 to 13b and all are placed within the genus Gondwanaspis (Feist & McNamara 2007). Only two of the Kimberley species have been formally named: G. spinosa Feist & McNamara, 2007 and G. dracula Feist & McNamara, 2007, due to paucity of material of the other taxa. Gondwanaspis is typified by a very low convexity, wide cephalon, poorly defined glabellar lobes and presence of spines or protuberances on the anterior margin of the cranidium. Feist & McNamara (2007) have suggested that the absence of an anterior cephalic arch seen in other odontopleurids is because of a downward flexure of the anterior margin. As a result Gondwanaspis, unlike other odontopleurids, instead of having to assume both a ‘resting’ and an ‘active’ posture, could assume a single posture.

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**Figure 3.** Evolution in species of the scutelluid trilobite Telopeltis from the Late Devonian (Frasnian) of the northern Canning Basin, Western Australia.
posture. The effect of this, along with the low convex cephalon and wide genal areas, was that the eye would have been positioned laterally, so as to reduce a potential appreciable anterior blind spot.

Consistent ontogenetic changes occur in a wide range of odontopleurids. These suggest that in *Gondwanaspis* some of the cephalic features evolved by paedomorphosis. These include the poorly developed glabellar lobes, the frequent anterior position of the eye lobe, and the truncate frontal lobe (Feist & McNamara 2007).

Harpetida

Harpetid trilobites are particularly common in the Frasnian part of the Virgin Hills Formation (McNamara et al. 2009). Two genera have been described. Of these, *Eskoharpes* is the most diverse and long-ranging, with four species that extend from Zones 11 to 13b. The type species, *E. palanasus*, is the last known member of the order Harpetida. Four species of *Eskoharpes* (Figure 4) show evolutionary trends in decreasing convexity of the cephalon and increase in the brim width. These changes have been attributed to heterochrony, and as such represent the first record of heterochrony in harpetid trilobites (McNamara et al. 2009, p. 28). Reasonably complete ontogenies of the last species of *Eskoharpes*, *E. palanasus* (Zones 13a–b), and of the earliest species, *E. wandjina* (Zones 11–12), has enabled the role that heterochrony played in the evolution of *Eskoharpes* to be determined.

The morphological changes that occurred in the cephalon of *E. wandjina* during ontogeny between early meraspids and holaspids are not great. The early meraspid cephalon, like that of the holaspis, has a strongly vaulted glabella and genal areas. The brim undergoes little relative increase in width between meraspids and the large holaspids. In meraspids the genal roll (see McNamara et al. 2009, text-Figure 2) is a little narrower than in larger specimens, but it was steeply inclined in all growth stages. The phylogenetically younger *E. palanasus* underwent much greater morphological change during ontogeny. During the meraspid phase of growth the brim became relatively wider; the external rim relatively narrower; the glabella broader, but less inflated and less steeply inclined; the genal areas less swollen; the genal roll more shallowly inclined; axial and posterior furrows less incised; and the alar furrows more pronounced (Figure 4).

The meraspid cephalon of this last species of *Eskoharpes* resemble both the meraspid and holaspid cephalon of the earlier species, *E. wandjina* and *E. boltoni* (Zone 12). The fact that *E. palanasus* underwent a greater degree of

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**Heterochrony in *Eskoharpes***

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- **Decrease in convexity**
  - *E. palanasus/guthae*

- **Increase in brim width**

- **Peramorphosis**

- **E. wandjina**

**Ontogenetic development**

Figure 4. Peramorphic evolution in species of the harpetid trilobite *Eskoharpes* from the Late Devonian (Frasnian) of the northern Canning Basin, Western Australia (after McNamara et al. 2009, text-Figure 5).
morphological change during ontogeny than earlier species, indicates evolution by peramorphism. The phylogenetically younger species do not attain the same size as the earliest species, *E. wandjina*, but compare in size to the Zone 12 species, *E. boltoni*. Although actual growth rates are not known, the greater morphological development in the younger species might have arisen from an acceleration in growth rates. The main morphological features that can be described as peramorphic are brim width, and genal roll, glabella and genal vaulting. This represents the first record of peramorphosis in Devonian trilobites (McNamara et al. 2009).

**Phacopida**

The phacopid *Acuticryphops acuticeps* (Kayser 1889) became increasingly common prior to the Frasnian/Famennian mass extinction event (Feist et al. 2009). A paedomorphic reduction in eye lens number has been documented in *A. acuticeps* which occurs not only in the fore-reef facies of the Late Devonian reefs of Western Australia, but also in a number of locations worldwide, such as Montagne Noire and Morocco (Feist 1995; Crónier et al. 2004; Feist et al. 2009). In the material from the Montagne Noire and Morocco eye reduction occurred intraspecifically. However, in the Virgin Hills Formation the paedomorphic reduction occurred between two species, *A. acuticeps* from Zone 13a and *A. klapperi* Feist et al. 2009 from Zone 13b (Figure 5). *A. acuticeps* has between 6 and 13 lenses in each eye. In *A. klapperi* it was reduced to between 3 and 6 lenses.

Six species of early Famennian phacopids have been described from the Virgin Hills Formation (Feist et al. 2009). Phacopids have not been found immediately after the mass extinction event. The first occurrence is in the middle triangularis zone. In Europe only blind phacopids are known in the earliest Famennian. However in the Canning Basin reef environment initial recovery following the mass extinction involved oculated forms, notably species of *Houseops*. The three species of this genus, described by Feist et al. (2009), *H. canningensis*, *H. beckeri* and *H. sp. A*, are thought to have evolved from conservative oculated ancestors that had survived the end Frasnian biocrises in reefal shallow water niches. Unlike the trends in eye reduction that occur in *Acuticryphops* in the latest Frasnian, descendant lineages in the Famennian show increasing number of lenses in the eye, increased cephalic vaulting and effacement. The earliest form of *Houseops*, *H. sp. A*. 25 lenses per eye, *A. beckeri* 48 lenses, and the youngest species *A. camingensis* 59. Given that the cephalas of all three species are of a similar size, then it can be presumed that

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**Figure 5.** Paedomorphic eye reduction in species of the phacopid trilobite *Acuticryphops* from the Late Devonian (Frasnian) of the northern Canning Basin, Western Australia.
the increase in lens number is a peramorphic trait, either by acceleration, or predispacement.

**Proetida**

The most abundant trilobite order found in the Virgin Hills Formation is the Proetida, with three genera and 15 species (Feist & McNamara in prep.). Evolutionary trends occur in a number of clades, with changes affecting, in particular, the eyes. In an undescribed drevermaniine genus large eyes and palpebral lobes are present in species between Zones 11 and Zone 13b. However the three species that occur in this genus show a progressive, albeit small, paedomorphic decrease in eye size (Figure 6). From these oculted proetids evolved the *Palpebralia* lineage. This had a worldwide distribution in off-shore or deeper ramp environments (McNamara & Feist 2008). *Palpebralia* underwent evolutionary trends in eye-reduction and straightening of the palpebral suture. In the Virgin Hills Formation five different morphs of *P. palpebralis* with a variable degree of regression of the palpebral lobe can be distinguished with four taxa of *Palpebralia* being blind (McNamara & Feist 2008). The eye reduction in the undescribed drevermaniine and in *Palpebralia* both occurred by paedomorphic reduction in size and in number of lenses in the eye. Another proetid, the blind *Pteroparia*, is an extreme paedomorphic form which displays an extreme backward migration of the facial suture, extending this trend that is a feature of the *Pteroparia* evolutionary lineage elsewhere (Feist & Clarkson 1989).

**Discussion**

During the late Frasnian, evolutionary trends in scutelluid, phacopid and a number of proetid lineages involved, among others, a reduction in eye lens number and diminution in size of the eye in a number of unrelated lineages. These reductions were induced by the operation of paedomorphic processes and show that heterochrony is a significant factor in convergent evolution. McNamara (1986) argued that paedomorphosis was the dominant form of heterochrony in Cambrian trilobites. It appears to have likewise been more common than peramorphosis in the late Devonian trilobites discussed here, although some of the Devonian trilobites do also show evidence for peramorphic processes, in particular the development of the brim in harpetids and the increase in eye lens number in some phacopids during the early Famennian.

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![Figure 6. Paedomorphic eye reduction in three lineages of proetid trilobites from the Late Devonian (Frasnian) of the northern Canning Basin, Western Australia.](image-url)
The early Cambrian oryctocephalids also show a predominance of paedomorphosis. Although this had some affect on eye position it was more targeted on thoracic and pygidial segment number. The nature of the Devonian material is such that details of thoracic segment number are not known and so it is not possible to determine if heterochrony had any significant effect on the segment numbers generated during ontogeny. However, in groups such the Phacopina segment number was fixed at 11 in all families. This reflects a post-Cambrian ‘developmental hardening’, as suggested by McNamara (1986), whereby there was a greater fluidity in thoracic segment number at lower taxonomic levels in the Cambrian compared with the post-Cambrian. Variation in segment number could even occur intraspecifically in some early Cambrian taxa, such as members of the Emuellidae (Paterson & Edgecombe 2006), this variation declining from the Middle Cambrian (Watts 2007). In the oryctocephalids it varied intraspecifically.

As well as the Cambrian and Devonian examples discussed here showing examples of convergent evolution in thoracic and pygidial segment number in Cambrian forms and eye size and lens number in Devonian taxa, both also show changes in exoskeletal convexity along lineages. In the case of the Cambrian oryctocephalids, this involved an increase in overall convexity. In the Devonian harpeditids and scutelluids, this involved a decrease in cephalic convexity. While it has been argued that increasing convexity can confer a selective advantage to the trilobite in terms of improved visual capability (McNamara et al. 2003, 2006), there is no obvious selective advantage to reduced convexity, although one possibility is that it could have improved the ability of the trilobites to burrow in the sediment. Alternatively it could indicate that there had been a reduction in the selection pressure for improved vision. This could have been by a reduction in predation pressure during the lead up to the Frasnian/Famennian mass extinction event.

It has been suggested (Feist et al. 2009; McNamara & Feist 2008) that reduction in lens number in a number of scutelluid, phacopid and proetid lineages may reflect selection associated with global sea level rise in the late Devonian. This culminated in an increase in water depth immediately prior to the final extinction event, the so-called Upper Kellwasser extinction. Reappearance of oculated phacopids and peramorphic increase in lens number in the early Famennian correlates with a period of regression and thus shallowing of water in the marginal slope environment (Feist et al. 2009). Profound eustatic perturbations during the late Devonian may thus have played a significant role in determining which type of heterochrony prevailed.

Conclusions

In his attempts in *On the Origin of Species* to explain the nature of intraspecific variation, the raw material upon which natural selection operates, Darwin stressed the importance of changes to development. This surprisingly unheralded aspect of Darwin’s work has been the subject of increased interest in recent years, where the role of developmental repatterning in evolutionary change has been shown to have played a major role in evolution. Darwin was also concerned that what he perceived as the poor fossil record did little to support his model of natural selection. However, many studies, especially within the last 30 years, have shown that the fossil record is sufficiently extensive to be used to demonstrate not only the patterns of evolution, but also their processes. In particular developmental repatterning, in the form of heterochrony has been shown to have been significant in the evolution of many groups of vertebrates and invertebrates.

The nature of the pattern of development of trilobites, especially with the progressive decreases through ontogeny in the number of thoracic segments, has encouraged a relatively large number of studies of the effect of heterochrony on the evolution of the group. These have shown the overwhelming importance of paedomorphosis, with many Cambrian clades having experienced reductions in the number of thoracic segments through time. By contrast, studies of heterochrony in later Palaeozoic trilobites have demonstrated more the significance of allometric changes, such as to cephalic shape and to eye size. While these studies have illustrated the continuing importance of heterochrony in the evolution of these later trilobites, both paedomorphosis and peramorphosis have been shown to have played significant roles in evolutionary trends in many clades.

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Polymorphism, variation and evolutionary change in early vertebrates from the Gogo Formation, Western Australia

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Abstract

The imperfection of the fossil record was used by Charles Darwin to explain the lack of evidence for "organs of extreme perfection and complication", which under his theory of natural selection must have evolved through a series of gradual transitions. In addition, a major premise in the theory of natural selection is that variation between organisms is required so selection for particular traits can occur. The fossil record has subsequently revealed a small number of sites comprising fossils of exceptional preservation including the Gogo Formation of Western Australia. Here a unique Late Devonian (Frasnian) reef fauna, with exceptional three-dimensional preservation of macrofossils combined with unprecedented soft-tissue preservation has preserved examples of the transitional forms and morphological variation Darwin predicted. The most significant discoveries have contributed: insights into reproductive biology, including the oldest known vertebrate embryos and evidence of sexual dimorphism with internal fertilization; the anatomy and variation present in the earliest gnathostomes, the placoderms, provides evidence of directional selection; some of the earliest morphological changes required in the transition from an aquatic to land environment are seen in the primitive tetrapodomorph, Gogonasus.

Keywords: Darwin, placoderm, reproduction, heterochrony, evolutionary trends, evolution

Introduction

Today Charles Darwin is most closely associated with the biological sciences; however, he was first recognised as a scientist in the field of geology receiving the Wollaston Medal, the Geological Society of London's highest honour in 1859 (Darwin & Barlow 1958). After graduating from Cambridge University Darwin worked as a field assistant to the geologist Adam Sedgwick with whom he obtained valuable practical experience in the observation and interpretation of geological structures and fossils. During the early stages of the voyage of the Beagle he read the Principles of Geology by Charles Lyell and was greatly influenced by the theory of uniformitarianism (Darwin & Barlow 1958). The study of stratigraphy was in its early phase but it had already been noted that the further back in the rock record you went the more dissimilar plants and animals appeared from extant forms (e.g. Cuvier 1821). Whilst on his voyage Darwin (1859) recognised many fossils in the rock record and posed the question "By what mechanism did new species replace old ones?" Unfortunately Darwin’s account of the fossil record in Australia was not inspiring (Darwin 1859). However, he recognised that for his theory of evolution to be fully accepted evidence from the fossil record was paramount as it clearly showed changes in life through time.

Darwin acknowledged that there were many problems with the data obtained from the fossil record, which needed to be overcome prior to undertaking any evolutionary study with respect to fossils. The first is preservation bias – hard parts are preserved in greater detail and number than soft parts. This leads to the problem that of missing data – this can be the absence of fossils themselves from time periods or the absence of parts of the fossils themselves requiring interpretation and reconstruction on the part of the palaeontologist. Sites that yield fossils of exceptional preservation and in high quantities have in recent years alleviated these problems to a large extent. But we still must be careful not to place too much emphasis on: 1. The incompleteness of the fossil record thereby not recognising the wealth of information it can provide; 2. The large amount of data we have already obtained from the fossil record thereby not accepting the limitations and biases inherent in the geological record of our Earth.

Despite these problems, palaeontologists have made huge advances in the understanding of past life and evolutionary processes in recent years. The Devonian Reef, which crops out along the Lennard shelf in the Canning Basin (Figure 1A), has yielded many remarkable fossil sites (see Playford et al. 2009 for a full review), the Gogo Formation having the most diverse fauna with over 40 genera of fish preserved as original bone in addition to invertebrates and the reefal structures (see Long 2006, Long & Trinajstic 2010 for a full review). Recently new technologies, especially computerised tomography (CT), have opened up novel avenues of investigating fossils and this has led to the discovery of many morphological features, not all of them bone.
Preservation and preparation of the fossils

The standard method of preparation was devised at the British Museum of Natural History by Harry Toombs and comprises sequential acetic acid (8–10%) baths where the carbonate is disaggregated to expose the bone (Rixon 1976). Unfortunately, recent discoveries of soft tissue structures have indicated that this method has also dissolved much muscle tissue over the years. New methods, using a lesser concentration of acid (5–8%), are preserving the soft tissue and bony structures in much greater detail (Long et al. 2008).

The partial decomposition of the fish, prior to fossilisation, is thought to have aided their preservation. The breakdown of fats results in the formation of a compound called adipocere, a low density, water insoluble substance (Zangerl 1971; Berner 1981), which is the precursor for the calcium carbonate concretions, the fossil forming the nucleus (Figure 1B). The rapid formation of the nodule combined with the overall lack of high-level tectonic forces in the region after burial of the reef complexes (Playford et al. 2009) has resulted in the high level of preservation (Long & Trinajstic 2010). Recently the first soft tissues including muscle fibres (Figure 2A) and an umbilical cord (Figure 2A, C) have been recovered (Trinajstic et al. 2007; Long et al. 2008). In addition extensive musculature has now been recovered from a yet unpublished acanthodian (“spiny shark”) and actinopterygians (ray fin fishes).

The muscle is mostly mineralised and in rare cases individual crystals of hydroxyapatite replace individual cells providing incredible structural detail (Trinajstic et al. 2007; Long & Trinajstic 2010). Scanning electron microscopy has shown incredible detail of the muscle structure in a number of fossil taxa including nerve tissue running between muscle fibres and blood capillaries (Figure 2D).

Figure 1. The Bugle Gap area of the Canning Basin. A, the Devonian reef outcrop at Bugle Gap with the inter-reef basins containing the fossil bearing nodules. B, A Gogo nodule containing a fossil actinopterygian (boney fish) with some soft tissue preserved.
Reproduction in the fossil record

The premise of survival of the fittest is central to Darwin's evolutionary theory, and although this expression is often attributed to Darwin, it was actually coined by Mr Herbert Spencer and not used by Darwin until the later edition of "The Origin of Species" (1869). Survival in evolutionary terms is measured as reproductive success and different reproductive strategies have evolved in order to maximise the species chance at survival. The two main reproductive strategies can be summarised as:

1. Producing many offspring with little parental care in order that some will survive; or
2. Producing few offspring with large amounts of parental care increasing the chances that most will survive.

These strategies represent the extremes of a continuum but are helpful in looking at different strategies animals and plants use. But how does one determine reproductive strategies within the fossil record?

Evidence of reproduction is very rare in the vertebrate fossil record. The recent discovery of embryos within ptyctodonts (Placodermi) from the Gogo Formation has provided the earliest evidence of internal fertilisation and live birth in the fossil record (Long et al. 2008, 2009; Ahlberg et al. 2009). Placoderms (fishes with the head and thorax covered by an armour of bony dermal plates) were the dominant members of the vertebrate marine community in the Devonian. The presence of an umbilical cord attaching the embryo to the mother provides the earliest evidence for matrotrophy, where the mother provided nutrition to the embryo, in the fossil record (Figure 2A-C, E). Following this discovery a further three embryos were found in ptyctodonts (Long et al. 2008) and two embryos were discovered in arthrodires (Long et al. 2009), the dominant group of Late Devonian placoderms. In addition pelvic claspers were also identified within the arthrodires providing crucial evidence for internal fertilisation within the arthrodires (Ahlberg et al. 2009; Long et al. 2009).

Figure 2. Materpiscis – the mother fish. A. post-cranial region of Materpiscis showing the umbilical cord and soft tissue. B. Reconstruction of the mother fish giving birth (with permission Dr John Long). C. CT scan showing the umbilical cord underneath a dermal plate. D. SEM of muscle fibres with capillary running between them from the arthrodire Eastmanosteus. E. CT scan of the tooth plates of Materpiscis. CT scans taken at ANU by Prof. Tim Senden.
The recent advance in three-dimensional imaging of bone means that fossils can be virtually dissected and histological information obtained non-destructively. Of the structures reveal through micro-CT perhaps the umbilical cord from *Materpiscis* (the mother fish) is the best known (Long *et al.* 2008). This tiny, coiled structure changed scientific thinking about reproduction in the earliest jawed fish, the placoderms. The structure was first recognised macroscopically, during preparation of the fish, sitting on the surface of the newly prepared area. However, there was an overlying body plate from the fossil embryo making examination of the earliest umbilical cord ever discovered difficult. In recent years collaboration with Drs Tim Senden and Arjay Limay from ANU has resulted in ultra-fine micro CT imagery of key Gogo material. Micro -CT scans of the specimen allowed us to trace to path of the umbilical cord, from a crystalline mass thought to be the yolk sac to the embryonic bones (Figure 2C). In addition, virtual thin sectioning was able to show the internal structure of the embryonic bones and teeth without having to destroy them (Figure 2E). The bone histology enabled us to determine that the small bones inside the adult fish were definitely an embryo and not its last supper (Figure 2C, E). The distinctive tooth structure (Figure 2E) confirmed this as we could confidently identify the embryo as the same species as the mother.

Natural selection and variation within the fossil record

Darwin recognised that populations comprise individuals that vary from one another and that selection of one variant over another could lead to evolutionary change. The recognition of variation in the fossil record is dependent on the preservation of the specimen, the number of specimens available and the ontogeny of the specimens available (McKinney & McNamara 1990). Many of the fish fossils from the Gogo Formation are mono specific genera, meaning that studies of variation are impossible, but amongst the arthrodires, there are several genera that comprise multiple specimens at various growth stages (Trinajstic & McNamara 1999; Trinajstic & Hazelton 2007; Trinajstic & Dennis Bryan 2009).

Several studies have now been undertaken on polymorphism within the arthrodires and its evolutionary significance. The first study on Australian fossil fishes was on the lateral line system in the arthrodire *Incisoscutum ritchiei* (Dennis & Miles 1981). Differences were noted not just between individuals, but also on the left and right sides of the fish (Trinajstic & Dennis Bryan 2009). The rostral plate (Figure 3A-C), which is the most anterior median plate of the head shield, was also found to be highly variable. In ancestral forms such as *Compagopiscis* and *Incisoscutum* (Figure 3C) the rostral plate has three forms, T-shaped, triangular and anteriorly protruding triangular. The fossil record from Gogo indicates that there was selection for one morph – the triangular morph, and in descendents the rostral plate is always triangular (Trinajstic & Dennis Bryan 2009). In addition, there is also selection for an increase in the length of the rostral plate within the Camuropiscidae (Miles & Dennis 1979) with descendents species having a longer rostral plate then ancestor species (Figure 3C), an example of directional selection (Trinajstic & McNamara 1999; Trinajstic & Dennis Bryan 2009). The mechanism of this elongation has been determined to be peramorphic – or an increase in the time of growth compared to other dermal plates (Trinajstic & McNamara 1999). These evolutionary mechanisms are further explained below.

Ontogeny and heterochrony

Recent studies of growth and development have been possible in four genera of arthrodiran placoderms: *Incisoscutum* (Dennis & Miles 1981), *Eastmanosteus* (Dennis-Bryan 1987) *Tubonasus* (Long 1988) and *Camuropiscis* (Trinajstic & Dennis-Bryan 2009). Trinajstic & McNamara (1999) recognised considerable variation in body form within *Compagopiscis croucheri*, which they attributed to allometry – i.e., differences between size and shape during growth. It was determined that lengthwise growth occurred prior to breadth-wise growth indicating...
that juveniles had a more gracile appearance than adults (Trinajstic & McNamara 1999). This discovery led to the synonymy of two genera Compagopiscis and Gogosteus (Trinajstic & Hazelton 2007).

Within the diversification of the placoderms there were a number of homeomorphic trends, and many of these parallel changes seem to involve morphological aspects of locomotion (Carr 1995). Many of these changes can be attributed to heterochrony - changes in the rate and timing of development (McKinney & McNamara 1990). The presence of a long trunk shield, more than one median dorsal plate and scales covering the body behind the shoulder girdle are considered primitive characters for placoderms (Miles & Young 1977; Goujet 1984; Goujet & Young 2004). Within the ptyctodonts there is a trend for reduction in the body armour, including the loss of the spinal plate, posterior ventral plates and median dorsal plate elements, and the loss of post thoracic scales (Figure 4). A similar trend is seen in the arthrodires with more primitive forms such as Holopena having a tail covered in scales and an enclosed pectoral fin, and more derived forms such as Menamarpis having a naked tail and an open pectoral fin (Figure 4). Carr (1995) suggested that the loss of body scales increased flexibility in arthrodires and similar selective pressures on ptyctodonts have resulted in a similar solution for increased swimming ability (Figure 4). In addition, the loss of the spinal plate and posterior lateral plate opened up the area for the pectoral fin allowing greater manoeuvrability of the fin. Information obtained from the study of placoderm embryos (Long et al. 2008, 2009) showed that not all bones ossified at the same time, the bones associated with respiration and feeding ossifying first and the dermal bones of the trunk armour ossify later. This suggests that the trend for the reduction in the number of dermal plates, evident through placoderm evolution, is the result of paedomorphosis. The combination of having greater pectoral fin movement and more streamlined body shape would result in an increased swimming ability. At the end of the Famennian arthrodires represented the top order predators in the Devonian seas.

The completeness of the fossil record

Darwin recognised that many of the morphological transitions required for speciation by natural selection were missing from the fossil record. "I remember well the time when the thought of the structure of the eye made me cold all over." He attributed the lack of transitional forms to the imperfection of the geological record (Darwin 1859). However, since Darwin’s time, knowledge of transitional species within the fossil record has greatly increased with one of the better-known transitions being the transition of the fin into the limb. One significant Tetrapodomorph, Gogonasus is known from the Gogo Formation. The exact phylogenetic position of Gogonasus remains unresolved (Long et al. 1997, 2006; Ahlberg et al. 2007; Clack 2009; Holland & Long 2009; Long & Trinajstic 2010); however, its position as a Tetrapodomorph is undisputed. The transition of fins to limbs requires strong muscles in the upper arm to support locomotion of land.

One anomaly in this transition seemed to be Panderichthys a fish that had a tetrapod - like braincase and teeth and no dorsal or anal fin; however, it appeared to have retained fin rays whilst also having bones homologous to the proximal part of the tetrapod limb skeleton. CT scanning of the specimen from Talinn in Estonian confirmed the presence of four distal radials indicating that fingers were not an evolutionary novelty of tetrapods but instead evolved from pre-existing distal radials common to all sarcopteyygians (Boisvert et al. 2008). Gogonasus is significant due to the exceptional preservation found at Gogo indicating not just the articulated fin skeleton but also the position of the cartilage filled spaces between the ossification (Long et al. 2006). Additional morphological information has been obtained through micro-CT scanning at ANU showing
the path of sensory line canals, the internal structure of the ear and nose and details of the fore-fin skeletal structures.

Future work in fossil imaging

To understand evolutionary sequences, what features are ancestral and what are derived, the first appearance of each novel morphological feature needs to be determined. A current controversy in vertebrate evolution is the presence or absence of teeth in early vertebrates. The presence of morphological structures, which determine the presence of true teeth, have been determined in the infragnathals (= lower jaw bone) of placoderms. This data suggests that teeth evolved only once in vertebrates, contra to Smith & Johanson (2003) and that the gnathostome tooth condition was established within arthrodires (Rücklin et al. 2009). Synchrotron scanning shows histological features at a subcellular detail in three dimensions. The placoderms from the Gogo Formation have been important to these studies with the dental elements showing the patterns common to tooth replacement (Figure 5A–B). CT scans done at ANU have shown the internal structure of the tooth suggesting the presence of immature teeth forming within the infragnathal (Figure 5C). The latest imaging technology, synchrotron scanning, is being used to aid in the resolution of this problem.

Summary

Deposits of exceptional preservation such as the Gogo Formation demonstrate many morphological features not apparent in less well-preserved faunas. From this a better understanding of the morphology of extinct faunas can be ascertained. In addition, it has been possible to study variation within and between species, ontogenetic variation and evolutionary trends within the fossil record. The fossil record is far more complete than in Darwin’s time giving evidence for the stepwise acquisition of characters. One of the best known transitions is that of fin to limb and tetrapodomorph taxa from the Gogo Formation have provided much morphological data important in this current study.

Figure 5. Arthrodire infragnathals (lower toothplates). A. Infragnathals of Compagopiscis showing tooth rows (arrow). B. Infragnathal of Bullerichthyes showing change to a crushing dentition. C. CT scan of the infragnathal of Compagopiscis showing replacement teeth (arrow).
Increasingly computerized tomography is being used in the study of fossils with exceptional preservation providing increased resolution and understanding of histological features non-destructively.

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The power of stratigraphy in determining biological evolutionary patterns

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Abstract

Biological evolution can be reconstructed from a number of pathways, including analysis of synoptic species variation, developmental biology (or embryology), palaeontology, and in more recent times use of microbiology and genetic science. The modern environment provides mechanisms and drivers that underpin biological evolution, \textit{viz.}, predation, inter-species competition, intra-species competition, changes in environment, changes in food sources, expansion of species population into neighbouring niches, amongst others. Using the modern environment as an example, there are innumerable and complex processes that result in complexity of stratigraphic sequences and biostratigraphic sequences. If properly addressed and categorised, and applied to the geological record, such information provides a reliable and robust interpretation of the fossil record, and while the synoptic approach for extant and fossil species is useful and has provided insights into speciation, the palaeontologic approach combined with stratigraphy, which is diachronous, holds to be the most useful because it involves tens to hundred of millions of years, and thousands of species. In this paper, the focus is on the use of palaeontology and the use of stratigraphy within which changes in species are recorded, but to begin with we describe some key background principles, processes and factors of geology, biology and evolution that underpin modern ecology, biological evolution, sedimentology and stratigraphy and the use of stratigraphy in evolutionary palaeontological studies; these include: uniformitarianism; gradations; mutations in organisms; biotic assemblages and ecology with respect to habitat; lateral habitat tolerance of organisms and its implications for evolution; skeletal contribution to sediments; the relatively poor record (contribution) of modern assemblages to the fossil record; ecological and population processes underpinning evolution as “drivers” and “determinants”; differential response of organisms to pressures and environmental changes; sedimentology, facies, and habitats; changes in facies laterally and vertically to develop stratigraphic sequences; changes in lithology macrostratigraphically, microstratigraphically, geochemically, or isotopically driven, for instance, by climate and tectonism; and geological processes and the incompleteness of the stratigraphic record. The different types of stratigraphic sequences are explored in their usefulness in interpreting the palaeontological record in terms of trends in biological evolution, and several of the best documented fossil sequences are noted and discussed. Stratigraphy is a powerful and important tool to set the geological stage for inferring evolutionary lineages, understanding evolutionary changes, and separating types of palaeontological sequences useful for interpreting lineages because it helps identify the framework in which the fossils occur, \textit{e.g.}, is a vertical sequence of fossils illustrating anatomical changes the result of stacking of facies and hence a stacking of the synoptic assemblages, or is it the result of diachronous changes?

Keywords: stratigraphy, palaeontology, evolution, stratigraphic types

Introduction

Construction of lineages in biological evolution and development of the theory of biological evolution have been based by a variety of techniques, ranging from interpreting synoptic species variation, palaeontology, embryology, and, more recently, use of microbiology and genetic science (Syvanen 1985; Mitton 1994; Mindell 1997; Weygoldt 1998; Katz 2002; Tishkoff & Kidd 2004; Regier et al. 2005; Richardson & Palmer 2007). In point of fact, investigations of biological evolution have proceeded essentially on four broad fronts: 1. that involving products, such as extant speciation, fossils and their synoptic and diachronous speciation, and biostratigraphy; 2. that involving studies of field ecology and micro-ecology, which have resulted in the understanding of interactions between organisms, such as predator-prey relationships, and species-and-habitat relationships, helping to explain processes that drive evolution; 3. that involving manipulative experiments in the laboratory on organisms such as bacteria or \textit{Drosophila}; and 4. that involving study of microbiological and genetic processes, through the advent of high-resolution microscopy and genetic science techniques, whereby the processes of evolutionary change are genetically and biochemically determined; in fact, major
advances in understanding biological evolution have occurred in recent years with the advent of genetic science, where lineages have been determined by DNA and by exploring mechanisms of genetic transfer. Combined, all have provided strong evidence of the workings and products of biological evolution.

The tenet of this paper, however, is that while the variety of techniques described above, without doubt, have been very useful, and have added enormously to an understanding of the processes and products of biological evolution, it is the palaeontological record, spanning >500 million years, with many thick sequences of sedimentary accumulations, and encompassing the length and breadth of continental geology and oceanic basins, that holds the largest library of information on the phenomenon of biological evolution. In other words, if biological evolution has been operating since life began on Earth, then it is in the fossil record, in the pages of the book of the Earth, that the evidence is embedded in abundance. Modern analyses of extant synoptic speciation, the various laboratory-based experimental manipulative techniques such as selective breeding or those involving microbiology, and the use of genetics and biochemistry are "here and now" techniques, i.e., they reside and derive from the Holocene, and cannot compare to the wealth of evidence held in the Earth. It is our contention that, to date, the full extent of this palaeontological history has not been systematically explored and utilised, nor explored within a formalised stratigraphic framework.

Fossils are not always readily preserved. In modern and Holocene environments, for instance, the (recent) fossil record is fragmentary, and from a diverse biota of skeletal and non-skeletal organisms, depending on environmental setting and taphonomy, only a small proportion may be preserved. In the modern and Holocene environments there also is (and has been) bioturbation, prevailing erosion, storms, transport, and accumulation of thanatocoenoses, and there are local environmental and climate changes that alter the composition of biological assemblages. These factors have also been present in the geological record, which has rendered the stratigraphic sequences complex; but, in addition, there have been hiatuses, intra-formational erosional episodes, disconformities, angular unconformities, and tectonism that can locally remove sections of stratigraphic sequences and alter an ideal biostratigraphic sequence of fossils (Figure 1). Antagonists of the Theory of Biological Evolution focus on what is missing, and even for many scientists there has been an implicit movement away from using the fossil record in a meaningful way to construct patterns of biological evolution. We argue that rather than concentrating on what is missing in the fossil record, enough is present and enough can be sought for researchers to appreciate what is actually preserved and use that as windows into palaeontologic patterns. If correctly interpreted and used, palaeontology in the stratigraphic record provides a powerful tool to decipher evolutionary patterns diachronously. Consequently, to

Figure 1. The complexity of the stratigraphic record (adapted and modified from Moore et al. 1952). This diagram, originally used by Moore et al. (1952) to illustrate complexities involved in using fossil assemblages for stratigraphic correlations, with the occurrences of hiatuses, unconformities and erosional removal of strata, equally could be used to highlight the incompleteness of the fossil record, and also to illustrate that fossils within a stratum occur as "assemblages" (whether biocoenoses, or thanatocoenoses).
assess how evolutionary patterns may be preserved, to assess the robustness of the sequences for use in determining lineages, and to aid palaeontologists and evolutionary biologists and palaeobiologists in their study of lineages, we aim to identify the nature of biological evolution processes (i.e., its "drivers" and "determinants"), the way that evolving organisms may be preserved, and the nature of stratigraphic sequences wherein fossils are embedded.

With the work carried out to date on biological evolution in the palaeontological record there has been a focus on species within a given genus, or genera within a family, often dictated by the nature of the outcrop and the speciality of the researcher. While the results have shown biological evolution operating in the fossil record, the full extent of the complex nature of assemblage interactions, animal-habitat interactions, and the multiplicity of evolutionary patterns present within the strata of the Earth has not been fully explored. For instance, if there were several "drivers" and "determinants" underpinning evolutionary change in a number of species that comprise an assemblage of, say, 100 different organisms within a given habitat, a palaeontologist working in the Palaeozoic and dedicated to studying corals, may not be focusing on the trilobites, graptolites, gastropods, calcareous algae, and other fossils present, which may be manifesting evolutionary changes, while another palaeontologist, if working within the same set of strata may have only focused on gastropods. Yet, proper analysis of the whole assemblage may show changes in many of its components and that evolutionary changes proceeded in a complex, diachronous, and in a temporally variable manner (some following gradualism, some following punctuated equilibria). It may also show different "drivers" and "determinants" underpinning the differential evolutionary changes in the various (now fossil) organisms. Unfortunately, holistic palaeontological studies of assemblages of organisms are not common, and while the studies that have been undertaken have been admirable and useful, there have not been enough palaeontologists to undertake such a deductive and systematic task worldwide. As such, the story of biological evolution in the palaeontological record, though it has provided important patterns and principles here and there, has been opportunistic and fragmentary.

This paper is partly a review of established concepts, principles and techniques, particularly those in early days of the development of the Theory of Biological Evolution by Darwin, Wallace and others, to illustrate that the early development of the Theory was not based on a robust palaeontological record, and partly a review of the foundations of geological, biological, and ecological science to develop a robust stratigraphic framework to assess palaeontologic changes from a palaeontological (palaeobiology) evolutionary perspective. Thereafter, we focus on types of stratigraphic sequences and fossil sequences and their use in interpreting evolutionary lineages. We describe types of stratigraphy as important tools in reconstructing biological evolution and provide stratigraphic frameworks for deciphering evolutionary patterns. We also emphasise the assemblage approach to unravelling evolutionary patterns, with a focus that different drivers and determinants will be affecting different organisms in the assemblages. Finally, we revisit some classic palaeontological case studies with focus on equids, Mononykus, Microaster, ammonites, and Gryphaea, that each in their own way provides different expressions of how palaeontology, biological evolution, and stratigraphy are related and expressed, and how palaeontology in concert with stratigraphy contributes to a more robust understanding of evolutionary lineages and evolutionary associations.

Note that this paper is not concerned with gradualism or punctuated equilibria as phenomena of the palaeontological record, as these focus on rates of appearances of new species or the stability of a given species, and how biological evolution may proceed. Rather we examine the various stratigraphic and biostratigraphic sequences within which the fossil record may be embedded, the reliability of these sequences, and how to use stratigraphy effectively. Thus, regardless of whether gradualism or punctuated equilibrium are the prevailing process of evolutionary change for a given species, or whether it is both, and regardless of whether gradual morphological change is evident, or paedomorphosis or peramorphosis is evident, we focus on stratigraphy, and formally define the various stratigraphic frameworks within which the diachronous assemblages are embedded.

The adjectival descriptor "synoptic" refers to those processes, or products (such as biota) that occur at the same time, or within the same time plane. It is synonymous with "isochronous". Extant biotic assemblages are clearly "synoptic assemblages". Fossil assemblages where they can be shown to have existed in the same time plane are "synoptic fossil assemblages" and the use of such assemblages or other fossil species in the same time plane is "synoptic palaeontology". The adjectival descriptor "diachronous" refers to that processes, or products (such as biota), that occur through time as manifest in the stratigraphic record. The study of fossils through the stratigraphic column, effectively through time, is diachronous palaeontology.

A review of history of early approaches in determining biological evolution

Charles Darwin arrived at his Theory of Biological Evolution from a number of pathways, synthesising information from a range of disciplines (Darwin 1859): information obtained during the voyage of the Beagle on extant spatial biological variation (e.g., his conclusions on the Rhea and other South American fauna that illustrate modern speciation and the variation across habitats and food types; Darwin 1846); developmental biology; work on beetles; and short term selective breeding with pigeons. Darwin arrived at his conclusions without recourse to detailed palaeontological evidence. This is not to say that the works of geologists and palaeontologists of the time did not influence him, or that he was unaware of the palaeontological record. Indeed, he himself had collected fossils in stratigraphic context, particularly in South America in relation to coral reefs (Darwin 1844), and flightless birds and extinct mammals (Darwin 1846), and Darwin foremost considered himself a geologist rather than a biologist, and thus was well aware of the
paleontological record available when writing On the Origin of Species. But he was also aware of the incompleteness of the fossil record in the 1800s. However, at the time of writing On the Origin of Species, paleontology and geological time could not be used in a robust manner in any detailed analyses because critical information was mostly missing and stratigraphic/paleontological sequences had not been fully explored at that time (cf. Sudbury 1958).

Wallace came to a similar conclusion to Darwin regarding biological evolution and the origin of species, but his focus was on contemporary biota, and he developed his theory mainly from synoptic patterns, with a focus on gradations between species based on his biogeographical observations in South America (Wallace 1852) and the Malay Archipelago (Wallace 1855). While being aware of the paleontological literature of the time (Wallace 1855), Wallace was primarily a zoologist and did not share Darwin's passion for geology and paleontology.

In addition to Darwin and Wallace, the proponents of the principle of natural selection in the Theory of Biological Evolution, were three others who published less developed ideas embodying the principle of natural selection, all of which were derived from different paths of study but involving modern synoptic patterns. These others were: a physician who derived the principle from observations of human skin colour (Wells 1818); an orchardist who developed the principle from experience with culling trees (Matthew 1831); and a zoologist with a special interest in ornithology, particularly the classification of bird varieties (Blyth 1835).

The sources and style of data and information that led Darwin, Wallace and others to their conclusions, while a synthesis of a number of pathways, were simpler than those of today, where microbiology, cell biology, genetics, biochemistry, cladistics, developmental biology, and micro-anatomy of fossils, amongst others, are making contributions to the Science of Biological Evolution.

However, to place the stratigraphic approach we are describing into a context, and refine it as a tool for deciphering evolutionary lineages and patterns from other scientific approaches, we will attempt to categorise the sources and style of data and information that led Darwin and his contemporaries to arrive at the theory of biological evolution. While modern approaches to unravelling, understanding, and supporting biological evolution are based on a number of scientific disciplines, ranging from genetics, biochemistry, embryology, amongst others, in the past, there were four cornerstones in developing evolutionary theory (Figure 2):

1. synoptic species variation
2. developmental biology
3. palaeontology
4. selective breeding

With synoptic species, synthesis of linkages and evolutionary patterns were obtained from interpreting variations in biota, and gradations in the anatomy of biota, adapted for their various modes of living (i.e., speciation, as species adaptation and response to different environments, different food types, and predation, amongst other controls and pressures). Thus, linkages were inferred by analysis of biota within the one time plane. The synoptic approach is particularly powerful if spatial gradations occur in the species, or where speciation can be linked to habitat variation, food types, feeding behaviour, or other animal behaviour. Axiomatically, for Darwin and Wallace, the one time plane for their reconstructions of evolutionary linkages was the contemporary late Holocene. Thus, the modern synoptic species variation was the main approach of Wallace and one of the main approaches of Darwin.

Developmental change, in the form of heterochrony (see McNamara this volume), also has been used as a tool in inferring evolutionary patterns (formerly expressed in the once popular phrase coined by Haeckel (1866): “ontogeny recapitulates phylogeny”, or simply “recapitulation” (Gould 1977). Here the element of time is captured in the short term in the ontogeny of the organism (i.e., the life of an individual). Darwin also used developmental change to some extent to develop his Theory, and other authors have explored this component of biological development as an indicator of lineages, and evolutionary trends. Ontogenetic changes are also used in the fossil record where, for accretionary shells (such as molluscs), the earlier stages of shelly organisms are preserved embedded in their interior (e.g., a protoconch). Accepting that developmental change provides clues to evolutionary lineages, fossil developmental change thus also is an important tool in determining palaeontological lineages (McKinney & McNamara 1991; McNamara 1994, 1995, 1997). Developmental palaeontology (ontogeny) has been used successfully in graptolites (Sudbury 1958), trilobites (McNamara 1986; McNamara et al. 2003, 2006), echinoids (McNamara 1988, 1990), ammonites (Trueman 1922; Zakharov 1988; Dommergues 1990), and brachiopods (McNamara 1983).

Selective breeding provided short term information that the strongest or fittest or most favourable characteristics could be artificially selected (Matthew 1831; Darwin 1859) thus paving the way to providing a mechanism that could be naturally occurring, a mechanism that Darwin, with later regret, termed natural selection.

Palaeontology as a tool in studies of biological evolution adds the dimension of time to determining evolutionary patterns, and it is particularly relevant to determining lineages because evolutionary trends are best expressed across time (i.e., diachronously). Fossil sequences can span tens to hundreds of millions of years, and so there is the aspect that there is a greater chance that lineages and incremental changes in organisms can be detected. That is, while other pathways of exploring Evolution Science provide good results, and in their own way make significant contributions to the field, they are firmly locked up in the “present”, i.e., the “here and now”, and there also is a component of having to extrapolate backwards in time to make sense of evolutionary linkages and lineages. Nonetheless, modern biochemical, genetic, and microbiological approaches provide valuable insights into the various mechanisms of biological evolution. The fossil record, on the other hand, holds the key to providing data and information on what has already happened, and has happened over hundreds of millions of years. As mentioned earlier, considering
The synoptic approach in interpreting speciation in modern and ancient settings

Synoptic approach

The synoptic plane: the modern environment (extant species) e.g., finches from the Galapagos Islands, used to infer speciation and lineages

Ancient synoptic planes

Synoptic planes can also be used in the fossil record: with reliable age dating, an ancient time plane can be used to infer speciation and lineages, effectively replicating, palaeontologically, the approach using the Galapagos finches.

Ammonites in a synoptic plane

Monograptus in a synoptic plane

Tetradium in a synoptic plane

Developmental change and evolution (heterochrony)

Developmental stages of fossils captured (embedded) in the earlier stages of an accreting skeleton

Figure 2. Some of the procedures used in the development of the Theory of Biological Evolution: A. The synoptic approach, in this case, using the finches of the Galapagos Islands, superimposed on a map of the Archipelago, as an example for the modern fauna (Gould 1837, 1841; Darwin 1845), ammonites for a Mesozoic time plane, Monograptus for a Silurian time plane, and Tetradium for an Ordovician time plane (for Tetradium palaeozoogeography see Webby & Semeniuk 1971). B. Developmental changes (heterochrony) evident in Monograptus revolutus and Monograptus argentus (modified from Bulman 1933; Sudbury 1958), and in the sutures of an ammonite (after Clarkson 1979); arrows on Monograptus argentus show the directional change of the orientation of the aperture of the thecae.

Where palaeontology is focused within the one time plane, assessing fossil biodiversity (at generic level and species level) would be termed synoptic palaeontology.

Some background principles in geology, ecology, and evolution

Use in stratigraphic sequences of palaeontology and interpretation of the changes in morphology of fossils requires an understanding of some principles in geology, ecology, and ecological processes that underpin evolution. This section provides a brief description of a number of key principles and processes that are required as background to interpreting the palaeontological record from an evolutionary perspective. However, we emphasise that the subject matter to be covered here is wide ranging and to be exhaustively covered would

the length and breadth of the Earth, and the depth of sedimentary strata accumulated, the stratigraphic record and its fossil content exposed in cliffs and quarries, explored and excavated to date, represents but a fraction of what the Earth holds in archive. We consider that the stratigraphic and palaeontological record holds the best long term evidence and record of biological evolution patterns.

Particularly if well dated, but even in robust sedimentary sequences that are not dated absolutely, palaeontology shows changes in organisms through the stratigraphic record in a temporally absolute, or in a relative way, with the pulses of appearances, extinctions, and anatomical/skeletal changes, effectively adding valuable information to determining evolutionary patterns. This approach can be termed the “diachronous procedure/data/information”.

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1. uniformitarianism
2. gradations
3. mutations occurring in organisms
4. ecological and population processes underpinning evolution as “drivers” and “determinants”
5. composition of biotic assemblages and their ecology with respect to habitat
6. lateral tolerances of organisms and their implications to evolutionary change
7. contribution of biota to sedimentary sequences as benthos, nekton, and plankton, and exogenic material
8. the relatively poor record (contribution) of modern assemblages to the fossil record
9. differential response of organisms in assemblages to pressures and environmental changes
10. sedimentology, facies, and habitats
11. changes in facies laterally and vertically to develop stratigraphic sequences
12. environmental changes such as climate changes and tectonically-driven sedimentary changes resulting in changes in lithology macrostratigraphically, microstratigraphically, geochemically, or isotopically
13. geological processes and the incompleteness of the stratigraphic record

These are briefly described below, but the reader is referred to other works dealing with the subject matter more fully. In each description, the relevance to understanding evolution in the stratigraphic record in terms of the principles, processes, or factors underpinning evolution is noted.

Uniformitarianism, first espoused as a principle by James Hutton (1788), has been a cornerstone of geology. Essentially it is summarised in the adage: the present is the key to the past. As such, interpretation of past sedimentological events, biological processes, development of biotic assemblages, drivers for evolution, expression of hydrochemistry, amongst many others rests on understanding similar or the same processes and products in the modern environment. While it is a clear principle in the geological sciences, e.g., modern models and modern phenomena can be applied to interpreting ancient sequences in disciplines as diverse as sedimentology, volcanology, and stratigraphy (cf. Ginsburg 1975; Reineck & Singh 1980; Cas & Wright 1989), it is also applicable to the biological and ecological sciences, though not as consistently used therein in comparisons of modern and ancient processes and products. Uniformitarianism is one of the foundations of ideas and principles expressed in this paper.

The identification of gradation between products, regardless of whether they are abiotic or biotic, especially when it is in temporal sequence and if used geographically, is a powerful tool in determining associations and inter-relationships. Abiotically, for instance, grainsize of sediment may gradationally change laterally (synoptically) in response to gradients in energy, providing insights into the relationship between grainsize of substrates and (wave, tidal, or wind) energy levels. In concert, the biological composition within an assemblage may change in response to such grainsizegradations. Gradations may also be expressed at the species level. For instance, an organism may change its form in response to a hydrochemical gradient or grainsize gradients (e.g., Avicennia marina, a mangrove, at the local scale physiognomically changes across a tidal flat from tree to shrub to dwarf shrub in response to a salinity gradient, or at the regional scale changes from forest-dominated to heath-dominated in response to a climate gradient; Semeniuk et al. 1978; Semeniuk & Wurm 1987). While synoptically a gradation in a product or an organism is reflecting a response to synoptic gradients geographically, climatically, hydrochemically, a gradation if expressed over time (i.e., diachronously), also shows that products are responding to some process or processes temporally. Such gradations, if they occur palaeontologically are important, as they show association of an organism temporally, and that the gradual change of an organism is occurring over time. Gradations between fossils synoptically over large geographic distances, or between facies (habitat) changes are showing inter-relationship of organisms across synoptic gradients. In palaeontology, gradations between species diachronously through a stratigraphic sequence, as well as synoptically across palaeogeographic regions are important tools in determining evolutionary associations and lineages. They show the inter-relationships between species. The evolutionary gradation of the horse foot (MacFadden 1988; MacFadden & Hubbert 1988) and the thecae of monograptids (Sudbury 1958) are good examples of diachronous gradation (Figure 3).

Mutations in organisms are a fundamental tenet of biological evolution (Muller 1932; Freese 1959; Papadopoulos et al. 1999; Eyre-Walker & Keightley 2007). The detailed processes involved and how DNA is modified are not relevant to this paper, rather, we focus on the outcome, that is, with mutations, the organism is changing, with the changes occurring potentially in different anatomical and physiological parts of the organism. In time, if the mutations accumulate, new species will derive from ancestral species. Within an assemblage of organisms composed of different species with varying propensity to adapt, or tolerate environmental change, or undergoing various types of mutation, different species will mutate in different ways, or at different rates, or not at all, to the various pressure(s) of the environment. Such differential responses of organisms is exemplified by mammals: within 150 million years since their appearance on Earth, they have developed different mechanisms to deal with...
Figure 3. Gradations in form in fossils as a basis for determining lineages. A. Gradation in horse feet (after McFadden 1988 and McFadden & Hubbert 1988). B. Gradations in form of monograptids (after Sudbury 1958). In both examples, the lineages are diachronous.

exothermia generated by the metabolism of their fuel (food) – radiator ears for elephants, epidermal evaporative cooling for humans, evaporative exchange in a labyrinth of nasal passages in camels, and evaporative exchange in the tongue of dogs, amongst others (Willmer et al. 2000; Cain III et al. 2006; Narasimhan 2008). The importance of the principle of mutation is that organisms within their environment and within the assemblages within that environment are (differentially) mutating, and through time this can be expressed as species changes. Palaeontologists focused on one fossil group will detect such changes within their speciality group, and another will detect changes in another group. The critical factor is that mutations generally will be occurring in all species, though these mutations may not necessarily be expressed as evolutionary changes unless the mutation is beneficial and then it is expressed as a new species. A thorough examination of all biota in well-preserved stratigraphic sequences will find many organisms changing and that evolution is proceeding on many fronts in many different species. Many of these changes can be attributed to developmental repatterning (heterochrony) (McNamara 1995, 1997, this volume).

In a given environment and within a given biological assemblage, an individual of a species in a population may be subject to predation, the effects of microbiology, intra-species competition, or inter-species competition, changes in environmental conditions, or changes in food sources. The species may also be incrementally expanding into adjoining habitats, expanding its range to exploit new food sources, or more effectively using its existing food resources within its existing habitats (Figure 4). The terms “drivers” and “determinants” actually encompass a range of phenomena, of mixed meaning, viz., they may be processes external to the organism (e.g., a predator, or a change in environmental conditions such as the regional cooling of the climate), or may be how an organism (internal to a population) responds to a stable environment, or responds to a locally modifying environment. Combined with various mutations of individuals within a population, these “drivers” and “determinants” can result in anatomical, skeletal, and physiological changes, i.e., the evolution of the species, or the development of new species. Examples of the effects of predation are the co-evolution of cheetah and antelope, where speed and hunting proficiency of the cheetah is being matched by speed and avoidance by the antelopes, or the co-evolution of the string-ray and soldier crab, where soldier crabs develop burrowing behaviour in response to sediment excavation by string-rays (Unno & Semeniuk 2008). In the fossil record McNamara (1994) has shown the importance of predation pressure in the co-evolution of cassid gastropods and spatangoid echinoids. Examples of the effects of microbiology are the resistance to disease in fauna, or the evolving association of soil microflora and nutrient uptake by vascular plant roots.

Intra-species competition, especially sexual competition, can result in development of anatomical features such as bright plumage or coloured crustacean claws. Inter-species competition for habitat space or food sources can result in anatomical modifications in a species to make it more proficient in surviving in its habitat. Changes in environmental conditions, such as in climate, substrates, hydrology or hydrochemistry can underpin species adaptation and anatomical and physiological changes. The evolution of the woolly mammoth is an example of this. Similarly, changes in food sources can drive anatomical changes – the evolution of horse teeth as their food sources changed from forest-dominated conditions to grass-plain conditions and they changed from being browsers to grazers. Species may also be incrementally expanding into adjoining habitats: for example, terrestrial plants belonging to the Verbanacea and the Myrtacea encroached progressively from terrestrial habitats to marginal shore habitats to high tidal habitats (to become Avicennia marina and Osbornia octodonta), with changes in anatomy, physiology and reproduction strategies; other species, notably the finches of the Galapagos Islands expanded their range and speciated to exploit new food sources. Finally, organisms can develop anatomical changes to more effectively utilise their existing food sources.
Drivers/Determinants that can lead to Biological Evolution, or to extinction

various drivers/determinants that are not environmentally determined, and generally not stratigraphically evident, unless features such as gut contents, or shell drilling are indentified, otherwise determined by inference e.g. changes in feeding chelipeds of crabs

Figure 4. Drivers and determinants that can lead to biological evolution, or to extinction.

resources within their existing habitats. The development of specialised feeding claws and cheliped hairs of the fiddler crab for scraping slime and diatomaceous films off tidal flats, and the cutting claw of crabs that feed on algal-turf on rocky shores are examples. Thus, the "drivers" and "determinants" acting on a species within a habitat can result in extension of the distribution of the organism forming a new species at the periphery of a habitat (peripatric speciation), or through local pressures such as predators, or through more efficient use of food sources (amongst many other examples) can result in development of new species within the habitat (sympatric speciation), as summarised in Figure 5.

A derivative of this concept of "drivers" and "determinants" acting on a species is that not all "drivers" and "determinants" are necessarily environmentally determined, or driven (e.g., intraspecies competition, or more effective use of food resources), and may not be evident stratigraphically. Figure 4 shows that of the many that act on the organism, the effects generally do not have sedimentological, microchemical, or isotopic signatures. The effects actually will be manifest in the evolution of the species responding to these "drivers" and "determinants". Exceptions are where the stomach contents of predators or browsers or grazers are fossilised, and then there is a direct predator-prey or direct feeder-food relationship and direct evidence of gastropod predation, such as gastropod boreholes in other molluscs or echinoids. Drivers involving changes of food sources and changes in climate, grainsize, and hydrochemistry, are environmentally determined, and may be detected stratigraphically (see McNamara 1990).

Given that the eight "drivers" and "determinants" underpin evolutionary changes within an assemblage of organisms in a given habitat, as described above, there can be differential response of organisms within an assemblage to the "drivers" and "determinants", and
Further, different species within an assemblage will be acted upon or influenced by different “drivers” and “determinants”. Thus, the ecological pressures and environmental changes can have varying effects on the different species within an assemblage, and the changes induced may proceed at different rates (see later, after description of stratigraphic types).

The species composition of benthic assemblages can markedly vary with habitat, and in fact this is the basis of habitat-focused ecology. There is a wealth of literature recording these patterns. It is well known, for instance, within a given biogeographic region and climate region, for marine environments, for example, that there are distinct benthic biotic assemblages in sandy environments, as compared to muddy sand, or mud environments (Figure 6). Such assemblages are related to substrate types, salinity, and water depth (see Dampier Archipelago; Gulf of California, Gulf of Mexico, Leschenault Inlet estuary; Shark Bay; the Wadden Sea; the Woods Hole region; Semeniuk et al. 1982; Jones 2004; Parker 1960, 1964; Dürr & Semeniuk 2000; T A Semeniuk 2000; Semeniuk & Wurm 2000; Logan et al. 1970, 1974; Wolff 1983; Parker 1975). Similar patterns of assemblage-to-habitat relationships exist on tidal flats (sand, muddy or sand-to-mud graded tidal flats), often with biota exhibiting zonation in relationship to environmental gradients (cf. mangrove zonation, and benthic fauna zonation; Bererra et al. 2006, Chakraborty & Choudhury 1985, Crane 1975, Degrera et al. 2003, Dittmann 2000, Jaramillo & Lunecke 1988, Jaramillo et al. 1993, McLachlan 1996, McLachlan et al. 1993, Ono 1962, Otani et al. 2008, Sass & Watabe 2008), and in estuaries and coastal environments such as the Wadden Sea (Wolff 1983), the Leschenault Inlet Estuary (Semeniuk & Withers 2000) and the tidal flats of the Canning Coast (Semeniuk 2008; and Figure 6, which shows the variety of molluscan fauna on tidal flats, with the “drivers” and “determinants” superimposed). Similarly, the ecological functioning and processes within a given biogeographic region and climate region can vary accordingly to habitat. The same principles apply to terrestrial environments, such as forested mountains, grassy savannah plains, riverine plains, heathland terrains, wetlands, amongst many others.

Various organisms have varying tolerance to environmental change laterally, and this has major implications in evolutionary development. For instance, within a suite of adjoining habitats varying from sand to muddy sand to mud, and varying from saline to hypersaline, or varying from marine to estuarine, to tidal flat, some species cross habitat boundaries, while others are environmentally restricted (Figure 7). Local works in Western Australia on the fauna of estuaries (Semeniuk & Withers 2000), mangroves (Semeniuk 1983; Semeniuk & Wurm 1987) and soldier crabs (Unno & Semeniuk 2009) and elsewhere globally on tidal flats (as listed above on the zonation of benthic fauna) exemplify this. Some of these tolerances may have derived from a given species expanding its habitat tolerances, and encroaching into adjoining habitats. The implications are that species with broad environmental and habitat tolerances may be able to cope with habitat changes or other environmental changes, while environmentally restricted species may not, and may be replaced by fitter mutational variants, or become extinct.

Within a stratigraphic sequence of accreted sediment, whether the sequence is homogeneous, multilayered, or complexly heterogeneous, biota can contribute to such sequences as benthos, nekton, and plankton, and exogenic biological material. Not all components may be preserved in sub-recent or pre-Holocene sequences, due to various taphonomic processes, bioturbation, diageneric, or even low grade metamorphism, but modern environments do show accumulation of benthic biota, nekton and nekton products (such as fragmented shell in excreta), and plankton. The latter may contribute directly as skeletons and skeletal particles (e.g., diatoms, zooplankton exo-skeletons, and foraminifers), or as decomposed organic material. Exogenic material may comprise skeletons of terrestrial biota deposited into marine or coastal environments, or tree logs deposited into marine or coastal environments. The result is that in accreting sediments, axiomatically, fossils may accumulate, and the palaeontological assemblages may be wholly benthic, mixed benthic and planktonic/nektonic, or wholly planktonic/nektonic.
Figure 6. Simplified mollusc assemblages on tidal flats along the Canning Coast, Western Australia (after Semeniuk 2008), showing key species within contrasting but adjoining sediment types, viz., sand versus mud, and the complexity of species composition within habitats. Not shown are echinoderms, polychaetes, crustacea, benthic vertebrates, and other fauna within the assemblages. The drivers and determinants above the assemblages illustrate that these factors and processes are operating on all components of the assemblage. Bar scale alongside the molluscs is 1 cm.

Figure 7. Simplified diagram to illustrate the environmental tolerances of selected species of fauna in subtidal marine, tidal, and estuarine environments in terms of sand, muddy sand, and mud substrates (or habitats). Some species are habitat-restricted because of grain size influences, food sources, and salinity (see Mictyris occidentalis as described by Unno & Semeniuk 2009), while others inhabit a range of substrate (habitat) types (e.g., Avicennia marina, Tellina deltiloidis, and Nassarius burchardi as described by Semeniuk & Wurm 1987, 2000). Some species cross environmental boundaries, occurring in estuarine and marine settings. This diagram does not address depth occurrence, or (wave and tidal) energy effects on species occurrence. Information on molluscan fauna adapted from Abbott & Dance 2000; Beesley et al. 1998; Semeniuk & Wurm 2000; Wells 1984; Wells & Bryce 2000; Wilson 1993, 1993b; Wilson & Gillett 1974).
In terms of benthic (or benthonic), planktonic and nektonic fossils, most palaeontologists focus on the macrofauna, i.e., the benthos, which are the most conspicuous and readily available. However, planktonic or nektonic fossils raining down directly onto the sediment floor also can be important components of the assemblages as they provide primary information in their own right in terms of evolutionary changes, and hold potential to provide supplementary information about the water column and other environmental factors that may not be evident macroscopically in the sediments and in the stratigraphy. Where present, they should be explored hand-in-hand with the macrofauna to assess the environmental stability or consistency of the stratigraphic sequence wherein evolutionary changes in fossils are being investigated. Assemblage changes or species changes in planktonic and nektonic fossils through time, even though the sedimentary pile within which they are accumulating may not show sedimentary evolution or basin evolution, implicate some form of changes in the environment that is not being expressed sedimentologically, e.g., changes in climate, hydrochemistry, or food source changes, or predation pressure that are occurring in the water column. Planktonic or nektonic fossils also can transported to shore or nearshore environments, e.g., the modern cephalopods cuttlefish Sepia and the ramshorn shell Spirula spirula, transported from oceanic environments to sandy shores and incorporated into beaches in Holocene and Pleistocene sequences (Semeniuk 1997, 2008). While the shore environments may be sedimentologically and ecologically relatively stable, repetitive and homogenous, the transported fossils may be signalling changes in the water column in the adjoining oceanic regime.

As a consequence of taphonomy (e.g., shell breakage, bioturbation, shell dissolution) and differential synsedimentary diagenesis, there can be generally a relatively poor record of preservation of living modern skeletal assemblages in the sub-recent sedimentary deposits, and by extrapolation, in the fossil record. For instance, the abundance and diversity of the living skeletal faunal assemblages in Shark Bay (Logan et al. 1970), Rockingham seagrass bank (Searle et al. 1988; Semeniuk 1997), the Dampier Archipelago (Semeniuk et al. 1982), Leschenault Inlet Estuary (Semeniuk et al. 2000), and the coastal zone of the Canning Basin (Semeniuk 2008), are not as well represented as whole and recognisable skeletal remains in the sub-recent sedimentary deposits. Close examination of the sedimentary deposits neontologically, however, generally shows faunal remains progressively reduced to sand-sized or smaller fragments, or in various stages of pitting on their way to skeletal degradation by dissolution, marine weathering, or algal boring. Skeletal remains in terrestrial environments are even more poorly preserved. This principle applies to the fossil record, and in general, it can be concluded that the fossil record generally is a relatively poor representation of what once existed from the point of view of locating whole and partly fragmented fossils. To circumvent this problem, Semeniuk (1973) in a study of Ordovician fossil assemblages, constructed the palaeo-ecological compositions of the assemblages using whole fossils, fragmented fossils, and sand-sized fragments of fossils where they were petrographically recognisable, and the same principle applies to sub-recent and Pleistocene skeletal remains in the Quaternary sequences. However, the modern sedimentary-and-skeletal-fragment examples illustrate that while there is degradation of the fossil record, the ancient stratigraphic sequences actually illustrate that enough is preserved to be able to be used palaeontologically and palaeoecologically (cf., the comparisons of Pleistocene and Holocene molluscan fauna in seagrass bank environments described in Semeniuk (1997), and the comparisons of Pleistocene and Holocene foraminiferal assemblages from marginal seagrass bank environments described in T A Semeniuk (2005).

There are a number of ecological and population processes operating in modern environments that underpin biological evolutionary changes. We term these evolution "drivers" and "determinants".

Sedimentology is the study of structures, composition, and grainsizes of sediments, and similar sediments, or suites of inter-related sediments, occurring in a given location are referred to as facies. There can be gravel facies, sand facies, mud facies, or carbonate sand facies versus quartz sand facies and so on. Habitats that benthic biota occupy, for example, in marine and coastal environments, are the result of sediment types (or facies) functioning in combination with hydrological and hydrochemical characteristics. The organism responds to living and feeding on a favourable habitat comprised of a given substrate, and hydrological and hydrochemical setting. The same principle applies to soils - they also form facies, and can be the basis of habitats for soil fauna, soil microbiota, vegetation, and macrofauna.

Sediments and facies can vary laterally and accrete vertically to develop stratigraphic sequences. This is Walther's Rule (Walther 1893-1894; Krumbein & Sloss 1963), where generally sediments in lateral relationships tend eventually to overlie each other. This is best exemplified by shoaling sequences where the sediments are arranged in parallel facies and perpendicular to environmental gradients such as water depth, hydrochemistry, or (wave, tidal, or wind) energy, and as sediments accrete and shoal to shallower water depths, or accrete to become emergent above a waterline, they sedimentologically adjust in response to the progressively changing environmental conditions (Brock & Semeniuk 2009). The grainsize variation and structure-and-grain-size variation normal to tidal flat shores and sandy beach shores, for instance, form parallel facies that with progradation and shoaling form vertically distinct sedimentary (stratigraphic) sequences that vertically mirror the horizontal facies relationships (Semeniuk 1997, 2008). In this context, habitats, related to facies, and related to sediment distribution are preserved as vertically accreting stratigraphic packages. The palaeontologist and evolutionary palaeontologist just need to read this sequence in terms of a sequence of facies, or a sequence of palaeo-habitats.

However, sediments and facies do not necessarily remain constant and environmental perturbations, such as in climate and tectonism, can result in changes in lithology macrostratigraphically, microstratigraphically, geochemically, or isotopically. Climate changes, for instance, can affect $^{14}$O/$^{18}$O ratios in water and in skeletons of biota (and reflected therefore in isotopic
changes in the stratigraphic column). Tectonism can drive and alter sedimentologic effects, bringing in changes of sedimentary style and lithology.

The final matter to discuss is that geological crustal processes can markedly alter the stratigraphic sequences. Uplift, mountain-building, folding, erosion, planation, and so on, can remove sections of the stratigraphic sequences, and result in incompleteness of the stratigraphic record. This has major consequences locally for the fossil record (Figure 1).

A synthesis of these matters described above, as they relate to biological evolution and evolution manifest in the palaeontological record is provided below.

An organism in the modern environment, in its biogeographic range as determined by habitat setting and climate, is complexly interacting with the abiotic factors and with other organisms in its search for living space, harvesting/hunting of food, in evading predators, and reproducing. Also, the sedimentary environment (or habitat) is changing, or shoaling, or in some way being modified lithologically, macrostratigraphically, microstratigraphically, geochemically, or isotopically. Essentially and generally, nothing is static, and the evolutionary biologist and evolutionary palaeontologist must incorporate these factors into their thinking, reconstructions, and interpretations. For instance, from modern considerations of ecological processes, composition of assemblages, changes in assemblages in the short term and the long term, differential response of organisms to environmental and ecological changes and pressures, the complexity of stratigraphy, and the other matters described above, it is clear that interpreting the fossil record in an evolutionary perspective can be a very complicated matter, particularly because it is fragmentary. However, it can be carried out if there is an understanding of ecological processes, of modern dynamics in biological assemblages, and of the types of stratigraphic frameworks that fossils are embedded in and how to use them. We emphasise, again, that the present is the key to the past, and a thorough understanding of modern processes leading to evolutionary change, preservation of fossils, and development of stratigraphy is the key to interpreting the fossil record.

Types of stratigraphic sequences

Fossils reside in sedimentary accumulations that form stratigraphic sequences, and to understand fossil occurrences and evolutionary changes, the various types of stratigraphic sequences and their significance to the palaeontological record need to be described. In a sedimentary basin, where evolutionary changes in fossils are to be described and interpreted, ideally, laterally there would be thousands of kilometres of stratigraphic sequence as rock exposure (e.g., the Permo-Triassic stratigraphy of the Sydney Basin, exposed as the cliff shores along the eastern seaboard of New South Wales; Australia; Packham 1969), and thousands of metres of vertical stratigraphic section extending over time intervals of millions of years of sedimentary accumulation. Such stratigraphic sequences, if fossiliferous, would provide synoptic and diachronous information on fossil species and fossil assemblages, wherein the various confounding factors generating palaeontological change could be explored and teased apart.

In detail, sedimentary sequences are complex and varied; they record deposition in fluvial, aeolian, lacustrine, glacial, shoreline, marine shelf, and deep-sea environments, amongst others (Reineck & Singh 1980). Depending on tectonism, and occurrence of subsiding basins, they develop as thin sequences, or thick sequences, and depending on whether the external environment (such as climate) and crustal environment are stable, they develop into homogeneous packages, or layered sequences, or heterogeneous and complex packages. In this paper, for purposes of setting the palaeontological record in a context and framework, the stratigraphic sequences relate to those that are relatively thick, i.e., spanning intervals of > 10 m, and ideally spanning intervals > 100 m.

Leaving aside the effects of tectonism and other geological processes that can remove, fragment, or disrupt the ideal sedimentary sequences, and hence complicate stratigraphic sequences and disrupt their vertical and lateral continuity, we recognise various types of stratigraphic sequences hosting fossil deposits. They range from the relatively lithologically homogeneous, to the lithologically repetitive, to the simply layered, to the heterogeneous and complex. The sedimentary sequences we recognised for use in the principles proffered in this paper, ordered from the most simple and homogeneous to the most complex and heterogeneous, are (Figure 8):

Sequence Type 1: macrostratigraphically lithologically homogeneous, as well as microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous;

Sequence Type 2: macrostratigraphically lithologically homogeneous, but not homogeneous microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous;

Sequence Type 3: composed of a two-layered or a three-layered sequence, with each layer macrostratigraphically lithologically homogeneous; within each layer, the sediments may or may not be microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous, but this factor needs to be noted; the contact between the lithological layers can be sharp, or commonly are gradational;

Sequence Type 4: composed of a lithologically multi-layered sedimentary sequence, often representing the vertical accretion of laterally equivalent facies and hence representing a shoaling-upward package, or a deepening sedimentary sequence; each of the lithologically distinct layers are macrostratigraphically lithologically homogeneous; and generally (depending on the depositional regime) also microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous; the contact between the lithological layers can be sharp, or commonly are gradational;

Sequence Type 5: composed of a lithologically coarse-scale repetitive sedimentary sequence, often representing the vertical accretion of alternating sedimentary events...
Figure 8. The eight types of stratigraphic sequences. These sequences are generalised and do not refer to specific types of lithology or to environmental setting.

(e.g., relatively moderately thick upward-shoaling packages of marine sediment, with sedimentary units on a metre scale; see Reineck & Singh 1980; or sand to coal cyclic deposition); in the literature these types of sequences have been termed "cycloths" (see Jackson 1997); each of the lithologically distinct layers may be macrostratigraphically homogeneous; and generally also microlithologically, microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous; given the repetitive nature of the alternating lithological sequence and that the lower part of the whole sedimentary package represents the
oldest part of the sequence, and the upper part represents the youngest part; examining each of the individual lithologies in the shoaling package, in turn, diachronously along the sequence effectively provides a similar nature of stratigraphy as Sequences Type 1 and Type 2, though each lithology actually is alternating; where such sedimentary packages accumulate to considerable thickness, and span millions of years, they form a powerful template of sedimentary units within which to study palaeontological changes, because rather than observing fossil changes in one lithology diachronously, these types of cyclic packages provide the opportunity to concurrently study several sediment types (habitats) and their fossil content over the same time interval; further, in a system where the overlying lithologies are in cyclic sedimentary packages, they are part of the lateral facies (habitats) pattern and effectively provide a degree of synchronicity of fossil assemblages in the same stratigraphic column.

Sequence Type 6: composed of a lithologically fine-scale repetitive sedimentary sequence, often representing the vertical accretion of alternating sedimentary events (e.g., accumulating flood-tide and ebb-tide tidal flat sediments on a centimetre scale; see Reineck & Singh 1980), or repetitive or episodic catastrophic events, e.g., accumulating submarine turbidites (Krumbein & Sloss 1963; Reineck & Singh 1980; Boggs 1987) triggered perhaps by earthquakes, that record a basal traction flow of sand or coarse silt, grading and fining-upwards to suspension deposited fine silt or clay; these also are called "rhythmites" (see Jackson 1997), referring to their rhythmic layering of lithology; the sequence of sand overlain by muddier layers is also commonly termed a "couplet". Each of the lithologically distinct layers in these turbidites or rhythmites may be lithologically homogeneous; and generally also microstratigraphically, micropalaeontologically, microchemically, and isotopically homogeneous; given the repetitive nature of the alternating lithological sequence, composed say, of sand and silt for tidal flats, or composed of sand and grading to fine silt or clay for turbidites, the lower part of the whole sedimentary package represents the oldest part of the sequence, and the upper part represents the youngest part of the sequence – examining the sequence as an alternating bipartite or tripartite system, these sedimentary sequences are equivalent to the Sequences Type 1 and Type 2, in that focussing on one of the lithologies through the time interval of the stratigraphic sequence provides diachronous fossil information across a relatively homogeneous lithology (albeit consistently sandwiched between the second lithology); in addition, for turbidites, because of the mode of their deposition, the lower part of each fining-upward package may provide bentho-dominated fossil assemblages, and the upper part, plankton-and-nektont-dominated fossil assemblages.

Sequence Type 7: lithologically heterogeneously layered sediments, often representing the vertical accretion of various sedimentary environments; for example, a delta comprised of a heterogenous package of channel sediments, levee deposits, floodplain sediments, strand plain sediments (beach ridges, lagoon mud and peat), delta-front, and prodelta mud in itself forms a lithologically complex sedimentary package (Reineck & Singh 1980), but if the river channel and the deltaic accumulation are laterally migrating with channel switching, then the stratigraphy of sand, shelly sand, gravel, shelly mud and peat can become more complex, and if the delta migrates into a sequence of marine seagrass-style sedimentation that has its own sequence of lithologies (Hagan & Logan 1974), e.g., the contact of the Gascoyne Delta with the Wooramel Seagrass Bank (Davies 1970; Johnson 1982) then the complexity is further increased; with vertical continuity and with vertical disjunctions, these types of sedimentary sequences, though they may be fossiliferous, do not provide a robust stratigraphic framework for detailed diachronous palaeontological studies; at the least with this type of Sequence, if the packages occur within the same time interval (and this is most probable if within the Quaternary), there is some measure of synchronicity of sedimentary environments, even if they represent markedly different facies (habitats).

Sequence Type 8: this sequence is similar to Sequence Type 7, i.e., lithologically heterogeneously layered sediments, often representing the vertical accretion of various sedimentary environments, but with the complication that are numerous hiatuses, disconformities, and erosional intervals disrupting the sedimentary sequences, and removing stratigraphic sections. With the abundance of hiatuses, disconformities, and erosional intervals, Sequence Type 8 is the least reliable for detailed diachronous palaeontological studies for evolutionary purposes; however, if properly dated, the fossils therein can be used for synoptic palaeontological studies.

There has been no implication in the Sequence Types described above that they derive from marine or terrestrial environments, however, because of the heterogeneous nature of processes in terrestrial environments, the best examples of these sequences will be found in marine and coastal environments.

In regards to palaeontological content in stratigraphic sequences, researchers need to be aware of separating fossils that are autochthonous from those that are allochthonous, with the caveat that biota derived from the overlying water column and raining down on to the substrate can be considered to be palaeontologically autochthonous. Often sediments may contain autochthonous and allochthonous components. The shoaling beach sequence illustrates this: with translating wave energy, onshore winds, and general transport shorewards, the sedimentary layers of the beach system may contain autochthonous components such as Donax and Paphies, and in situ sand worm burrows, as well as allochthonous components such as nearshore and shallow subtidal benthos, and at the storm water levels skeletons of Sepia and Spirula spirula (the latter derived from oceanic waters). Tidal flats, in contrast, are generally of low energy, and contain a higher proportion of autochthonous components.

Difference levels of importance can be ascribed to the Sequence Types in terms of their usefulness to studies in evolution in palaeontology, and Sequence Types 1, 2, 3, 4, 5 and 6, are discussed further below.

Lithologically consistent stratigraphy, such as Sequence Type 1, provides a robust framework for determining evolutionary changes because confounding
factors such as migration of species from adjoining environments due to changes in climate or hydrochemistry or food types, etc., can be eliminated and the changes in the species (i.e., their evolution) can be gauged against an environmentally consistent framework. In this context, the drivers and determinants for evolution may be predators, microbiotic effects, intra-species competition, inter-species competition, and more effective use of food resources. Sequence Type 2 provides a less robust framework to determining evolutionary changes. Micromorphological, micropalaeontological, microchemical, and isotopic changes would signal that while macrostratigraphically the habitat appears consistent, there may be changes in climate, or hydrochemistry, or some other environmental parameter, and that the palaeontological changes are due to migration of biota from adjoining environments, or contributions from plankton from warmer (or cooler) water, or chemically different water. The carbonate mud cores from ocean basins extracted over the Quaternary interval exemplify this (Warne et al. 1981; Duncan et al. 1992): while macrostratigraphically relatively homogeneous, they show changes in foraminiferal assemblages and 18O/16O ratios indicating major climate changes (Emiliania 1955, 1966; Ericson et al. 1961) related to glacial and inter-glacial cycles (Imbrie & Imbrie 1979). Any fauna that remained in the environment (i.e., tolerant of the temperate change) may have changed due to a variety of drivers and determinants acting on them, but the change in the composition of the planktonic skeletal rain was due to environmental effects.

Sequence Types 3 and 4 show an environmental change, and most commonly are due to the lateral migration of one facies (habitat) into and overlying the other. Any fossil changes across the layers can be due to evolution of a species adjusting to the encroaching new substrates, or simply the change in habitat-linked species migrating as passengers with the migrating habitat.

Sequence Type 5 and 6 manifest some of the best types of stratigraphy for palaeontological studies. Whether composed of a lithologically coarse-scale repetitive sedimentary sequence, or fine-scale repetitive sedimentary sequence, they provide a diachronous sequence of repetitive lithologies that effectively mimic Sequence Types 1 and 2, but with the advantage that the coarse-scale repetitive sedimentary sequences preserve, on a vertical repetitive basis, the sequence of lithologies that are laterally equivalent. Effectively, the sediments of Sequence Type 5 preserve a record of facies (habitats) consistently migrating and remigrating across the site. As such, the fossils contained in each of the facies are represented in temporal sequence, and it is possible to determine changes in species diachronously that occur within any given facies (and there may be several to choose from), determine the lateral relation of assemblages with respect to the facies, determine which species were crossing facies boundaries during time of deposition, and which species (in time) eventually crossed facies boundaries. The sediments of Sequence Type 6 preserve a finer-scale record of depositional events that repetitively embed the fossils of the time. If Sequence Type 6 is a turbidite succession, then the repetitive layers embed the biostratigraphic record of the turbidite package or couplet, and the plankton in the upper part of the turbidite package or couplet. By being repetitive through time, this provides a consistent sequence of lithologies preserving alternating benthic and planktonic components.

Sequence Types 7 and 8 represent the least reliable stratigraphic systems for detailed diachronous palaeontological studies, but they can be still be useful. Even though generally comprised of short sections of stratigraphy, or environmentally un-related sections of stratigraphy, they can be used to infer depositional environments, and if well dated, they can be used to determine synoptic patterns. Fossils of horses and hominids occur in such sequences, and where well dated, they provided an environmental context for the horse fossils, and provide a temporal sequence and a synoptic sequence for the relationships of such fossils.

**Types of stratigraphic sequences and their use in interpreting evolutionary lineages**

The relationship of species and assemblages to sedimentary facies, and stratigraphic sequences are summarised in idealised diagrams in Figures 9-12. Figure 9A illustrates changes in species of the same genus (species A, B & C) across facies types that are sand, muddy sand, and mud, with no crossing of facies boundaries by any species. This is exemplified by species of *Uca* where, in a given region, they may occupy different substrate types and different tidal levels (Crane 1975). For instance, with the fiddler crabs in Western Australia (George & Jones 1982), *Uca mjobergi* inhabits sandy substrates, *Uca flammula* inhabits muddy sand substrates, and *Uca polita*

![Figure 9A](image-url)
Figure 11. Idealised diagram to show the differential and complicated manner that biological evolution may proceed in assemblages. The diagram shows laterally equivalent sediments (substrates, or habitat) of sand, muddy sand, and mud with several species in each habitat. Some species such as A, D, F and G cross habitat boundaries. The species variably diachronously change into new species in response to the drivers and determinants shown in Figure 6. Some species only change in a given habitat, some do not change at all, and some change into different species when in a different habitat because of the variation in drivers and determinants. This diagram should be viewed in combination with Figures 6 and 9A.

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Figure 12. Some theoretical examples of species evolution within the context of the stratigraphic sequence types, and with the type of driver/determinant involved. A. Species evolution within a homogenous stratigraphy, driven by predators, or change in food type, or more effective use of food. B. Species evolution within a homogenous stratigraphy, driven by predation (and the development of spines in species B1, B2, B3), or intra-species competition (and the development of ornamentation in species C1, C2, C3). C. Species evolution (D1 to D2) within two sets of homogenous stratigraphy, with the original species (D1) encroaching to outside its habitat. D. Species change diachronously within a macrostratigraphically homogenous system, with migration of species from adjoining habitats or climate. E. Species change (D1 to D2) diachronously within a macrostratigraphically prograded system, with migration of species D2 from adjoining habitats.

are shown in Figure 12. Evolution of a species in Sequence Type 1 is diagrammatically shown as a species progressively changing from A1 to A4. The driver/determinant may be predators, changes in food, or more effective use of food resources (Figure 12A). Evolution of two species in Sequence Type 1 is diagrammatically shown in Figure 12B, with the species progressively changing from B1 to B3 and C1 to C3, with the driver/determinant in one species being a predator, resulting in the development of protective spines, and intra-species sexual competition in the other, resulting in anatomical ornamentation. The crossing of a facies boundary and peripatric speciation is shown in Figure 12C. Here, species D1 remains unmodified in the mud facies, but at some stage encroaches into the muddy sand facies, becoming a different species (D2). Thereafter, species D1 and D2 remain unchanged.

The sequence of diagrams Figures 4, 6, 7, 8, 9, 10 and 12 illustrate the complexities of deciphering evolutionary patterns in a stratigraphic context, and the importance of having an understanding of the stratigraphic framework, the types of driver/determinant underpinning evolutionary changes, and the complexity of modern assemblages in terms of biological composition, and the tolerance levels of habitat change for given species.
Table 1

<table>
<thead>
<tr>
<th>Fossil group</th>
<th>Stratigraphic Sequence Type</th>
<th>Principle applied</th>
</tr>
</thead>
<tbody>
<tr>
<td>Graptolite Monograptus (Sudbury 1958)</td>
<td>Sequence Type 1</td>
<td>diachronous in homogeneous sequence as well as gradation (see Figure 13)</td>
</tr>
<tr>
<td>Ammonites (Cobban 1951)</td>
<td>Sequence Types 1 &amp; 2</td>
<td>diachronous in homogeneous sequence</td>
</tr>
<tr>
<td>Echinoid Micraster (Nichols 1959; McNamara 1989)</td>
<td>Sequence Type 2</td>
<td>diachronous in lithologically homogeneous sequence</td>
</tr>
<tr>
<td>Trilobite Arthricopesphilus (McNamara et al. 2003)</td>
<td>Sequence Type 2</td>
<td>diachronous in lithologically homogeneous sequence</td>
</tr>
<tr>
<td>Trilobites Olenellus and Olenelloides (McNamara 1978)</td>
<td>Sequence Type 2</td>
<td>synchronous in lithologically homogeneous sequence</td>
</tr>
<tr>
<td>Brachiopod Tegulorhynchia (McNamara 1983)</td>
<td>Sequence Type 4</td>
<td>diachronous in lithologically multi-layered sediment sequence</td>
</tr>
<tr>
<td>Echinoids Panister-Schizaster (McNamara &amp; Philip 1980)</td>
<td>Sequence Type 4</td>
<td>diachronous in lithologically multi-layered sediment sequence</td>
</tr>
<tr>
<td>Bivalve Gryphaea (Gould 1980; Rubilar 2005)</td>
<td>Sequence Type 7; Small-scale Sequence Type 1</td>
<td>gradation dominant in diachronous fragmented and scattered stratigraphy, but locally, diachronous in homogeneous sequence</td>
</tr>
<tr>
<td>Equids (McFadden 1988; McFadden &amp; Hubbert 1988)</td>
<td>Sequence Types 7 &amp; 8</td>
<td>gradation dominant and synoptic analyses, and diachronous lineages</td>
</tr>
</tbody>
</table>

There have been several classic studies of fossils in sequences that have been used as standards for inferring evolutionary patterns. Some of the notable examples are fossil horses, the graptolite *Monograptus*, the echinoid *Micraster*, ammonites, trilobites, brachiopods and the oyster *Gryphaea*. Their stratigraphic context is briefly described in Table 1 in terms of the stratigraphic framework in which they are embedded and what principles of analysis were applied.

Stratigraphic sequences within and across sedimentary basins

The focus on stratigraphy in the text above has been on stratigraphic sequence types. Such sequences may be relatively well preserved within a sedimentary basin (such as the example of the sedimentary rocks in the Sydney Basin mentioned above), where there is lateral and vertical continuity, and provide the best settings for the investigations of palaeontology from an evolutionary perspective, bearing in mind that even in well exposed basins, there will be the eight Sequence Types described above. However, in the real geological world of faults, folding, uplift and erosion, stratigraphic sequences are often fragmentary. This is not to say that they cannot be used palaeontologically for evolutionary studies, and indeed, some of the best studied fossils have occurred in such stratigraphic fragments, but in these contexts, the palaeontologist needs to have well-dated sequences, and then rely on gradations, synoptic comparisons, and small scale diachronous sequences. Across sedimentary basins, ordered from the most robust to the most fragmentary, with the latter relying on synoptic information and gradation to reconstruct lineages and associations, we recognise the seven levels of preservation (Figure 14). These are described with regard to their characteristics, and what techniques are best used to analyse them.

- cyclothems or rhythmites comprising the lithologic sequence, both representing some of the ideal types of stratigraphy to unravel evolutionary lineages;
- homogenous, monotonous lithologic sequence, one of the ideal sequences of stratigraphy to unravel evolutionary lineages;
- homogenous, monotonous lithologic sequence, but with isotopic and microchemical, and microstratigraphic variation – a near ideal sequence of stratigraphy to unravel evolutionary lineages;
- relatively well preserved basin stratigraphy showing gross and subtle facies superposition; fossils therein manifest real and apparent evolution (that is, stacking of already speciated organisms, or true evolutionary change within the stratigraphic sequence);
- relatively well preserved basin stratigraphy, but all in the same time plane (fossil synoptic plane); analysis would include basin facies variation and synoptic speciation (= synoptic plane);
- fragmented isolated stratigraphy but all largely in the same time plane of speciation (fossil synoptic plane) though scattered geographically (across the globe and across basins); and
- fragmented isolated stratigraphy – requires the gradation approach; the fragmentary record of equids is an example.
Figure 13. Sequence of *Monograptus triangulatus* from the shales of Rheidol Gorge, showing evolution of the monograptids (adapted after Sudbury 1958).

Discussion and conclusions

Darwin and Wallace focused on modern biota synoptically in interpreting natural species radiation across geographic regions, such as in south-east Asia, or the Galapagos Islands. It was a useful and valid approach and allowed them to interpret speciation in a context of geographic and environmental setting. Darwin, of course, supplemented this approach with taxonomic work on barnacles and beetles, selective breeding of pigeons, and with limited use of palaeontology. If the synoptic approach could be used positively in the modern environment to infer associations, relationships, and lineages, it can also be used palaeontologically to study biodiversity and inter-relationships in the fossil record. With well dated sequences, the identification of the speciation of organisms, say within the same genus, within the stratigraphic record, is utilising the synoptic approach of Darwin and Wallace. While it is palaeontological in scope, if Darwin's approach of synoptic analysis is valid, then the palaeontological synoptic approach is equally as valid. All that is involved is another time plane. In effect, if Darwin existed a million years into the future, he would have been analysing and explaining the variation in ratites, for instance, in a fossil time plane, by dealing with fossil anatomy and fossil spatial variation and not living anatomy and living spatial variations. However, what is required if a synoptic approach is used in the palaeontological record is an understanding of the palaeoecological setting of the fossils, interpreting species radiation in the stratigraphic record can be very useful if the fossil bearing horizons are well dated so that the researcher is sure that the variation is within time equivalent horizons, but becomes more powerful when the environmental setting and palaeoecological associations are known. This provides the researcher with insights into the factors underpinning palaeobiogeographic variations, and separating various strands of environment-induced speciation, e.g., is the species variability related to substrates changes, or faunal associations, or geographic (climatic) variation.
While lineages and relationships can be inferred from anatomy and developmental biology (such as embryology, and even palaeo-embryology, as preserved in the skeletal fossil record), they can be fragmentary, as the palaeontological record often is - but this does not diminish the power of the use of such anatomical comparisons; and nor that of embryology.

Palaeontology provides one of the most powerful tools to explore biological evolution, as Darwin himself was aware. Fossils cross large time intervals and spatially large tracts of geological basins. Colloquially, they can be viewed as the alphabet of the story of biological evolution in the "pages of the book of the Earth". However, as modern ecology is complex, and the result of many interacting processes and products, then palaeoecology, palaeoecology, and palaeo-evolution in the palaeontological record also are complex. The problems that ecologists face in unravelling ecological stories in the modern environment are magnified in the palaeontological record because of the loss of the record through diagenesis, general taphonomic processes, and the impact of Earth processes (such as crust movements, and erosion) on the stratigraphic record. However, palaeontology as a tool to study biological evolution has one major advantage - it involves large intervals of time, at species, genus, and family levels. To date, however, the material in which fossil are embedded (i.e., the stratigraphy) has not been rigorously enough explored to define the reliability of sequences so that they can be of use in interpreting, in a robust manner, the nature of the palaeontological record from a biological evolution perspective. We hope that in this paper we have pointed a way, in a preliminary manner, to refine and define stratigraphic frameworks so that the nature of the "pages of the book of the Earth" can be assessed, because where palaeontology is linked to a well established stratigraphy, its use becomes more powerful. The vertical changes in organism form/anatomy at species, generic, and family levels, reflecting temporal changes in
organism development, embedded in well dated stratigraphic sequences, provide the best means for interpreting evolutionary changes over time.

Care needs to be exercised in interpreting fossil records where there have been changes induced by lateral facies migration, or climate shifts, or other environmental changes, or missing parts of the stratigraphic record. Where stratigraphic sequences provide a consistent framework of lithology and microlithology (i.e., a relatively homogeneous stratigraphy), or repetitive lithology, spanning large intervals of time, then stratigraphic sequences provide a robust framework for interpreting biological/palaeontological changes that may be manifest across that time interval without having to tenuously interpret or peer through and adjust for regional facies changes, climate changes, or hydrochemical changes.

Additionally, we hope this paper has highlighted that if ecologists need to be aware of sedimentology and abiotic factors that drive ecological functioning and the development of assemblages and the constraining of species to specific habitats, then the reverse needs to be addressed — that palaeontologists working in ancient sequences need to be more holistic, integrating sedimentology, stratigraphy, and evidence of climate changes, and working with assemblages wherein the different organisms are responding differentially to pressures in the environment. If complexity is a reality in modern ecology, then it is a reality in palaeoecology. To date there has been a focus on individual species, or genera, as examples of evolution, and not a description of the entire assemblage within which the evolution of a given species or genus is embedded. The documentation of evolutionary change also has generally not been undertaken within a framework of stratigraphic sequences, i.e., evolutionary palaeontologists generally have not specialised in palaeo-sedimentology or basin analysis, and conversely, palaeo-sedimentologists, stratigraphers, and basin analysts have generally not specialised in evolutionary palaeontology. In these latter contexts, palaeo-sedimentologists, stratigraphers, and basin analysts have tended to use palaeontology to reconstruct palaeo-environments, or for biostratigraphic correlation. We suggest that the approach to evolutionary palaeontology needs to be more holistic (i.e., multidisciplinary and integrated) in the same way that modern autoecology and ecology tend to be holistic.

Palaeontologists and palaeoecologists need to explore the reasons why there would be faunal changes in the stratigraphic sequences and the answers lie in the modern settings, in the sedimentology, climate changes, facies changes, and ecological assemblages. These provide the information base and models to explain fossil assemblages. In other words, Hutton's adage, "the present is the key to the past", needs to be applied to evolutionary palaeontology and palaeoecology. The modern alphabet of autoecology, ecology, ecological functioning, sedimentology, and how stratigraphic sequences develop provides the key to reading the story of evolution in the palaeontological record.

We have also emphasised that different types of stratigraphic sequences may express different types of faunal changes, and hence there will be complexity expressed in stratigraphic/fossil sequences. Some of the complexity in interpreting the fossil record results from variation in the species concept (i.e., whether there are species variation temporarily or spatially, and thus whether some of the species changes reflect a variable perception of a species by different researchers), but complexity in interpreting the fossil record also can result from interpreting the various expressions of the stratigraphic record, viz., thin versus thick homogeneous stratigraphic sequences, thin versus thick heterogeneous stratigraphic sequences, shoaling or deepening stratigraphic sequences, and how these effect or are manifest in the palaeontologic record. Additionally, complexity in interpreting the fossil record also can result where there are fragmentary though well dated stratigraphic sequences. There is also a need to separate fossil changes that may be expressed at the species level, at the generic level, and family level. One also needs to separate rapid changes expressed over short time intervals, rather than in thin stratigraphic sequences or thick stratigraphic sequences, from slow changes in fossil anatomy.

The shifting stratigraphic record can be gross and clearly changing lithologically, or subtle, with both reflecting changes in climate, basin sedimentary patterns, and hydrochemistry. Subtle changes may be the microchemical or microbiotic that reflect climate changes while the overall lithology may appear constant. For instance, Quaternary deep sea oozes composed of carbonate mud, and appearing lithologically similar at the gross scale, contain changes in microfossils, or changes in oxygen isotope ratios, or changes in diagenetic patterns, such that the climate record, and species changes are largely locked in at the microscale. For interpreting fossil sequences for use in biological evolution, we have ordered the stratigraphic sequences that host fossils from most fragmentary (wherein one would rely on synoptic information and gradations to reconstruct lineages and associations in combination with radiometric dating), to the most robust involving thick sequences of homogenous lithologies, or cyclothsms, or rhythmites (including turbidites).

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Darwin's Tree of Life and challenges from modern genetics

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Abstract

The tree of life has been a central organising principle in biology for centuries. Darwin provided a mechanism - descent with modification - through which a tree of life could be explained and understood. Since his time a central project of biology has been the elucidation of the structure of the tree (phylogenetics). Recently, following the success of molecular data in allowing very wide and deep comparisons of taxa from throughout life, challenges to the metaphor of life as a tree have emerged. The challenges arise from observations that not all inheritance of genes, and hence of characteristics, is through descent; some alleles in a given taxon may be derived by lateral transfer from another organism, sometimes in a very different domain of life. This reticulate inheritance, if common and widespread, would mean that life would be better viewed as a net than a tree. This paper provides an empirical argument why, at least for the multicellular domains of life, rejection of a tree of life is premature and tree-like inheritance through descent with modification predominates over reticulate inheritance through lateral gene transfer.

Keywords: Darwin, phylogenetics, Tree of Life, genetics, lateral gene transfer

Introduction

A recent series of papers (Doolittle 1999; Dagan & Martin 2006), popularized in a cover article in New Scientist during the Darwin bicentenary (Lawton 2009), have made a strong claim: that Darwin's idea of a 'tree of life', an overarching concept in evolutionary biology since publication of On The Origin of Species, is wrong.

The concept of a single tree of life was central to Darwin's thinking and to the development of his theory of evolution by natural selection (Padian 2008). A core project of evolutionary biology for the last 150 years has been to elucidate details of the tree. However, the New Scientist article claimed that "today the project lies in tatters, torn to pieces by an onslaught of negative evidence", that "many biologists now argue that the tree concept is obsolete and needs to be discarded" and that "the tree of life ... has turned out to be a figment of our imagination".

This paper reviews the conceptual history and antecedents of the tree of life, discusses the challenge to the concept provided by new evidence, and argues that, at least in the multicellular domains of life, the pattern of variation observed in the real world provides strong evidence that life does indeed have a tree-like structure and that Darwin's tree of life continues to be a useful concept.

Darwin's Tree of Life and its antecedents

The first evidence that Darwin viewed life as tree-like comes from a sketch on p.36 of his Notebook B (c. July 1837, one year after the return of the Beagle to England; see van Wyhe, 2002–9). The sketch shows a branching diagram rooted at the base, each node having two or more branches arising from it. Some terminals in the tree bear cross-bars (representing extant taxa) while others lack them (representing extinct taxa). The accompanying notes show that Darwin was considering concepts of relatedness (some taxa being more closely related than others) and extinction (particularly the need to keep the numbers of species constant from one generation to another).

Three principal antecedents to Darwin's tree are likely to have influenced his thinking. The first is the scala naturae (often called the Great Chain of Being), a mediaeval concept of the universe in which all nature is arranged in a natural and immutable hierarchical order, with the inanimate world at base and God at the apex. In intermediate positions (from the base, in order) are vegetable forms, animals (sometimes in order from least to most useful), commoners, nobles, angels and apostles. Many representations of the scala naturae are found in mediaeval literature, and the concept would undoubtedly have been familiar to Darwin. While the scala naturae is not strictly tree-like, it is rigidly hierarchical and accommodates all natural forms in a single structure, properties of Darwin's tree also.

The second antecedent is the classical system of classification (categorization) developed by Greek philosophers, particularly Plato and Aristotle, and applied to many natural and conceptual systems from the mediaeval period onwards. In classical categorization, classes are definable, exclusive and exhaustive: that is, any class should belong unambiguously to one and only one higher-order class, and any class should contain all subclasses that have the same defining properties.
Beginning with Aristotle, the natural world was seen by many natural historians as a model system for classical categorization. Increasingly sophisticated systems were developed to accommodate knowledge, in the biological realm culminating in Linnaeus’ Systema Naturae. While generally conceptualised during this period as a “boxes within boxes” system, a classical classification may also be represented as a tree, with the most inclusive category as the root and any node having only one parent and at least one child. Again, Darwin was clearly very familiar with classical categorization, discussing it at length in the *Origin*, and Darwin’s tree of life shares the same properties.

The third antecedent, again one with which Darwin would have been very familiar, is the biological key, developed from “tables” of relationships around the middle of the Seventeenth Century (see Nelson & Platnick 1981 for a discussion of the history of keys and other biological tree structures). Keys are a special class of dichotomizing classification, and are often represented in a tree-like form with a root and a branching, tree-like structure. Biological keys are closely related to classical categorizations, and the two are often more or less interchangeable.

With these antecedents, Darwin would have been very familiar with the representation of knowledge as a tree and with the use of trees to represent biological systems and taxonomic relationships. The tree first sketched in Darwin’s notebook in 1837 became the sole figure in the *Origin*, an indication of the importance he placed in the concept of a tree of life.

In Darwin’s tree and most of its antecedents, every node (except the root) has exactly one ancestor node and two or more descendent nodes, and for every node (taxon) there is a single line of descent from the root. This presupposes four main conceptual properties of life. Firstly, the fact that every taxon is connected to every other precludes the pre-Darwinian concept of spontaneous generation, in which new living organisms arise *de novo* from non-living matter. Secondly, the fact that the tree is rooted presumes that evolution is unidirectional; once extinct, a taxon cannot be recreated. Thirdly, the fact that every taxon has only one direct ancestor presupposes that a given taxon cannot arise twice independently. Lastly, the fact that every taxon has a single line of descent presupposes that all inheritance is by descent (with modification).

### Calculating Darwin’s tree

Darwin’s critical concept of descent with modification, one of the two core ideas of the *Origin* (the other was natural selection), has been one of the most productive ideas in biology. It provided a theoretical basis for classical biological categorization and, by providing an argument for the existence of a natural classification (one which reflects the pattern of evolutionary descent) greatly contributed to the development of post-Linnaean classification systems. Understanding evolutionary patterns in turn has provided an underpinning framework for virtually the whole of biology.

For close to a century after publication of the *Origin*, the tree of life acted more as a guiding principle than as a methodological tool. Many alternative systems of classification were erected, each claiming to be natural, but there was no method for rigorously testing classifications for goodness of fit with the actual pattern of evolution or with the observed pattern of distribution of characters, nor could alternative classifications be compared on any grounds other than utility and preference. Trees were frequently drawn, most notably those of Haeckel (Haeckel 1866), but more as artistic expressions of a set of loose ideas of relationships than as rigorous, testable hypotheses.

This situation changed dramatically in the 1950s with the development of cladistic (phylogenetic) methodologies by Hennig (1950; 1966). Hennig realized that descent with modification provided a powerful tool for constructing hypothetical trees of life (phylogenies) and for testing these hypotheses against independent data sets. The breakthrough came in the recognition that some shared characteristics – those shared because they are novelties or modifications within the evolutionary history of the group concerned – are informative of relatedness, while other shared characters – those shared because they are unmodified from the ancestral state – are not informative of relatedness at the level of interest. Following Hennig, mathematical algorithms were developed to derive trees from sets of observations of character states in taxa (see Cavalli-Sforza & Edwards 1967; Nei 1996 for reviews).

The conceptual basis for phylogenetic analysis is simple. If evolution by descent with modification has occurred, then character states that have become modified during the evolution of a group should be distributed within the terminal taxa of the group in a way that encodes information about the underlying pattern of evolution (Figure 1). Phylogenetic analysis seeks to uncover a pattern of branching that best explains the observed pattern of distribution of character states in these terminals. This is done using a nominated criterion of goodness of fit, such as parsimony, likelihood or

![Figure 1. A simple, imaginary phylogeny of four organisms. Boxes represent extant terminal taxa; lines represent the lines of descent of the taxa; symbols represent modifications of character states, showing the pattern of descent and the distribution of states in the terminal taxa. Phylogenetic analyses are able to reconstruct the pattern of branching by analysing the distribution of states in the terminal taxa.](image-url)
bayesian probability. Of all the possible ways of arranging the taxa of interest into a tree, some trees provide a good explanation (under the nominated criterion) while others provide a poor one: the analysis methods search the set of possible trees for the best. An implicit assumption is that trees derived from such algorithms are candidates for parts of the tree of life.

All methods for constructing phylogenetic trees allow that the best tree found may not explain all aspects of the observed distribution of character states. This is necessary because noise may creep into the phylogenetic signal through several processes. The two main sources of noise are errors of interpretation of character states and evolutionary processes other than direct descent with modification, such as lateral transfer of character states derived in one part of the tree directly to another part of the tree through hybridization and direct gene transfer.

Noise is identified, and accounted for, by assessments of congruence. A lack of congruence between two or more characters indicates that at least one of the characters is providing noise rather than signal to the analysis (Figure 2). Noise is filtered from the analysis by preferring trees that maximize congruence among characters.

Figure 2. The phylogeny of Figure 1 with noise added to the phylogenetic signal through lateral gene transfer. Phylogenetic analyses are usually still able to reconstruct the pattern of branching by analysing the distribution of states in the terminal taxa, taking into account congruence between characters, as long as the signal to noise ratio is not too severely compromised.

Two developments in the latter half of the twentieth century had a profound effect on phylogenetics, taking it into realms Darwin would have found unimaginable. The first was the development of the methods outlined above. The second was advances in gene technology, particularly in rapid and inexpensive DNA and RNA sequencing methods. These two factors – the ability to generate enormous amounts of potentially informative phylogenetic data and the ability of analyse the data rigorously – led to an explosion of interest in phylogenetics and the tree of life. The same factors also led to challenges to the validity of the entire conceptualization of life as a tree.

Challenging Darwin's tree

A major strength of genetic data in phylogenetic reconstruction is that all living organisms share many genes. This provides a depth and power to phylogenetic analysis that was impossible to gain from earlier morphological studies. Using appropriate molecular sequences, phylogenetic analyses can assess relationships between, for example, species of bacteria, algae, flowering plants and whales. The diversity of form across this set of organisms makes morphological comparison between them meaningless; the conservatism of their sequences, conversely, makes genetic comparisons richly meaningful.

As more and more sequences were accrued and such phylogenetically deep comparisons became commonplace from the early 1990s, incongruous examples of sequence relationships began to accumulate (see Doolittle 1999 for a review). Specific gene sequences that were postulated to have evolved in the Archaea were found in Eubacteria, and vice versa. It is now widely accepted that lateral gene transfer in and between eubacteria and archaebacteria is widespread (Jain et al. 1999; Dagan et al. 2008), and a number of mechanisms by which it occurs have been elucidated, including transfer of genes via virus and bacteriophage vectors and direct uptake of DNA fragments from the environment (Martin 1999; Thomas & Nielsen 2005). However, its frequency is not well established. Estimates of the proportion of prokaryotic genes that have been transferred laterally at least once vary from 2—60% (Ge et al. 2005; Lerat et al. 2005).

The role of lateral gene transfer in eukaryotes, particularly multicellular eukaryotes, is less clear. Sequences believed to have evolved in bacteria after the symbiosis event that gave rise to eukaryotes have been found in eukaryotic taxa (Keeling & Palmer 2008; Ros & Hurst 2009), and sequences believed to arise in one branch of eukaryotic life have been found in others (e.g. Lisch 2008; Alsmark et al. 2009). Cases of transfer of specific sequences into widely unrelated groups (such as between bacteria and mammals) presumably occurred deep in evolutionary history. Other mechanisms for transfer that have been postulated in eukaryotes include hybridisation, which appears to be common in some groups such as plants (although again its frequency is highly uncertain; see Ellstrand 1996 for a review). Transfer through hybridisation events may potentially involve large stretches of DNA including many genes.

Lateral gene transfer directly questions the validity of the tree of life. If evolution of organisms is principally driven by descent with modification, then a tree is an appropriate metaphor and representation. If, however, most evolution is driven by lateral transfers of genes then, as some authors have claimed, life is a web (Hilario & Gogarten 1993) and viewing it as a tree is counterproductive. This view has been claimed as a paradigm shift in biology by some (O'Malley & Boucher 2005).
Testing Darwin's tree

Rather than arguing from first principles whether trees or nets are the best representations for the phylogenetic structure of life, it would be useful to have an empirical test of the goodness of fit of different representations. This in turn would provide some indication of the significance (as against the mere existence) of hybridization and lateral gene transfer in the evolution of any group of organisms. In fact, such an assessment is possible, and indeed is inherent in the structure of phylogenetic analysis.

Consider an imaginary world in which lateral gene transfer greatly predominates over descent with modification, and is random. The pattern of evolution would be a closely reticulating net, with genes (and hence their phenotypic expression as characteristics of organisms) jumping widely and randomly between different strands of the net during evolutionary time. A result of such frequent transfer would be that alleles and their characteristics will be distributed randomly across extant taxa. In such a world, phylogenetic analysis using algorithms that seek to identify a tree-like pattern would be characterized by gross incongruence. Two or more analyses based on independent subsamples of data or molecular sequences would be very likely to give different (incongruent) tree topologies.

Compare this with a second imaginary world in which descent with modification greatly predominates over lateral gene transfer. The opposite outcome would be expected – alleles and character states would be highly patterned in extant taxa, and two or more phylogenetic analyses based on independent subsamples of data would usually give similar (congruent) topologies.

How does the real world compare with these two imaginary worlds? In general amongst plants and multicellular animals there is a striking degree of congruence between independent phylogenetic analyses of the same group of taxa, as indeed there is between modern phylogenetic analyses and classifications based on traditional, pre-phylogenetic inferences. For example, in a recent change from a 90-year old classification (based on Engler & Prantl 1905) to a modern classification (APG III 1990) at the Western Australian Herbarium, there were 53 cases spread over 226 families in which genera or groups of genera were reallocated to new families.

On one hand, this result could be regarded as indicating a substantial problem of lack of congruence between the traditional and modern classification (involving 23% of families). However, almost all of the cases of incongruence can be explained by factors other than lateral gene transfer, particularly the failure of traditional classifications to adequately reflect relationships by descent (monophyly), difficulties in accurately interpreting homologies, and sampling artefacts. Thus, there is a >80% congruence between old and new classifications. Similarly, the APG III system itself is based on the striking congruence between independent data sets, and is regarded as approaching stability in most areas (APG III 1990).

Even in the bacterial domains, attempts to extract congruent tree-like patterns from amongst the noise of random lateral transfers appear successful (Puigbò et al. 2009). The world observed through phylogenetic analysis appears to be a world in which lateral gene transfer is not so rife as to destroy the tree of life. Of course, if lateral gene transfer is non-random, instead involving coordinated jumps of large parts of genomes, then the observed phylogenetic congruence in the real world cannot be regarded as evidence against ubiquitous lateral gene transfer. However, most proposed mechanisms for transfer (infections by viruses, hybridization and direct uptake of DNA from the environment) are essentially random events, and empirical evidence suggests that, while they undoubtedly occur, they do not significantly challenge the validity of Darwin's tree.

Conclusions

In multicellular life, congruence between trees obtained by phylogenetic analysis of independent data sets is commonplace. Indeed, cases of incongruence are intensely interesting and are the exceptions that prove the rule. This provides empirical evidence that random lateral gene transfer is not rife, although it undoubtedly exists. This in turn suggests that a tree-form representation of life – Darwin's tree – is an appropriate metaphor and framework principle. It would be premature to reject it at this stage.

The demonstrated existence of some lateral gene transfer shows that some reticulations do occur in the tree of life. Such reticulations may be common in some groups, particularly among prokaryotes, but it should not be assumed that they break the tree metaphor until it can be demonstrated in those groups that phylogenetic congruence is rare rather than common.

Most methods of phylogenetic analysis assume a tree-like structure and force a tree-like result. Work to find analysis methods that can handle reticulations continues (see e.g. Linder & Riesberg 2004; Reeves & Richards 2007). However, if phylogenetically meaningful network algorithms can be developed we will have a situation in phylogenetics akin to that in astronomy. Radio astronomers and visible-light astronomers do not argue as to which method provides the best view of the universe. Rather, their telescopes are regarded as complementary. Similarly, the evolution of life appears to have tree-like and network-like aspects, and the use of "telescopes" that recover tree-like signal and net-like signal are complementary rather than competitive approaches.

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Lamarck and Immunity: Somatic and Germline Evolution of Antibody Genes

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Abstract
Current work on the mechanism of hypermutation of somatically rearranged antibody variable (V) genes shows that the most likely mechanism involves both direct DNA modification (deamination of cytosines to uracils by AID deaminase) and strand nicking plus mRNA editing (deamination of adenosine to inosine via the ADAR1 deaminase) coupled to a reverse transcription process to fix RNA sequence modifications in V gene DNA – most likely involving the repair enzyme DNA polymerase eta (q) known to be an efficient reverse transcriptase in vitro. The DNA sequence patterns of families of similar germline V genes reveals that many features of somatically mutated and antigen-selected variable genes appear written into the germline V gene arrays of the immune system. Lamarckian gene feedback and cellular reverse transcription, coupled to Darwinian antigen binding selection of somatically mutated V genes, are concepts which appear necessary for a more complete understanding how the V gene complex has evolved. Antibody variable (V) genes of the immune system have therefore been used to test ideas on reverse transcriptase-coupled soma-to-germline feedback in a complex multicellular system. Such feedback constitutes a violation of Weismann’s Barrier and thus support for some type of Lamarckian gene feedback operative during the evolution of the vertebrate immune system.

Keywords: Lamarck, immunity, somatic and germline evolution, antibody genes; evolution

Introduction
In this paper I will review the main findings of our studies on the mechanism of antigen-driven somatic hypermutation of rearranged antibody (immunoglobulin, Ig) variable region genes (so called VDJs) and the impact of this somatic genetic diversity on the germline V segment repertoire. I will then draw general conclusions on the origins of genome diversity. Many details of this work have already been covered in major reviews (Steele et al. 1993; Rothenfluh et al. 1995; Steele et al. 1997; Blanden et al. 1998) and in our 1998 book Lamarck’s Signature (Steele et al. 1998). More recent work will be cited in the body of the text.

General Concepts: Molecular-Cellular Immunology and Evolution
It is generally agreed that the primary evolutionary purpose of the immune system of vertebrates is the protection of the individual against disease. The proteins and carbohydrates which make up the cell walls, viral coats and secreted microbial toxins constitute the foreign antigens which individual immune systems need to react against to preserve the integrity of the body. The system consists of highly mobile blood white cells (lymphocytes) which come in two main categories, B cells and T cells which circulate from blood to lymph via a complex network of lymphatic vessels and capillaries. The complexity of the system almost rivals that of the brain and central nervous system (which in contrast consists of sessile or non-mobile nerve cells and fibres which generate their complexity in both their sheer cell numbers and cell-cell synaptic connections). The progenitors of the white cell lineages (B and T lymphocytes, monocytes, neutrophils, mast cells, polymorphonuclear leucocytes etc.) arise from stem cells in the bone marrow which produce many millions of hemopoietic cells on a daily basis (and, of course, the senescence of many other hemopoietic-derived cells as they exit the system). Hormonal and cytokine cell-to-cell communication no doubt allows the system to be co-ordinately controlled.

The primary evolutionary strategy of the immune system has been shaped by two selective forces, a) the requirement to respond to unexpected antigens thrown up by new infectious diseases, and b) the need to prevent autoimmune reactions against self antigens. This has meant that during vertebrate evolution the immune system has developed strategies to learn to recognise and respond to the antigenic universe both during ontogeny (somatic recognition strategy during life in individual animals) and phylogeny (a germ line strategy for antigen recognition). The founding concepts of modern immunology are based on the Clonal Selection Theory of Acquired Immunity of Sir MacFarlane Burnet (Burnet 1959). A good summary of the theory can be found in the Scientific American article by Ada and Nossal published in 1987.
Darwinian Selection

Thus ‘Darwinian Selection’ principles are the first key component of the learning mechanism at the molecular, cell and whole animal levels. Clones of somatic B or T lymphocytes live or die depending on their recognition of ‘self’ or ‘non-self’. In particular somatic mutant B cells (below) live or die depending on the binding affinity of their mutant cell surface antibody receptor for antigen. With respect to B cells The Clonal Selection Theory posits an array of B cells emerging early in ontogeny each displaying a different antigen receptor on their surface membrane i.e. “one cell makes one antibody”. Early proof of this concept was provided by Sir Gustav Nossal (Ada & Nossal 1987). Of course the most immediate antigens an emerging B cell from the bone marrow would confront would be those proteins and carbohydrates (mainly in membranes but also in the fluid phase) presented by ‘self’. Burnet postulated a clonal deletion or purging mechanism to rid the body of such potentially auto-reactive lymphocytes. And we now know after 50 years of research that a variety of mechanisms help to establish and maintain self tolerance based on Burnet’s ‘clonal deletion’ concept – they include clonal abortion, clonal anergy, clonal suppression (via regulator T cells), V receptor editing and V gene replacement (Nemazee 2006; Chen et al. 1995).

All those other B cells that escape this process of course constitute the anti-nonself recognition repertoire from which foreign antigens select anti-nonself clones (see Figure 1) and many go on to become longer lived ‘memory cells’ for recall later by the same antigen. Similar, although different processes, of ‘negative’ and ‘positive’ selection, occurs for T cells as they mature in the thymus (Steele et al. 1993).

An important modification was made to Burnet’s theory in the 1970s when Alistair Cunningham proposed that most antibody diversity actually appears after antigenic stimulation, that is during the course of the immune response (Cunningham 1977). We now recognise this process by the phenomenon of antigen driven “somatic hypermutation” of rearranged immunoglobulin V genes (VDJs) which underpins the phenomenon of the affinity maturation of antibodies during an immune response (Berek & Milstein 1987, 1988).

Lamarckian Gene Feedback Loops

The other learning mechanisms contributing to the repertoire of antigen recognition in both ontogeny and phylogeny we propose invoke roles for reverse transcription and soma-to-germline gene feedback (Steele 1979; Steele et al. 1998; Blanden et al. 1998; Steele et al. 1998). These will be elaborated on further below. In short, such processes allow ‘directional’ fine tuning and maintenance of functional V gene repertoires both during life and over evolutionary time.

Figure 1. Clonal selection.
Steele: Lamarck and immunity

Central Dogma of Molecular Biology

Transcription (~ $10^{-3}$ - $10^{-4}$)

DNA Replication

$10^{-8}$ - $10^{-11}$

DNA → RNA → PROTEIN

Reverse Transcription (~ $10^{-3}$ - $10^{-4}$)

Figure 2. Central dogma of molecular biology: the frequencies represent point mutations per replication event per bp. Thus DNA replication is a relatively high fidelity copying process with errors occurring at a maximum rate of about one nucleotide substitution per 100 million bases replicated.

These feedback loops are enshrined in, or are modifications of, the Central Dogma of Molecular Biology (Figure 2) and Weismann’s Barrier (Figure 3) – the first defines the rules for information flow at the molecular level and the second, a cellular theory, prohibits somatic genetic information (RNA/DNA) being fed-back to germline DNA in germ cells. This author believes that these two fundamental ‘biological theorems’ have been confused in the past, particularly in such widely read books by the philosopher and author Arthur Koestler (Koestler 1978). It was proposed that the Weismann Barrier can be selectively breached without violating what we know about molecular biological processes in general and be compatible with Darwinian natural selection principles – thus it could be imagined that somatic genetic information in the form of mRNA amplified in the soma could be available for transfer and integration into the genome of a germ cell and thus be inherited by progeny. This formed the basis of the Somatic Selection Hypothesis (Steele 1979) summarised schematically in Figure 4. For V genes in the immune system it was imagined that antigen-selected mutant VDJ genes could be selected by antigen and the mRNA taken up by a harmless endogenous retroviral vector (endogenous RNA virus, ERV) and delivered to germ cells where the RNA could be copied into DNA via a reverse transcriptase (thought to be provided primarily by the ERV). Independent support for this general scheme can be seen in the ground breaking work of Corrado Spadafora and colleagues initiated in the late 1980s which will be discussed below (reviewed in Smith & Spadafora 2005; Spadafora 2008).

The mechanism of somatic hypermutation appears to also require a RNA intermediate and thus a reverse transcriptase step to fix somatic RNA mutations in lymphocyte DNA (Steele & Pollard 1987; Steele et al. 1997; Steele 2009). We will discuss these data and analyses in more detail below.

Weismann’s Barrier

Differentiation

Germ Cells → Somatic Cells

Soma-to-Germline Feedback

Figure 3. Weismann’s Barrier.

Research Strategy in Antibody Diversity

For over 25 years our research strategy has depended on two parallel research programs, a) an analysis of the mechanism of antigen-driven somatic hypermutation, and b) how this somatic genetic diversity might impact on the diversity and “genetic quality” of the germline V
Weismann's Barrier Selectively Permeable

Weismann's Barrier

Differentiation

Germ Cells

Somatic Cells

Soma-to-Germline Feedback

Somatic Selection Hypothesis, 1979

Figure 4. Somatic selection hypothesis, 1979.

gene arrays at the immunoglobulin locus in vertebrates. This work has allowed us to conclude that a significant portion of the somatic mutation and antigen-selection pattern in antibody variable genes (~80%) is indeed written into the germline V gene arrays at Ig loci.

Rearrangement, Gene Expression and Somatic Hypermutation of VDJ genes

A critical factor in the analysis depends on what has been established about the germline and somatic expression of immunoglobulin genes - they have clear 'germline' and 'somatic' configurations (Figure 5 and see Honjo et al. 2004). These facts allow us to infer and deduce that genetic information has indeed flowed from the somatic compartment to the germ cell compartment over evolutionary time.

The figure shows a schematic outline of a mammalian immunoglobulin heavy chain in its germline configuration and its somatic configuration. The germline, or unrearranged DNA configuration, exists in germ cells and all non-lymphoid cells in the body (e.g. kidney cells, liver cells, etc., Honjo et al. 2004). Thus on the left hand side (5' side) are the array of so-called 'V-elements' or 'V-segments', which would typically encode approximately 95 amino acids and the 100-200 V-elements are encoded in a span of chromosomal DNA of about 1 Mb in the human genome. This repertoire of unrearranged V-elements lies about 100kb upstream (in the transcriptional sense) of very short genetic elements termed diversity (D) and joining (J) regions. There are 10-30 D regions and 4-5 J regions at typical mammalian IgH loci (together they would encode after VDJ assembly approximately 25 additional amino acids). Further downstream, encompassing about 10 Kb lie successively the intronic enhancer and nuclear Matrix Attachment Region (EIMAR) and then the Ig class switch region DNA repeat elements and then a series of constant region exons encompassing Ig heavy chain isotypes, mu (μ), delta (δ), the various γ chain subclasses (IgG1, IgG2a, IgG2b IgG3) and then the α chains for secretory IgA and ε chains for mast cell binding and allergy-activating IgE antibodies. Further downstream is the 3' enhancer region (Honjo et al. 2004).

The various Ig classes reflect the functional properties of the antibody once antigen has been bound by the antigen combining site. The functional properties would include Complement activation and thus opsonisation of foreign particles for phagocytosis by monocyte scavenger cells (e.g. macrophages). The antigen binding site is a heterodimer of a light (L) and heavy (H) chain so antigen binding and thus antigen-mediated selection can only
occur on a fully assembled Ig molecule or a B cell that displays such an antigen receptor on its surface membrane.

A key process not shown in Figure 5 is immunoglobulin class switching (CSR) whereby following cytokine signalling from other lymphocytes (T cells) and white cells, the B cell will switch from transcribing and assembling IgM heavy chains (υ chains), and reposition the productively assembled VDJ gene further downstream in front of one of the downstream Ig isotypes. This is a looping out DNA recombination mechanism such that the B cell retains the original selected VDJ but now has it joined to a different set of constant region exons (Honjo et al. 2004).

It is already clear that Ig loci display a degree of genetic complexity not observed in more straightforward single-copy housekeeping or tissue-specific protein coding genes. T-cell receptor genes also display the same general genetic organisation and expression strategy (but typically do not normally somatically hypermutate their assembled VDJ genes). There is evidence that the protocadherin synaptic receptor genes in the central nervous system show a similar variable-to-constant rearranging strategy as seen for immunoglobulins and T-cell receptor genes but in these cases it is executed at the RNA level by an alternative splicing mechanism (for a mini-review see Chess 2005).

Germline V-elements per se are never transcribed into RNA for inclusion in a mRNA prior to translation into Ig proteins. In this sense they are transcriptionally and translationally silent. As such V-elements or their products are never the direct targets of antigen-binding selection. This type of antigen-mediated somatic selection is only directed to a fully assembled VDJ gene in the...
context of a light chain VJ gene co-expressed in the same B cell (and thus clonally selected).

VDJs are therefore the substrates for both RNA polymerase II transcription and somatic hypermutation. It is important to note that additional mutational errors are introduced by the DNA rearrangement process at the V-D and D-J borders (termed 'junctional diversity') and because the process is stochastic only a minor portion (about 10% of all rearrangements of IgH chains) are 'productive' i.e. in the correct translational reading frame (Honjo et al. 2004). This critical point will be discussed later in the context of fused 'VD' pseudogenes at chicken IgH loci (Rothenfluh et al. 1995).

Thus a germline repertoire of 100 functional VH elements, 20 D and 5 J regions can theoretically encode 100 x 20 x 5 or 10,000 VDJ regions; similarly 100 functional VL elements and 5 J regions would encode 500 VL. Together there is a potential combinatorial germline repertoire of perhaps 10,000 x 500 or 5 x 10^6 unique antibody specificities. Following antigenic stimulation and somatic hypermutation this potential repertoire could perhaps increase another order of magnitude or two (Berek & Milstein 1987, 1988). In reality ongoing antigen selection sifts and focuses the response for higher affinity antibodies so the full potential is unlikely to be realised in any individual (and of course the upper limit would be set by the total number of B cells generated from the bone marrow at any given point in time).

To summarise, genetic information in the form of unrearranged V-elements is never subject to direct antigen binding selection on the intact antibody or Ig receptor bearing cell. In contrast B cells expressing fully rearranged VDJ (heavy chain) and VJ (light chain) genes are subject to direct antigen-binding selection. It is this crucial distinction that demarcates the germline from the somatic configuration and thus allows deductions on the origin of highly non-random DNA sequence patterns.

The Germinal Centre and Affinity-Based Selection

A naïve B cell in the periphery can be selected by antigen to immediately secrete its encoded antibody or it can migrate to the primary follicle in lymphoid tissue to become a founder B cell in a Germinal Centre (termed GC). One or just a few B cells locate in a follicle and they multiply to form small colonies of 10,000 to 20,000 cells. Due to antigen-binding competition between pre-existing low affinity antibody and antigen-antibody complexes displayed on follicular dendritic cells within the GC, only the mutated B cells displaying viable high affinity antibodies survive – the rest die by the programmed cell death process called apoptosis (>90% of all B cells in a Germinal Centre die there). In this way the mutated B cell survivors become antibody secreting cells and memory^ cells and they bear the signature of non-random DNA sequence modifications.

Figure 6. Wu-Kabat variability plots. Thirty somatically mutated derivatives of the mouse VH-1186.2 heavy chain variable gene assembled as V(D) is in mature anti-NP antibodies. Variability = Number difference at a position / Frequency of most common at that position. VDJ DNA sequences at top; translated protein sequences at bottom. Adapted from Steele et al. (1993).

The Mechanism of Somatic Hypermutation

The dominant current model of somatic hypermutation, “The DNA Deamination” model is DNA-based. i.e. all the mutational events occur directly at the DNA level (Di Noia & Neuberger 2007; Teng & Papavasiiliou 2007). The main first step entails deamination of Cytosine to Uracil by the enzyme activation-induced cytidine deaminase (AID) which targets Cytosines in the context of WRCY hot spots (W = A or T, R = A or G purines, and Y = C or T pyrimidines). The resulting C-to-U lesions in DNA are either repaired by a base excision DNA repair pathway (involving uracl
DNA glycosylase, UNG), or if not repaired, replicated over to produce C-to-T mutations. If repaired by UNG the resulting abasic site can be transformed into a nick in the DNA by an endonuclease termed apurinic apyrimidinic endonuclease (APE). Alternatively the G:U mispairs attract the mismatch repair heterodimer MSH2-MSH6 which also recruits the error-prone translesion DNA polymerase-η (eta) which introduces mutations in the repaired patch by targeting A:T base pairs at WA-sites (where W = A or T). These series of steps are very similar to the V targeted-nicking and error-prone repair model of somatic mutation of IgV genes first advanced by Brenner and Milstein in 1966.

However three sets of recent observations by our group are not easily reconciled with the standard model but are consistent with, or predicted, by the reverse transcriptase model (Steele 2009):

a) DNA polymerase-η the accepted and sole A:T mutator in SHM is an efficient reverse transcriptase in vitro (Franklin et al. 2004);
b) The RNA editing signature of ADAR1-mediated A-to-I deamination, as instanced by the elevated A-to-G mutations, is embedded within the SHM pattern (Steele et al. 2006); and
c) The AID deaminase-linked RNA polymerase II RNA mutation signature, as instanced by elevated mutations at G sites (particularly G-to-C and G-to-A) is embedded within the SHM pattern (Steele 2009).

This work has led us to conclude that the weight of evidence now favours "The Reverse Transcriptase Model first advanced by Steele and Pollard in 1987. Thus somatic hypermutation in B lymphocytes involves:

a) Direct DNA deamination (C-to-U, thus giving rise to C-to-T and G-to-A mutations);

b) RNA Pol II copying deaminated DNA templates carrying U and abasic site lesions generates mutated mRNA (giving rise to G-to-C and G-to-A strand biased mutation signatures);
c) RNA deamination (editing) of mRNA causing Adenosine-to-Inosine mutations via ADAR1 deaminase (thus causing the A-to-G strand biased mutation signature); and
d) Error-prone reverse transcription by DNA Pol-η to fix the RNA mutations in B lymphocyte DNA and create further strand biased mutations viz. the transversions A-to-C and A-to-T.

To summarize, during somatic hypermutation both direct DNA mutations and a variety of RNA mutations are copied back into DNA (Steele 2009). As we have pointed out earlier (Steele et al. 1997) a role for a cellular reverse transcriptase such as DNA polymerase-η acting in its reverse transcriptase mode should no longer be a heretical concept given that "telomerase", a ribonucleic acid-protein particle has as its core function the capacity to copy the RNA repeat into a DNA repeat - a critical step in synthesis of the telomere multiple repeat chromosomal cap. That is "telomerase" itself is a cellular reverse transcriptase (Blackburn 1992).

Evolution of the Germline V-Segment Repertoire and Soma-to-Germline Feedback

Is there any evidence that somatically mutated variable genes can be fed back to the germline V-segment repertoire? It is possible to answer this question in the affirmative because germline V-segments can never be the targets of somatic hypermutation nor direct antigen-mediated selection at the protein level i.e. on an intact Ig antigen receptor on a mature B cell surface. This fact is

1. Pristine condition ("open reading frames" or minor defects)
2. Non-random mutation patterns (= Ag mediated somatic selection)
3. Insertion-deletions display a highly non-random distribution:
   * protein coding regions: triplet codons or multiples thereof
   * non-coding regions: variable length
4. Chicken V pseudogenes show non-random mutation patterns and features of somatic V->D->J rearrangement signature
5. Flanking and coding regions are evolving independently
6. Major sites of genetic recombination coincide with predicted sites of soma-to-germline retrotransposition

Figure 7. Key features of the repertoire Germline V Segments (Blanden et al. 1998).
often not addressed nor appreciated by those in the field speculating on the evolution of the V-segment repertoire. As we have documented elsewhere the germline V repertoires of families of similar V segments display all the hallmarks of strong somatic mutation and antigen-mediated selection i.e. a significant portion of the somatically mutated VDJ repertoire generated during evolutionary time in vertebrates has been fed back to the germline most likely by a reverse transcriptase intermediate step and targeted to unarranged V genes by homologous recombination (approx 280% of the assembled VDJ gene is comprised of the V element). Figure 7 summarises the main findings of this work which has been extensively published in refereed literature (Rothenfluh et al. 1994; Rothenfluh et al. 1995; Weill et al. 1998; Blanden et al. 1998; Zylstra et al. 2003).

In short, a highly non-random somatic mutation and selection signature dominates the DNA sequence pattern of families of similar V genes arrayed, usually in tandem, in the vertebrate germline.

As suggested above these are ‘subtle’ somatic mutation signatures – they are of a different class from the more obvious retro-sequence impact events that dominate vertebrate and mammalian genomes. They argue for a requirement for innovative ways of interpreting the DNA landscape of the genome. Thus sites of hyper-recombination near RNA splice site borders in the L-V intron make sense in this model (Weill et al. 1998) as do the strange features of chicken VH pseudogenes which all have fused ‘D’ bits in the correct reading frame (Rothenfluh et al. 1995; Ota & Nei 1995).

From our research thus far we therefore conclude:

1. Somatic hypermutation of antibody V genes operates by direct DNA and RNA base modifications coupled to reverse transcription and integration of mutated cDNA retrotranscripts back into chromosomal DNA within a B lymphocyte.
2. Over evolutionary time somatically mutated and selected (“successful”) V sequences from B lymphocytes have undergone homologous recombination into germline DNA, thus contributing to germline diversity and the maintenance of a functional germline V gene repertoire.

**Evidence from other systems**

Is Soma-to-Germline feedback a general phenomenon in complex biological systems? We address this by briefly reviewing the work of other groups.

**Corrado Spadafora**

From about the late 1980s to the present Corrado Spadafora and colleagues in Rome have published a series of important papers clearly showing that mammalian spermatozoa can take up foreign nucleic acid molecules and express the genetic information in progeny organisms. In particular mouse spermatozoa in vitro can absorb both foreign DNA and RNA, and if the latter then a LINE-1 derived reverse transcription step will be executed copying the RNA into DNA. In a small number of cases (≤ 10% ) the DNA sequences are integrated into the germline genome. In the majority of cases the sperm-absorbed DNA/RNA exists as extrachromosomal epipomides which replicate along with the host somatic cells during development displaying mosaic tissue expression (see reviews in Smith & Spadafora 2005; Spadafora 2008). This work clearly shows there is no physical barrier to uptake of DNA or RNA, although there may be additional developmental stages in spermogenesis when spermatozoa are susceptible to foreign nucleic acid uptake (Zoraqi & Spadafora 1997).

**Patrick Fogarty**

Using an innovative technique based on P-elements and delivering DNA transgenes intravenously in simple vesicles, Fogarty has shown that 50% of progeny from such male mice inherit the gene sequence (Fogarty 2002). The critical integration event requires a transposase. This works suggests that non-cellular DNA can readily transverse the testes tissue barriers, that normally quarantine the production of sperm, be integrated into the germline and be transmitted to progeny.

**Minoo Rassoulzadegan**

The group of Minoo Rassoulzadegan has shown that mature sperm carry more than just a compact haploid DNA nucleus (Rassoulzadegan et al. 2006). Thus sperm heads contain gene-specific regulatory RNAs (miRNA) which at fertilisation can have profound genetic effects in progeny. The phenomenon described involves an allele-specific “paramutation” effect of the Kd locus (important in mammalian development) yet the implications of the finding are far reaching. Certainly the effects can be transmitted to an additional breeding generation. The mechanism is unclear given that animal miRNA systems are not thought to amplify their miRNA precursors by a double stranded RNA polymerase as in plants. Perhaps the transgenerational effects are based on long lived RNA molecules? However the whole phenomenon raises the possibility of germine fixation of such epigenetic intermediary effects via a reverse transcription step at some level of the RNA regulatory process.

**John Mattick**

Since the mid 1990s John Mattick and colleagues have been documenting the extent and importance of the RNA regulatory networks of what we now call the extended “transcriptome” (Mattick 2007; Mattick et al. 2009). Thus non-protein coding regions produce ncRNAs which are regulatory in nature, regulating gene-specific expression of protein coding genes. Only about 2% of the entire mammalian ‘transcriptome’ codes for proteins – the rest (>98% genome) are involved in specific gene regulation in a multilayered complex best described as the “RNA regulatory universe”. In more recent papers Mattick concedes the necessity for some form of soma-to-germline feedback to be operative (Mattick 2009) to ensure that selected genetic changes at this level contribute to the evolution of complex systems, particularly the brain and central nervous system (Mattick & Mehler 2008).

**Lars Holmgren**

For a number of years Holmgren and colleagues have studied the potential genetic consequences in metastases of horizontal transfer of tumor genes via dispersal and
uptake of apoptotic bodies (Bersmedh et al. 2001; Ehnfors et al. 2009). These studies clearly show that if the laterally spreading DNA confers a selective advantage on the recipient cell then integration of the DNA is manifest and the DNA sequences propagated to progeny cells. We speculated on this type of somatic gene transfer in the late 1970s (Steele 1979).

Genetic Cargo of Sperm?

This is an appropriate question given the interesting findings of Spadafora and Rassoulzadegan we have just discussed. Indeed when one considers an ovum at about the time of natural fertilization there are more questions than answers raised by the phenomenon (Figure 8).

Have we become so used to an image like this that we have forgotten how truly amazing it really is. Apparently one sperm succeeds in the race to fertilisation (one possibility is arrowed). Given conventional wisdom all the other attached sperm have no further say in the genetic outcome. Apart from the non-Mendelian routes of genetic transfer in the experiments of Spadafora and Rassoulzadegan we have known for many years (e.g. Keissling et al. 1987) that sperm heads have clusters of attached endogenous retroviruses - to what end one might ask? Moreover, ERV concentrations are very high in seminal fluid (>10^7 per ml) and ERVs are emitted in copious quantities from activated lymphocytes (they also are prominent in Germinal Centres following immunisation). ERVs have been observed coating the female placenta (see Rothenfluh 1995 for more references of this type). Again the question arises - to what biological purpose should cells of the immune system and reproductive tissue be so predominantly associated with either ERV production or unexpected ERV tissue localisation?

Concluding Remarks

We conclude that both Darwinian antigen-binding selection and Lamarckian soma-to-germline feedback play key roles in the evolution of antibody variable genes. There is also evidence supporting the view that reverse transcription is central to a better understanding of the somatic and germline evolution of these genes. The work of a number of groups suggest that the ease of gene movement between cells, whether they be germline or somatic, suggests that soma-to-germline feedback is likely to be general in complex biological systems and contributes to genome diversity. Thus Weismann’s Barrier is viewed as being selectively permeable to somatic genetic information provided it is beneficial to both parent and progeny organisms (Figure 9). Acquired somatic genetic information (“experience”) may therefore not be lost with the death of the individual but be propagated to progeny who would then be selected in a Darwinian manner for fitness.

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The Genomic Drive Hypothesis and Punctuated Evolutionary Taxonations, or Radiations

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Abstract

Orthodox evolutionary theory does not accord with what palaeontologists usually find in the fossil record, which mainly indicates long periods of stasis, interspersed with relatively short periods of rapid change, that is, macro or micro punctuational evolutionary taxonations. This is usually known as punctuated equilibrium. A novel hypothesis we have called Genomic Drive, points towards Transposable Elements (TEs) as powerful facilitators of evolution and as essential for induction of periodic changes in the rate of evolution. The Genomic Drive hypothesis, which is supported by current data, if confirmed, will open the way for the reconciliation of evolutionary theory with the findings of most palaeontologists. It may also help to explain the extraordinary fecundity of some orders, and the paucity of species in others, and why there are “fossil species”.

Keywords: Evolution; the Genomic Drive hypothesis; transposable elements; taxonation; punctuated equilibrium; gradualism; stasis; extinction; fossil record

Introduction

Discovered by Barbara McClintock in the 1950s (McClintock 1950, 1956, 1984), TEs were authoritatively written off thirty years later as parasitic, junk, or selfish DNA, which we would be better off without (Orgel & Crick 1980; Doolittle & Sapienza 1980). However, during the last decade a large number of researchers have noted that the evolutionary potential of taxa can benefit from the presence of TEs (Kidwell & Lisch 2001; Bowon and Jordon 2002; Kazazian 2004; Feschotte & Pritham 2007; Goodier & Kazazian Jr. 2008) and many others. Building on this foundation, we developed the Genomic Drive hypothesis, the major elements of which were recently published as an unnamed synthesis (Oliver & Greene 2009).

Genomic Drive, according to our hypothesis, is a powerful facilitator of evolution in sexually reproducing eukaryotes. It is the process by which germ line or early embryo genomes engineer coding, regulatory, karyotypic, or other changes to their own genome. Transposable elements (TEs) (see Table 1) are the major facilitators of evolution by Genomic Drive (Oliver & Greene 2009). Other genomic content, such as simple sequence repeats (SSRs) also make some contribution (Kashi & King 2006; King et al. 2006). Of course we do not deny that many other factors also facilitate evolution and may possibly result in punctuation events on some occasions. Some examples are: whole genome duplications, endosymbiosis, horizontal gene transfer (especially in bacteria) point mutations, insertions and deletions, and other such well known phenomena. We also acknowledge that their may be some as yet unknown phenomena that help to facilitate evolution and that may also give rise to punctuation events. We present Genomic Drive as a hypothesised major facilitator of evolution, but certainly do not claim that there are no other significant facilitators of evolution. Indeed, some phenomena such as point mutation highly complement Genomic Drive by allowing newly engineered DNA sequences to diversify. A notable example of this is the ape-specific GLUD2 gene, which encodes a glutamate dehydrogenase enzyme involved in neurotransmitter recycling. Derived from a retrotransposed copy of GLUD1 that has undergone critical nucleotide substitution events, GLUD2 appears to have significantly increased the cognitive powers of the apes (Burki & Kaessmann 2004).

Major Principles of the Genomic Drive Hypothesis

TEs (Transposable Elements) are ubiquitous, comprising 20% to 80% of most genomes, and are extremely ancient; they are powerful facilitators of evolution. We have proposed this powerful facilitation of evolution by TEs, as the Genomic Drive hypothesis. Successful taxa do not destroy TEs, but strongly control transposition of TEs in the soma, where they are often damaging and cannot be inherited. However, they allow some TE activity in the germ line and the early embryo, where they can generate potentially useful variation in progeny, for natural selection to work on. Thus Genomic Drive can cause genetic changes of great magnitude and variety within germ line genomes, making such genomes flexible and dynamic, so that they drive their own
evolution and the evolution of their resultant phenotype. Genomic Drive can cause many genomic alterations that cannot be caused by any other mutagens. The de novo synthesis of new, or orphan, genes from TEs, and perhaps other non-coding DNA, has recently been confirmed in fruit fly and humans. Genomic Drive can build, sculpt, and reformat genomes by both active and passive means. Active Genomic Drive is due to the active transposition of TEs, from either a heterogenous or homogenous population of TEs. Passive Genomic Drive is due to ectopic recombinations between homologous TE insertions. Such ectopic recombinations are common only when there are large homogeneous populations of TEs. TEs can infiltrate germ lines by endogenous de novo synthesis, e.g. SINEs, SVAs, by exogenous invasions by retroviruses e.g. ERVs and LTRs, and by horizontal transfer between taxa, mostly by DNA-TEs. New integrations of germ line genomes by TEs, or modifications to existing TEs, or various stresses experienced by the phenotype, can result in intermittent bursts of TE activity. We propose that this can result in punctuational evolutionary taxonations or radiations, usually known as punctuated equilibrium.

Although sometimes harmful to some individuals, TEs can be very beneficial to lineages. The result of this is lineage selection for lineages endowed with a suitable repertoire of TEs; this endows such lineages with enhanced evolutionary potential. Taxa or lineages deficient in active TEs, and with heterogenous populations of inactive TEs, tend to be non-fecund, tend to prolonged stasis, and eventually may become extinct. Conversely, taxa or lineages well endowed with such TEs tend to be fecund, or species rich, as they taxonate readily. This could be called the evolution of evolvability. Cellular defences against excessive TE activity have resulted in the capacity of genomes to evolve epigenetic controls of TEs, which may further facilitate evolution or adaptation by epigenetic means.

In short, TEs, which we propose constitute the main engine of Genomic Drive, can result in the generation of widely divergent new taxa, fecund lineages, lineage selection, and punctuated equilibrium (Oliver & Greene 2009). Others, to give but one example, Goodier & Kazazian (2008), have clearly recognised the likelihood that bursts of TE transposition could accelerate taxonation, and that evolution has been adept at changing "junk" into treasure. However, they have stopped short of developing any hypotheses to this effect, and exploring the implications of such hypotheses.

Gradualism and Punctuated Equilibrium

Gradualism and Punctuated Equilibrium are two possible modes of evolution. Current orthodox evolutionary thought is dominated by an assumption that biological lineages evolve by the slow and gradual accumulation of adaptive mutations, that is, by gradualism, and that macroevolution (the origin of higher taxa) can be explained by an extrapolation of microevolution (the origin of races, varieties and species) into the distant past (Kutschera & Niklas 2004; and many others). This line of thought has been mostly dominant since Charles Darwin who, influenced by Lyell's concept of very slow changes in geology, regarded gradualism as fundamental to his theory. Darwin unreservedly said Natura non facit saltum (nature does not make a leap). Despite a number of early dissenters such as Bateson in the 1890s who strongly advocated evolution by discontinuous variation or sudden leaps, gradualism was eventually incorporated into neoDarwinism and the Modern Synthesis (Bowler 2003). However, many palaeontologists have found that gradualism does not concur with the majority of the fossil record. Instead, new species are found to arise abruptly and periodically and there are intermittent and often long periods of stasis, punctuated by periods of rapid change and branching speciation. These punctuations often occur during different periods in diverse lineages, so are apparently not always related to environmental changes. The observed persistence of ancestors in stasis, following the abrupt appearance of a descendant, is an indicator of punctuated equilibrium (Eldridge & Gould 1972; Stanley 1981; Eldridge 1986, 1995; Gould 2002). This is not to be confused with the hypothesis that fairly rapid, but gradualistic, evolution can occur in peripheral isolates, followed by the movement of the resulting new taxon back into the main population, giving the erroneous appearance of a gap in the fossil record.

Punctuated equilibrium, as detailed by the paleontologists cited above, has been observed in certain very fine grained strata, and entails intermittent periods of rapid evolutionary change, over an estimated 15,000 to 40,000 years (Gould 2002), which gives birth to a new taxon that remains little changed (i.e. in a period of stasis) until it becomes extinct, usually four to ten million years later. This taxon is often the progenitor of other taxa in the same lineage, while it is still extant. Contemporaneous, or successor taxa, in the same lineage eventually suffer the same fate. Of course, mass extinction events can interrupt this pattern, but they only
Transposable Elements Have Periodic Waves of Activity

Although retro-TEs can horizontally transfer between taxa only very rarely, new infiltrations of germ lines by retro-TEs can occur by de novo synthesis of SINEs, the fusion of SINEs into dimers, or the fusion of SINEs with other complex elements. Activating modifications to SINEs, and to the untranslated (promoter) regions of LINEs can also occur, and so on. Invasions of the germ line by exogenous retroviruses are also common, as are modifications to existing endogenous retroviruses or retroviral remnants. All of these intermittent events can result in transient waves of retrotransposition. Such intermittent waves of transposition often result in contemporaneous waves of retrocopies or retrogenes (these are sometimes called processed pseudogenes) which can sometimes be converted into useful new genes by other mutations. SINEs (especially Alu SINEs) are also thought to be typically activated in response to stresses on the host organism (Oliver & Greene 2009; Zeh et al. 2009). These waves of retrotransposition can therefore activate periods of rapid evolution punctuating the more normal near stasis of a taxon, giving punctuated equilibrium type evolution. In contrast to retro-TEs, many DNA-TEs can readily transfer horizontally from one taxon to another, sometimes between widely divergent lineages. There is often a dramatic wave of TE activity following on from a horizontal transfer event (Pace et al. 2008). However, all transposable elements, both Type I and Type II, can eventually succumb to the increased effectiveness of cellular controls such as methylation and interfering RNAs, and to crippling mutations which can eventually result in much reduced activity, and a possible return to near stasis in the affected taxon. But there are nearly always periodic new infiltrations of TEs in genomes by one means or another, to keep Genomic Drive going and to intermittently result in rapid evolution. If this does not occur then, according to the Genomic Drive hypothesis, extinction of the affected taxon is likely, if all other things are equal, or alternatively the taxon could become a fossil species. This is in agreement with the fossil record where extinction, aside from the mass extinctions, is the normal eventual fate of a taxon, but usually the lineage to which it belongs, survives. An example of this is the hominid lineage, where a number of earlier successful hominins which were in stasis, showing little variation over time, such as Homo erectus, succumbed to extinction but where Homo sapiens both survives and thrives (Eldridge 1986).

Genomic Drive in Mammals

The Human Genome is composed of about 45% TEs: ~42% are retro-TEs, made up of ~21% LINEs, ~13% SINEs, ~8% LTRs and ERVs. Most, but by no means all, of these are inactive, so some active Genomic Drive is constantly in humans. However, as nearly all of the LINEs are L1s and nearly all of the SINEs are the primate-specific Alu SINEs, there is a good potential for passive Genomic Drive, by means of such repetitious DNA promoting ectopic recombinations. A wide variety of DNA-TEs make up the other ~3% of TEs in the human genome, all of which are inactivated molecular fossils, but some have been exapted for cellular functions and are under positive selection, as in the SETMAR chimeric primate (anthropoids only – not prosimians) gene (Cordaux et al. 2006). TEs do cause disease in individuals, but in humans only slightly more than 0.5% of known genetic diseases are attributable to TEs. With ~356 extant species the primates are moderately fecund. Bursts of considerably increased TE activity have been associated with the major separations and divergences in the primate lineage, such as those of prosimians and Old World monkeys, and of Old World monkeys and apes (Oshina et al. 2003; Kim et al. 2004; Khan et al. 2006).

Quite atypically for mammals, the bats have many recently active DNA-TEs, some of which may be still active, as well as retro-TEs (Ray et al. 2007, 2008; Pritham & Feschotte 2007). Bats are correspondingly fecund, and with approximately 1000 extant species they comprise over 20% of all mammalian species. Bats evolved in an
early Eocene “big bang” ~52 million years ago (Simmons 2005) and appear to have taxonated rapidly. Rodents exhibit even greater fecundity, comprising close to 40% of all extant mammals, and these are well endowed with retro-TEs, but in at least some rodents (mice) individuals apparently pay a high price for the success of their lineage, as they have very many more TE-caused genetic diseases in individuals than do humans (Maksakova 2006). The bat and rodent orders contrast with the colugos, or “flying lemurs” (order Dermoptera) with only 2 to 4 species, but little is known about their TEs at present, except that they lack the 7SL derived SINEs that may have been a major factor in the successful radiations of the rodents and primates. More data on the genomes of colugos would be very valuable in assessing the consistency of their paucity of species with the Genomic Drive hypothesis.

With punctuated equilibrium evolution, as evidenced in the fossil record, stasis is the normal condition, and rapid change occurs rarely. Stasis is data, which must be accounted for in a satisfactory theory of evolution. “Living fossils” such as the Tuatara and the Coelacanth have been more or less in stasis for hundreds of millions of years. Information about the TEs in their genomes is scarce, but what there is suggests that these species have a paucity of TE activity, which is entirely consistent with the Genomic Drive hypothesis (Oliver & Greene 2009). The robustness of the Genomic Drive hypothesis as applied to the evolution of other phyla has scarcely been contemplated, but there is certainly evidence of long periods of stasis in some insects, and in crocodilians.

The Genomic Drive Hypothesis and Plants

TEs are also very active in plants and some angiosperm genomes are comprised of up to ~80% TEs. We have not yet extensively investigated the validity of the Genomic Drive hypothesis for plant evolution, but preliminary investigations indicate that plants also show punctuated equilibrium type taxonation. Plants have their fecund lineages, such as orchids in the monocots and daisies in the dicots, among the very numerous angiosperms, which evolved ~130 million years ago. Plants also have “fossil species” like the gymnosperm Ginkgo biloba, which has leaves similar in form and venation to those found in rocks deposited in the Mesozoic era (248–65 Mya) when ginkgo-like plants apparently had a worldwide distribution (Foster & Gifford 1974). Gymnosperms, which evolved ~350 million years ago, have relatively few species and seem to be in stasis, but are still very successful in terms of biomass, forming extensive forests in both the northern and southern hemispheres. Hybridisation giving sterile plants, followed by polyploidy to give fertile plants, is an observable and well documented example of punctuated equilibrium. The endosperm has also played a significant role in the evolution of many angiosperms by means of possible reproductive isolation caused by mismatches of the endosperm balance number (Johnson et al. 1980). The Genomic Drive hypothesis, when its probable application to plants is thoroughly investigated, may also help to explain the major transition of the angiosperms from their possible seed fern progenitors. However, another factor to consider is that the large advances in plant evolutionary forms are all associated with high global CO₂ levels at different periods of the earth’s history (Oliver et al. 2009).

Conclusions

Genomic Drive is a new hypothesis which still needs much development and testing, but it powerfully portrays the profound effects that waves of transposable element activity produce in intermittently driving evolution, and also the possible passive effects of homologous repertoires of inactive TEs. Much evidence suggests that it offers an explanation for stasis, and for rapid punctuational evolutionary taxonations and/or radiations, or punctuated equilibrium as it is usually called, as has been found in the fossil record. However, like all hypotheses it needs to be subjected to testing. If it is confirmed, it will offer a new conceptual foundation for much of evolutionary theory and will probably enable a reconciliation of the findings of paleontologists with biological evolutionary theory which has not been possible previously. It also seems likely that it, when fully developed, will be able to help to explain why some lineages are very fecund, while other lineages are quite non-fecund and why some lineages evolve rapidly while others linger in stasis and terminate in “living fossils,” and similar puzzles. Working out the relationship between TEs and evolution, in terms of cause and effect, seems likely to be a fruitful area of research well into the foreseeable future.

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References


New Understandings in Microbial (Bacterial) Evolution – a review

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Abstract

This review addresses the impact of the coming avalanche of genomic data and the convergence of fresh ideas on evolution on the pre-genetic concepts on bacterial evolution. The context is set with a brief historical account of the discovery of microbes and what Darwin wrote about them. The need to view bacterial evolution afresh in the 21st century is discussed. Current understanding of evolutionary forces and evolutionary mechanisms occurring in bacteria are outlined and secrets to the rapid evolution of bacteria are revealed. We conclude that the budding image of bacteria as gene-swapping entities stipulates a revision of such concepts as organism, species and evolution itself and propose a hypothesis that a bacterium is a 'composite entity' with a multiple decent of origin.

Keywords: microbial evolution; bacteria; evolution; evolutionary forces; evolutionary mechanisms

Finding the unseeable – what Darwin thought of microbes

In 1878, some 19 years after first publication of Darwin’s “On Origin of Species”, the French scientist Charles Sédillot proposed the word ‘microbe’ to refer to microscopic life (Bulloch 1938). However, predictions on the existence of minute organisms not visible to the naked eye long predate their discovery. As early as about 50 B.C. the Roman philosopher Titus Lucretius Carus speculated in his poem De Rerum Natural (On the Nature of the Universe) on the existence of invisible disease-causing entities, and in 36 B.C. Marcus Terentius Varro wrote that animals (animalia quaedam minuta) that cannot be followed by the eye were transferred through the air to other persons and caused serious illness (Cheesman 1964). We now think that Varro was referring to Plasmodium, the causative agent of malaria. Despite many centuries of philosophical and scientific speculation about their existence visual evidence for microbes was only first revealed to humans following improvements in microscopy during the 17th century, especially by the Dutch clothing merchant Antonie van Leeuwenhoek (van Leeuwenhoek 1684). Leeuwenhoek used the term ‘animalcule’ for the miniscule life forms he observed with his novel microscopes in various samples such as suspended teeth scrapings obtained from his friends and acquaintances. Much later the term ‘infusoria’ become popular to describe the abundant life forms seen in the microscopic world. However, apart from some interested scientists being aware of their existence there was little progress in knowledge of microbes during the next two centuries that followed their discovery. Whether these minute organisms were the cause or the products of biological or chemical processes were not clear to these early discoverers, and it was not until the beginnings of the science of microbiology by pioneers such as Louis Pasteur and Robert Koch in the mid-19th century that significant advances in understanding were made.

Studies on microbial biogeography also trace back to the days of Charles Darwin. It is commonly assumed that Darwin had nothing to say in his writings about microbes. However, this is not the case. He included microbes in his Beagle studies of the geographical distribution of organisms. Charles Darwin (1846) wrote “Generally the atmosphere is hazy; and this is caused by the falling of impalpably fine dust... I collected a little packet of this brown coloured fine dust... Professor Ehrenberg finds that this dust consists in great part of infusoria with siliceous shields, and of the siliceous tissue of plants. In five little packets which I sent him, he has ascertained no less than sixty-seven different organic forms! The infusoria, with the exception of two marine species, are all inhabitants of fresh-water. ... It is, however, a very singular fact, that, although Professor Ehrenberg knows many species of infusoria peculiar to Africa, he finds none of these in the dust which I sent him. On the other hand, he finds in it two species which hitherto he knows as living only in South America... After this fact one need not be surprised at the diffusion of the far lighter and smaller sporules of cryptogamic plants".

Darwin had made three very important evolutionary claims based on his various discussions about the microscopic world and these are critical arguments to understand his theory on evolution (O’Malley 2009).

1. All living entities, no matter how different they seem from animals and plants, undergo natural selection;
2. Microbes demonstrate that evolution is not a progression from simple to complex;
3. Microbes and their adaptive capacities are very important biological phenomena to understand the history of evolution on Earth.
The term microbes is used often to include both prokaryotic and eukaryotic microscopic organisms, in this paper we focus on one of the two domains of prokaryotic microorganisms – Bacteria, and in particular recent advances in our understanding of mechanisms affecting their evolution.

**Microbiology in the 21st century – why we need to view bacterial evolution afresh**

Although the majority of prokaryotic microbes (except for those causing serious diseases) have traditionally been considered as a minor part of life since their discovery in the seventeenth century, during the past few decades bacteria, as a general group of organisms, have rightly been given the greater attention they deserve. It is now widely accepted that microbes, both over time and space, have dominated a major portion of the history of life on earth. Microbes are the most ancient inhabitants of Earth. Some of the very old microfossils resembling bacteria found in Western Australia date from about 3.5 billion years ago (Schopf 1993). However, prokaryotic microbes are not only very ancient but also they are by far the most diverse and abundant forms of life on this planet. As a general type of organism, prokaryotes seem to be able to thrive on practically any substance, either organic or inorganic, that they can oxidise. They are ubiquitous in nature and occur not merely in fertile soils, fresh water ponds, ocean waters, plants, animals and the air but also in what is considered to be very extreme environments such as the super-heated hydrothermal vents, on the deep ocean floor, known as “black smokers” venting fluids at temperatures up to 350°C (Prieur et al. 1995), Antarctic ice floes (Lanoil et al. 2009), salt-saturated alkaline pools (Oren 2002), acid hot springs (Brierley & Brierley 1973), distilled water reservoirs (Moffett & Williams 1967) and even the upper atmosphere (Imshenetsky et al. 1979). The ability of these minute organisms to exploit such a cosmic range of environments is due to the tremendous breadth of genomic, and consequently physiological, variation found amongst them.

Until quite recently, our knowledge of prokaryotic organisms, and their metabolic diversity, was largely restricted to those bacteria commonly encountered everyday and that can be cultured in the laboratory under ambient conditions. However, since the advent of new molecular techniques and Metagenomics, which enabled sequencing of DNA extracted from communities of organisms, understanding of these microscopic forms have greatly expanded (Steele & Streit 2005). For example, a recent study by Fierer et al. (2007) used metagenomic analyses of a variety of samples of prairie, desert and rain forest soils to reveal that the average number of microbial species present in a single sample of soil probably surpasses the total number of microbial species that have been described and named to date (~7,500 archaea and bacteria, ~80,000 fungi and ~2,000 viruses). Thus, estimates and understanding of microbial diversity have taken a quantum leap early in the 21st century and it is fair to say that we are still only just beginning to understand the various evolutionary processes that lead to such a tremendous degree of ecological, morphological and physiological diversity in microbes. The key metabolic processes that have evolved in microbes have had a great influence in the history of this planet. Just as one example, the evolution of anaerobic photosynthesis contributed to the accumulation of oxygen in the Earth's atmosphere (Margulis 1970). The dawn of the Metagenomic era is promising to reveal new novel biochemical processes that exist in microbes but that have been concealed to humans so far (Steel & Streit 2005). When discovered, these no doubt will potentially revolutionize some of the basic concepts not only in biology but also in other fields of science.

**Dimension of bacteria – what we knew and what we now know**

Aspects of the bacterial cell

*Bacteria* are unicellular organisms usually ranging between 0.2 – 10 μm in size. As with many aspects of microbiology there are striking exceptions to this range with the largest known prokaryotic organism, *Thiomargarita namibiensis*, having cells up to 750 μm in diameter (Shalz et al. 1999). However, the norm is that bacterial cells are microscopic in size and need to be magnified about 100 times to be easily observed. In Stainer & van Niel (1962), used the current knowledge, to describe the principal features that distinguish a prokaryotic cell from a eukaryotic cell as follows:

Absence of internal membranes which separate the resting nucleus from the cytoplasm, and isolate the enzymatic machinery of photosynthesis and respiration in specific organelles.

Nuclear division by fission, not by mitosis, a characteristic possibly related to the presence of a single structure that carries all the genetic information of the cell. (As discussed below, it is now known that bacteria do not always carry their genetic information in a single structure.)

The presence of a cell wall that contains a specific mucopeptide as its strengthening element. (It is now known that the nature of the mucopeptide can be quite diverse amongst different species of archaea and bacteria. Furthermore, some bacteria, such as mycoplasmas, do not have a cell wall.)

Two other significant features that differ prokaryotes from eukaryotes are that their cytoplasm is immobile (cytoplasmic streaming, pseudopodial movement, endocytosis and exocytosis are absent) and they contain distinct 70S type ribosomes. While mechanisms of gene transfer between individual cells and recombination of DNA can occur, these processes never involve gametogenesis and zygote formation in prokaryotes (Krieg 2005). The method of prokaryotic reproduction is always asexual, commonly by a process called binary fission where a single cell first replicates its genome and then divides into two cells. Certain genera of bacteria, namely members of *Bacillus, Clostridium* and *Sporosarcina* may have two phases to their life cycle, vegetative cells and endospores (Nicholson et al. 2000). Endospores are not reproductive structures but are dormant survival bodies that are produced from the vegetative cell by a process called sporulation. This process is triggered
when the living, vegetative cells of these bacterial genera are exposed to stressful or harsh environmental conditions. As one of the hardest life forms known, the genera of bacteria that can produce endospores are able to withstand high temperatures, desiccation, freezing, excessive radiation, chemicals, the vacuum of space and many other environmental conditions that would easily kill eukaryotic organisms and vegetative bacterial cells (Nicholson et al. 2000). Being dormant survival structures endospores are metabolically inactive, somewhat like a plant seed, which are able to wait for the environment to again become favourable. Once environmental conditions improve, the endospore then germinates back into a living, vegetative bacterial cell that can grow and thrive.

**Bacterial genome architecture**

Bacterial genomes are compact structures and, in contrast to eukaryotic genomes, their protein-coding genes are virtually uninterrupted by introns. Therefore, the size of a bacterial genome is strongly linked with the number of genes it contains and as a result the evolutionary forces that act on individual genes have profound effects on overall genome architecture in these organisms (Kuo et al. 2009). The occurrence of repetitive and invert repeat regions of DNA sequence is a common feature of bacterial genomes (de Bruijn 1992; Shapiro 2005). Although it has been known for some time that in bacteria certain genes with a common function often occur in an operon (Jacob & Monod 1961), until recently, operons were thought to consist of both coding and non-coding, non-functional regions of DNA. Generally the term coding region is used to refer to DNA segments that contain the triplet genetic codes for amino acids that form polypeptides. It is now known that RNA and protein binding takes place on the so-called non-coding regions of an operon in order to fine-tune operon function (Shapiro 1999). These RNA and protein binding regions of operon DNA also contain specific codes of DNA sequence that interact with RNA or proteins that work as quite different codes to the well-known triplet genetic code for amino acids. Thus the concept we now have for the existence of multiple genetic codes in living organisms has come to be (Shapiro 1999). In addition to the commonly known triplet genetic code for amino acids it is now known that quite a wide range of other genetic codes in bacterial genomes such as transcription codes, replication codes, DNA segregation codes and codes for control signals for the level of expression of a certain protein (Shapiro 1999). These findings also suggest that the commonly occurring repetitive regions in bacterial genome are not just "junk DNA" as previously thought but that these segments of DNA in fact contain these other genetic codes which are essential for the proper functioning of a bacterium (Shapiro 2005).

**Multiple chromosomes, other replications and their shapes**

Until the advent and widespread application of genome-mapping studies, it was a common belief that all bacteria possessed a single circular chromosome. It is now known that this is not always the case – bacteria do not necessarily have a single chromosome nor are their chromosomes always circular. The presence of multiple chromosomes has been reported for a number of bacterial species; for example, two different chromosomes are known to exist in Agrobacterium tumefaciens, Leptospira interrogans, Brucella melitensis and Rhodobacter sphaeroides (Allardet-Servent et al. 1991, 1993; Choudhary et al. 1994; Zuerner et al. 1993) while three chromosomes are present in Burkholderia cepacia (Rodey et al. 1995). To date, two theories have been proposed for the evolution of multiple chromosomes in bacteria. One proposal is that the single chromosome splits into two or more smaller chromosomes. Evidence such a splitting of a single large chromosome to create multiple chromosomes has been reported for strains of Bacillus cereus (Carlson & Kolsto 1994). In this species the chromosomal splitting may be a relatively recent event in evolutionary terms, as contemporary strains of B. cereus with one or more chromosomes coexist. On the other hand the splitting of the chromosome in L. interrogans into two separate entities may have been a relatively ancient event as all strains of this species studied so far contain the two chromosomes (Zuerner et al. 1993).

The second mechanism proposed for generation of multiple chromosomes in bacteria is acquisition of the chromosome via lateral (horizontal) transfer of the DNA from another independent organism. Horizontal gene transfer is a very widespread process in bacteria that has played a very significant role in their evolution, as discussed further in the next section of this paper. Evidence for acquisition of a second chromosome via lateral (horizontal) transfer is found with Rhizobium sp. strain NGR234. This is a very promiscuous nitrogen fixing root nodule bacterial strain that can enter into symbiosis with legumes belonging to 112 genera representing all three sub-families of Leguminosae (Pueppke & Broughton 1999).

Given the existence of multiple chromosomes leads to the question – What are the benefits for bacteria of multiple chromosomes? Cole & Saint-Girons (1994) proposed that multiple chromosomes may have arisen in bacteria as an attempt by the cells to achieve faster overall rates of replication. It is well known that the capacity for rapid growth rates provides bacteria with strong advantages in competitive situations. However, the maintenance of multiple chromosomes across successive generations also requires the presence of an efficient system for chromosome partitioning, and this may cause a metabolic burden on the cell. These authors also suggested a possible reason for the evolution of multiple chromosomes in bacteria may be due to very strong selective pressure to maintain the second chromosome if it contains genes essential for bacterial growth or survival.

Until the 1980s the bacterial chromosome was also thought to only exist as a circular structure in the cytoplasm of the cell. However, during recent decades a range of interesting discoveries have been made relating to the diverse variety of shapes and sizes of bacterial chromosomes. Although the majority of known bacteria do contain a single circular chromosome, some bacterial chromosomes are linear molecules of DNA. A linear bacterial chromosome was first reported in the bacterial agent of Lyme disease, Borrelia burgdorferi (Bart et al. 1989; Ferdows & Barbour 1989). Since then other bacteria with linear chromosomes have been found in the genera Streptomyces (Lin et al. 1993) and Rhodococcus (Crespi et al. 1992). In some bacteria the situation is even more
complex with both circular and linear chromosomes being present, such as the coexistence of both linear (2.1 Mb) and circular (3 Mb) chromosomes in Agrobacterium tumefaciens. This species also contains two circular plasmids (450 kb and 200 kb; Allardet-Servent et al. 1993). Plasmids are double-stranded DNA molecules containing genetic information that can exist and replicate independently of the chromosome, but may also integrate with the chromosome. Plasmids often are stable and inherited in bacteria, but the genetic information they contain is not always essential for their growth and reproduction. However, plasmids can contain genes, such as antibiotic or heavy metal resistance that enhance cell survival in adverse or stressful conditions and thus provide a selective advantage for the cells that contain them. As with bacterial chromosomes, plasmids are commonly circular molecules of DNA, but linear plasmids occur in Mycobacterium xenopi, M. celatum and M. branderi even though these species each have a circular chromosome (Picardeau & Vincent, 1997). Species of Borrelia contain both linear and circular plasmids (Barbour 1988).

Bacterial evolutionary mechanisms – secrets for rapid evolution

The evolutionary mechanisms of a bacterial genome can be divided into three broad functional categories (Brown et al. 2001). Two of these categories (local changes in DNA sequence and rearrangements of DNA) exert their evolutionary effects by changes to the existing DNA (commonly inherited from the parent cell) present in a cell. The third mechanism, (lateral (horizontal) gene transfer) operates via the introduction of new genes into the cell that can provide it with novel metabolic capabilities that it did not previously have.

The first category, local DNA sequence changes, includes all situations of small local changes in the DNA sequence such as occur with the substitution of a single nucleotide, the deletion or insertion of one or a few nucleotides, or the scrambling of a few nucleotides etc. These small local changes in DNA sequence are generally thought of as being responsible for the slow evolution of proteins, and such changes in genetic information are generally transferred vertically from mother to daughter cells through successive generations. However, local sequence changes can also contribute to rapid evolution if these small sequence changes occur for example in a regulatory gene for a particular metabolic pathway. This could result in the complete shut down of the pathway and consequently could have a great impact on the evolutionary path of the organism in question.

The second broad category of evolutionary mechanism is DNA rearrangements within the genome of the bacterial cell (Michel 1999). These are often a consequence of the movement of genes between various locations on the chromosome or even between plasmids and the chromosome. This general process of gene movement is called transposition, and the simplest form of such a mobile gene is known as an insertion sequence (IS). An IS is a specialised segment of DNA that only contains information for functions involved in the movement of the segment from one DNA site to another. One important outcome of transposition is a rearrangement of some of the DNA of the cell’s genome, and depending on the nature of the genes affected there can be considerable effects on the organism itself, and the ecological niches it may occupy. There are a diverse range of mobile genetic elements now known to occur in bacteria (e.g. composite transposons, integrons, conjugative transposons), and the processes involved in their functioning within cells can cause substantial rearrangements of DNA as a consequence of events such as recombinational reshuffling, insertion sequence (IS) element related DNA inversion, deletion or partial genome duplication, site-specific recombination, transposition events, repetitive elements, correia elements and VCR elements (Buisine et al. 2002; Burrus et al. 2002; Burrus & Waldor 2004; Mazel et al. 1998; Chalmers & Blot 1999).

The third category of evolutionary mechanism is the main player in rapid evolution of bacterial genomes and this overall process is called lateral (horizontal) gene transfer (Gorgaten et al. 2002; Gorgaten & Townsend 2005). This overall process involves the transfer of DNA, and obviously the genetic information it contains, from one bacterial cell to another. There are three quite different ways in which a bacterium can gain DNA via lateral transfer from another cell. One process, called conjugation, is when there is DNA transfer from a donor cell to a recipient cell following direct cell-to-cell contact and involves bacterial plasmids in the process. The second way of gene transfer, known as transformation, occurs when a cell takes up exogenous DNA present in its environment and incorporates the foreign DNA into its genome. The third process of gene transfer, known as transduction, is the transfer of DNA between different bacteria by bacterial viruses, also known as bacteriophages. The evidence from many molecular-based studies of bacterial genomes is providing strong indications that these processes of genetic transfer are probably the most significant influence on rapid evolution in bacteria. Most bacteria share the ecological niches they inhabit with very diverse communities of organisms, and because of horizontal gene transfer they have potential access to a considerable portion of the community gene pool. There is growing evidence that within certain community gene pools, such as occur in soil populations of bacteria, there may be present what we would term “a flexible gene pool” that contains an ‘assortment’ of strain-specific genetic information that may provide additional properties enabling these bacterial species to adapt to special environments. The genes in this flexible gene pool are often carried on mobile genetic elements such as plasmids, genomic islands, etc., and can easily transfer among bacterial strains, species or even genera facilitating their relatively rapid evolution.

Evolutionary forces – news and views

There is a large repertoire of sequenced bacterial genomes now available; the average size of a small bacterial genome is estimated to be about 0.5 Mb while the larger bacterial genomes are around 10 Mb (Kuo et al. 2009). However, the smallest bacterial genome sequenced so far is only 0.02 Mb containing just 29 genes (http://
how pathogenic forms of some species may have a reduced genome size while free-living counterparts may have a considerably larger genome size (Ochman & Davalos 2006). Being sequestered inside a host, the pathogenic form may have restricted opportunities for gene uptake, and consequently lose pathways required for exogenous DNA incorporation as well as other genes that are not necessary for their growth and survival in a relatively stable niche inside a host organism. This leads to minimal genome sizes that are also known as resident genomes (Andersson and Kurland 1998). Powerful selection to minimize the material costs of cellular replication in some bacterial genomes in special niches or ecosystems is called genome streamlining (Giovannoni et al. 2005). Genomic streamlining in microbes is a consequence of selection for metabolic efficiency (Lynch 2006).

The larger genomes of the free-living strains indicates more recurrent gaining of new genes which may be required for metabolic versatility or more efficient selection for the maintenance of weakly beneficial genes in the genome. Kuo et al. (2009) propose that variation in level of genetic drift coupled with the inherent bias towards deletions in bacterial genomes are the key forces that govern the evolution of genome complexity in bacteria. The interplay among mutation, natural selection, and genetic drift is responsible for the vast diversity observed for the microbial genomes (Kuo et al. 2009).

It is apparent that we are still only at the beginning of uncovering the nature of diversity amongst bacteria, and our understanding of the complexity of processes at interplay in microbial evolution is in its infancy. The widespread occurrence of horizontal gene transfer between bacteria is a highly significant characteristic distinguishing them from eukaryotes, but researchers have only recently become aware of how important its role is in enabling rapid evolution in bacteria. Science is currently within an exciting period of microbiology as molecular advances provides new insights into the elegant complexity of processes at play in microbial evolution, and it is clear the knowledge gained will significantly influence our understanding of evolutionary processes affecting all life on our planet.

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Philosophical perspectives on Evolutionary Theory

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Abstract
Discussion of Darwinian evolutionary theory by philosophers has gone through a number of historical phases, from indifference (in the first hundred years), to criticism (in the 1960s and 70s), to enthusiasm and expansionism (since about 1980). This paper documents these phases and speculates about what, philosophically speaking, underlies them. It concludes with some comments on the present state of the evolutionary debate, where rapid and important changes within evolutionary theory may be passing by unnoticed by philosophers.

Keywords: Darwinism, evolutionary theory, philosophy of biology; evolution.

Introduction
Darwin once said that he had no aptitude for philosophy: “My power to follow a long and purely abstract train of thought is very limited; I should, moreover, never have succeeded with metaphysics or mathematics” (Darwin 1958). This was not false modesty; it was the simple truth. Nevertheless, he was a great synthesiser of facts and theories, and he was very thoughtful about scientific methods (he especially valued Sir John Herschel’s A Preliminary Discourse on the Study of Natural Philosophy; see Gildenhuys 2004), so he was somewhat akin to a philosopher. One of his outstanding attributes was his willingness to put forward prominently the main objections to his theory of evolution. Three objections stood out in 1859:

- There seemed to be a mismatch between the gradualism supposed by the theory and the discontinuities of the fossil record.
- There seemed to be a disconcerting lack of transitional species in the fossil record and in living biology.
- Many organisms and many of their organs seemed too perfectly adapted to their environments or too perfectly suited to their functions to have come about from the haphazard processes of mutation and natural selection.

Darwin thought that these objections could be answered, or would be answered in time. The other great absence from his theory was a coherent genetics, but there was no scientific genetics before Mendel, so Darwin and his followers were whistling in the dark on that matter. As things turned out, the neo-Darwinian synthesis of the 1930s supplied a form of genetics friendly to Darwinian theory. (For an analytical summary of contemporary Darwinian evolutionary theory, see Gregory 2009).

In more recent times, evolutionary theory has been expounded to non-specialist readers by various kinds of author. Biologists such as Richard Dawkins, Stephen Jay Gould, Steve Jones and Simon Conway Morris are prominent. So also are historians of science, such as Peter Bowler, Janet Browne, Adrian Desmond and James R. Moore. Equally likely, however, one might be introduced to evolutionary theory by a philosopher of biology, for example Michael Ruse, David Hull or Kim Sterelny. (For introductions to the philosophy of biology, see Lennox 2004; Sloan 2005; Griffiths 2008; other recent examples include Brandon 1996; Hull & Ruse 1998; Sterelny & Griffiths 1999; Hull 2001; Sterelny 2001; Pigliucci & Kaplan 2006; Hull & Ruse 2007; Rosenberg & McShea 2008.)

My subject in this paper is the relation between Darwinian evolutionary theory and the discipline of philosophy. I will divide the story of this relationship, much condensed and inevitably simplified, into four parts. (Grene & Depew 2004 provides a grand survey of the history of biological thought; see also Grene 1986.)

Indifference
For about one hundred years after the Origin the leading philosophers of Britain, America, Germany and France – the leading countries in the field – showed almost no interest in Darwin or Darwinism. They simply ignored the subject altogether. They largely ignored biology itself. This was not because they were intellectually insular. The leading philosophers, men such as Frege, Russell, Moore, Wittgenstein, Husserl, Heidegger, Carnap and Quine, almost all had interests outside philosophy, but those interests were in logic, mathematics, physics, perception, language and ethics. They were also often reacting against the synthesizing evolutionism – a very non-Darwinian evolutionism – of 19th century Hegelian idealists. None of them saw Darwin’s evolutionism as an antidote to Hegel’s metaphysical evolutionism. But more probably the main reason why the philosophers were uninterested in Darwinian theory was that they did not regard biology as a leading science. Of course a few philosophers were interested in biology, but they were not Darwinian in outlook. They were the vitalists, of whom Hans Driesch...
is the best-known example. But none of the leading philosophers took vitalism at all seriously.

Nor were the philosophers interested in theology, least of all in creationist theology, as a potential world-view. To this day, philosophers almost universally disdain creationism and the theory of intelligent design. In this, they are the descendants of David Hume and Immanuel Kant.

It should also be said that none of the philosophers held any enthusiasm for the ugly side of the Darwinian movement - its espousing of radical individualism and, far worse, of eugenicist authoritarianism. Eugenicism was popular amongst many biologists but not at all amongst philosophers.

Criticism

With the molecular biology revolution of the 1950s, the status of biology as a science changed dramatically, and this might have led to an upgrading of its prestige amongst the philosophers. However, at first quite the opposite happened. Darwinian evolutionism came under attack. The assault was led by one man, Karl Popper, but since he was widely regarded as the world's leading philosopher of science, this was no small confrontation. By Popper's time, the Darwinians had put together a formidable system. Darwin's "descent with modification" acting through the mechanism of natural selection, now working in tandem with Mendelian genetics, had become the established framework for much of the discipline of biology. Then the breakthrough into the molecular domain by Watson, Crick and many others showed that biology could be integrated with chemistry and presumably with physics. There seemed to be no longer any good reason for not taking biology seriously as a great science.

Popper, however, saw Darwinism as a pseudo-science, or at best as a "metaphysical research program". In his words, "To say that a species now living is adapted to its environment is, in fact, almost tautological. ... Adaptation or fitness is defined by modern evolutionists as survival value, and can be measured by actual success in survival: there is hardly any possibility of testing a theory as feeble as this. And yet [he adds], the theory is invaluable. ... Although it is metaphysical, it sheds much light upon very concrete and very practical researches" (Popper 1974; see also Hanson 2008). Popper was happy to accept the "modification by mutation" half of the Darwinian equation. What he attacked was the "natural selection" story, which he accused of vicious circularity. The problem turned on the definition of "fitness". If fitness is nothing other than survivability, then survival of the fittest is merely the survival of those who survive. The Darwinian theory thus seems irrefutable, since even in principle no evidence could be given that would count against the theory. The attributes of fitness that might explain survival are, Popper claimed, nothing other than the fact of survival itself. Behind Popper's objection is a Humean assumption that, wherever we have a causal story, the cause must be separately identifiable from the effect.

It was this argument that, I think, kick-started the philosophy of biology as a sub-discipline. I don't know to what extent Popper's argument was taken seriously amongst biologists (Hull 1999 suggests it was not), but it made an impact amongst philosophers, who set out to show that fitness could be identified separately from survival. The first generation of professional philosophers of biology, including David Hull, Michael Ruse, Michael Ghiselin, and Elliott Sober, were all defenders of Darwinism, defending it in part against the objection raised by Popper. This was a central topic of discussion amongst such philosophers in the 1960s and 70s. The end result was no doubt a victory for Darwinism. (See Sober 1984 and the essays in Sober 1994; more recently, chapter one of Pigliucci and Kaplan 2006). Popper had few supporters, and he retracted his key argument in 1978 (Popper 1978; see also Popper 1976 and Hull 1999; Hull points out various ways in which Darwin exhibited his theory as falsifiable).

Enthusiasm and expansionism

Having weathered this storm, Darwinism's reputation amongst philosophers went rather rapidly from being clouded by Popper's objection to being a paragon of good science and a paradigm that should be applied even outside biology. This third stage has been dominant since about 1980. We can call this the period of Darwinian enthusiasm, perhaps even of expansionism. The movement to expand Darwinism has been carried out by many thinkers. From within biology, E.O. Wilson led the charge, but many psychologists, social scientists and even philosophers have joined in the battle (Wilson 1975). The disciplines to be colonised were mainly psychology and the social sciences, but gradually the expansion has come to include philosophy itself. Perhaps the key figure amongst philosophers has been Daniel Dennett. To explain this movement it may help to see how Dennett arrived at the odd position of being a trumpet-blower for what he called "Darwin's dangerous idea" (Dennett 1995; for reviews see Orr 1996, and Gould 1997).

In the 1960s it came to be fairly widely agreed that philosophy had failed in one crucial area. It had failed to give any plausible account of the nature of the mind, even though the question had been central to philosophy since Descartes in the 17th century and even though Cartesian mind-body dualism suffered from its seemingly anti-scientific commitment to inexplicable interaction between material bodies and an unknowable non-material mind-stuff that supposedly makes up the mind. To go forward philosophy would have to cut this Gordian knot. The cutting was done by a small number of Australian and American philosophers, one of whom was Dennett. Henceforward it would be taken as given that the mind just is the brain. Mind-body materialism would be taken as an axiom. Whatever difficulties there might be in this, it was assumed they can't be worse than the difficulties in the Cartesian dualist assumption. The difficulties would be fully debated, but the solutions to any problems would be materialist solutions. (As a footnote to this, it is worth noting that Popper's friend, the great neuroscientist John Eccles, was a mind-body dualist. As late as the 1960s, neuroscience was not necessarily committed to materialism.)

But, if the mind just is the brain, what then is the brain? It is of course a biological organ. In that case,
whatever we say about the brain had better be based on biology, if we want to have any scientific credibility. And the only biology that can do the job is Darwinian biology. Hence philosophers such as Dennett, who had come out of the mind-body debate, declared themselves to be whole-hearted Darwinians. They then set out to convert the academic world – in psychology, the social sciences and philosophy – to their new world-view. (A rival school of thought, the computationalists, led by Hilary Putnam and Jerry Fodor, modelled the mind-brain relation on the computer, a line of argument that left room for the claim that the mind is the brain but it is not simply the brain, since it involves something like an algorithm working in the brain by means of which the world is represented. In recent times Fodor has emerged as a critic of Darwinian theory; see Fodor 2007 and Fodor & Piatelli-Palmarini (in press)).

This step marks an important change. I think, in the nature of how philosophy is done. Since the mid-19th century, when the Hegelian synthesis collapsed, the leading English-speaking philosophers had tried to avoid speculation like the plague. It was not their job, they insisted, to provide mankind with a synthesis of all knowledge. They saw themselves in two ways: either as searching for the foundations of knowledge (in logic or mathematics or perception) or as interpreters of language and of the ways that language shapes our shared social practices and world-view. Dennett and others broke with this self-imposed embargo on speculation. They supported Darwinism much like punters might support a horse: they took it to be the best horse in the field, and they backed it to the hilt. Darwinism will, they think, eventually explain to us not only the brain but also our social life and our morality and even our misbegotten tendencies towards religious enthusiasm. Darwinism will be, for all intents and purposes, a new theory of almost everything biological, social, and ethical. (For examples, see Millikan 1984; Sober & Wilson 1998; on religion, see Wilson 2003; on the theory of cultural evolution, see Boyd & Richerson, 2005.) Dennett describes it as a “universal acid; it eats through just about every traditional concept and leaves in its wake a revolutionized world-view”. He does not deny that cultural evolution occurs, but he denies that it displays any features inexplicable by evolutionary theory.

In some ways this is a reversion to Humeanism. It was David Hume’s main ambition in the 18th century to naturalise the mind, to see it as part of nature. Today Humean naturalisers are the dominant party in the English-speaking philosophical world, which dominates the discipline. But today we have moved beyond Hume’s naïve Newtonianism; instead we have what might be called naïve Darwinian naturalism. How productive this strategy has been is a matter of controversy. Few even of its supporters could claim that it has made the great questions of philosophy very much less intractable. And certainly some philosophers have argued in favour of a more modest form of Darwinism, such as T H Huxley and Gould). It seems clear that much is happening at the level of the genome and move between genomes in disconcerting ways (see Oliver & Graeme 2009).

What does all mean for the Darwinian system of ideas? That is beyond my competence. One obvious question is whether an unstable genome is consistent with the gradualism that is the default assumption of Darwinism (even though it has been denied by some Darwinians, such as T H Huxley and Gould). It seems clear that much is happening at the level of the genome that we do not at all understand. Given what we do know, it is quite possible that large-scale evolutionary modification might occur not incrementally but very abruptly. This possibility has the attraction that it might be seen as matching the radical discontinuity of the fossil record. Abandoning gradualism will be seen by some as abandoning Darwin; others will portray it as a revamped Darwinism, despite Darwin’s insistence from the start on incremental changes only. (For one unorthodox viewpoint, reporting on very recent research, see Ryan 2002 and Ryan 2009).

How does all this relate to philosophy? I’m not sure. Recent public debate about Darwinism has been driven by the challenge from creationism (aka “Intelligent Design”), but that is not an angle that interests many philosophers. Few if any philosophers have any sympathy for or interest in creationism (Fuller 2008, though a secular humanist, is a partial exception). A more interesting question is how far are they aware of

Reasons for rethinking?

Dennett-style Darwinism still dominates amongst philosophers. But in the last decade, it seems to me, much has happened to the Darwinian paradigm that the philosophers and social scientists have been so enthusiastically backing. Here I have to be very tentative. I’m not a biologist of any sort, so I can speak only as an observer. But what I seem to detect within biology is a paradigm shift, of the sort described by Kuhn. This time, however, it is not the selection and fitness part of the equation that is threatened, as Popper had supposed. It is the modification story that is being shaken up.

The genomic revolution was generally expected to be the completion of the Darwinian synthesis. Knowledge of the genome would finally show us in detail how the system works. Genes code for proteins, and knowledge of the genome will decode the code. But it has not turned out that way, for at least three reasons:

• Most – almost all – of the genome is non-coding. Thus, far from being a lean-and-mean reproducing machine honed by relentless competition, the genome looks more like a flabby couch potato unlikely to be competitive at any level.

• The coding part of the genome seems insufficient to do the work expected of it. There is no strong correlation between genotype and phenotype (on this “C-value enigma” see Gregory 2005). Thus, much of the work assumed to be performed by genes is now seen as lying in the province of epigenetics.

• The genome is not the stable hard-drive that ensures the smooth running of the biological software. Pieces of code move around within the genome and move between genomes in disconcerting ways (see Oliver & Graeme 2009).

What does all mean for the Darwinian system of ideas? That is beyond my competence. One obvious question is whether an unstable genome is consistent with the gradualism that is the default assumption of Darwinism (even though it has been denied by some Darwinians, such as T H Huxley and Gould). It seems clear that much is happening at the level of the genome that we do not at all understand. Given what we do know, it is quite possible that large-scale evolutionary modification might occur not incrementally but very abruptly. This possibility has the attraction that it might be seen as matching the radical discontinuity of the fossil record. Abandoning gradualism will be seen by some as abandoning Darwin; others will portray it as a revamped Darwinism, despite Darwin’s insistence from the start on incremental changes only. (For one unorthodox viewpoint, reporting on very recent research, see Ryan 2002 and Ryan 2009).

How does all this relate to philosophy? I’m not sure. Recent public debate about Darwinism has been driven by the challenge from creationism (aka “Intelligent Design”), but that is not an angle that interests many philosophers. Few if any philosophers have any sympathy for or interest in creationism (Fuller 2008, though a secular humanist, is a partial exception). A more interesting question is how far are they aware of
the unorthodox happenings within biology? The leading names in the philosophy of biology seem to be unperturbedly Darwinian. We will have to wait and see how all this plays out. I hope the philosophers do take the new genomics seriously. There is every reason why they should do so, since they might help us to think through the issues a little more systematically. (See, for one example, Griffiths & Stotz 2006.) But to do so will perhaps require dropping the Darwinian triumphalism that has been dominant for so long and making room for consideration of non-Darwinian theories of evolution. Darwin himself said at the end of his 1859 "Introduction": "I am convinced that natural selection has been the main but not the exclusive means of modification" (Darwin 1968: 69). The present question is whether the Darwinian theory of evolution is only one amongst a number of plausible evolutionary theories.

Acknowledgements I have benefited from regular conversations with Keith Oliver on these topics. I also thank this journal's anonymous reviewer for helpful criticisms.

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Coming to terms with biological evolution: a critique of the terms and perspectives embedded in the definition and description of some of its fundamental concepts

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Abstract

The abstract concepts embodied in the theory of biological evolution are difficult for most people to comprehend since humans are not genetically endowed with the cognitive mechanisms to directly perceive biological evolutionary events and must deal with them in a culturally derived intellectual manner. This can lead to inaccurate, misapplied, and poorly conceived terms, and the inappropriate changing of meanings of established terms. More effort should be made by authors when coining new terms or applying existing terms. By not addressing these issues of terms and meanings, future research may go in unproductive directions, thus delaying attainment of a better understanding of the mechanisms of biological evolution.

Keywords: biological evolution, evolutionary terms, science education

Introduction

From the time of the publication of Darwin’s *On the Origin of Species* (Darwin 1859), there have existed problems of misunderstanding and misapplication of fundamental concepts in the science of biological evolution, particularly concepts such as random variation, non-random natural selection and descent with modification from a common ancestor. This is despite claims by scientists (Gould 1996; Mayr 1997; Dawkins, 2009) that the concept of natural selection is simple to understand. For example, Weismann (1909) quoted T H Huxley as saying about Darwin’s idea of natural selection: “How extremely stupid not to have thought of that.”

However, it is evident that a majority of people, even when exposed to biological education, have difficulty in accurately grasping the fundamental concepts of biological evolution. Bishop & Anderson (1990) found that college students who had previously studied biology had three main misconceptions about biological evolution: (1) a teleological or need-driven idea of the adaptive process; (2) variation of traits within a population and subsequent differences in reproductive success were not recognised; and (3) a gradual variation of traits was perceived to occur in all members of the population at the same time. Gregory & Ellis (2009) studied students undertaking an advanced postgraduate degree in science and found that while post-graduate students had a better understanding of concepts of biological evolution than students at lower levels, there were still persistent misconceptions and a lack of working knowledge of biological evolutionary mechanisms even at this advanced level. Many other authors have observed a similar situation in studies of various groups from primary school level to secondary school level biology teachers (Demastes et al. 1995; Jonsen & Findley 1996; Larreamendy-Joerns & Ohlsson 1995; Ohlsson 1991; Zuzovsky 1994).

While various authors have put forward explanations for the continued misunderstanding of biological evolutionary concepts (e.g., the naïve schema of Larreamendy-Joerns & Ohlsson 1995; the event versus equilibration ontology of Ferrari & Chi 1998; or the prior disposition, understanding and parents’ education level, determined by Deniz et al. 2008), in this paper I suggest that part of the problem is etymologically related in that the embedded meanings of the terms and language employed in defining and describing the fundamental concepts of biological evolution create a (non-conscious) bias in the mind of the user towards a way of thinking that is non-scientific and inapplicable to the actual processes of biological evolution. Further, although the concepts of biological evolution such as natural selection, adaptation, common ancestry, etc., appear straightforward and simple to understand, these ideas contain abstract, statistical and temporal aspects which are not necessarily compatible with the natural perceptual and cognitive abilities of the human brain. Thus, throughout the paper there will be discussion of two ideas: (1) that of the problems with terminology including misleading, inappropriate or misapplied terms and (2) that of the genetic (“hardwired”) nature of human neurologically-based cognitive and perceptual frameworks, particularly in relation to language. In fact, the two ideas are inter-related, in that the nature of human “hardwiring” and its effect on cognitive and perceptual frameworks leads to the misunderstanding of concepts, and the coining and use of misleading, inappropriate or misapplied terms.

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The impact of words

Terms have different meanings to different scientists (and people in general, for that matter), depending on their path in life, or background, and the meaning conveyed to readers may not always be the one intended by the writer. Further, not all scientists fully understand the use of terms in their own discipline, or that in other related disciplines, nor can they coin appropriate terms. The misapplication of terms in the history of science, and the changes in meaning of a term in the history of a given discipline provide examples of this problem. Such misinterpretations, misapplications, and misunderstandings, and evolution of the meanings of terms is particularly relevant to the theory of biological evolution, as it is an arena that is mired in controversy, and terms need to be explicit, precise, and not open to misapplication and misinterpretation. Unfortunately, this is not the case, and I proffer the notion that two of the problems in the controversy and debate in biological evolution resides in: (1) the misuse, poor definition, and misunderstanding of terms; and (2) the incorrect and inappropriate coining of terms. These terms can create erroneous perceptions of what constitutes biological evolution, create resistance to the idea of biological evolution, and mislead research directions.

The influence of words on human emotions and thinking has been noted by philosophers and scientists from early in recorded history to the present day. Buddha in the 5th Century BC, advised that “Whatever words we utter should be chosen with care, for people will hear them and be influenced by them for good or evil.” This can be modified to the theme of this paper as: “Whatever words we utter should be chosen with care, for people will hear them and be influenced by them from their own perception, training and background.” Carl von Linné (Linnaeus 1707–1778) wrote: Nomina si nescis, peril cognitio rerum. “If you ignore names, actual knowledge vanishes.” Mark Twain (Samuel Clemens), a 19th Century author and social commentator, observed (as related in Paine 1917) that “A powerful agent is the right word: it lights the reader’s way and makes it plain.” Clearly, words are an important part of communication, and they are an important pathway for lighting the way to further and deeper understanding of a given subject matter.

Recent psychological and neurological studies have investigated how language, human behaviour and neural structures are interrelated (Chomsky 1965; Liberman & Whalen 2000; Scott & Johnsrude 2003; Coppola & Newport 2005; Dehaene-Lambertz et al. 2006; Friederici et al. 2006; Goldberg 2008; Ledoux & Camblin 2008). Several parts of the human brain are involved in language processing, particularly in the left hemisphere, such as Broca’s area, Wernicke’s area, and the inferior parietal lobule (Geschwind’s territory), so an argument can be made that human response to words, while having cultural causative factors (i.e., each culture has developed its own language and word meanings), also has genetic and hence biological evolutionary underpinnings. Human languages (and the underlying anatomical neural areas) have developed in a social context within common experiences of the physical world and largely dealt with a timescale spanning the current instant (several seconds) to a person’s lifetime (ideally spanning ~ 80–100 years). In that situation, does it matter that words may have imprecise or multiple meanings? After all, there are many non-verbal cues in social contexts which re-enforce verbal meanings. My thesis in this paper is that it does matter when an objective description is required, of processes (e.g., biological evolution, quantum mechanics, amongst others) which occur in the physical world and may have no relation to human social contexts or human time-scales, or common, everyday experiences. Thus, for many of the experiences and natural phenomena described by scientists, there is generally no direct human experience as a calibration, and hence it becomes even more important that words, terms and meanings are correctly conveyed. This is the realm of scientific terminology where nomenclature forms the basis of description and classification as employed in the Scientific Method, and is essential to Science and its communication.

Inherent in the principle of the Scientific Method is the assumption that the language or terms employed in scientific studies are defined such that there is a common understanding of the ideas being conveyed. This understanding of defined terms is a critical component in the process of reproducibility of results, without which scientists cannot be certain that they are talking unambiguously about the same topic. An example of an area where the clarity of scientific terminology is particularly important is in forensic science, especially in criminal cases where non-scientist members of the jury and judiciary are struggling to understand the expert evidence that may or may not convict a person (Edmond 2002).

Unfortunately, scientists are not perfectly logical machines, and the terms that they assign to phenomena are a product of the existing scientific knowledge, perpetuation of erroneous ideas, and the current culture of the times in which the scientists live. The convention of positive to negative flow of electricity in an electrical circuit is an example of the perpetuation of erroneous ideas. An initial conclusion (based on the observations and equipment available in the 1700s), was later proven erroneous (electrons flow from negative potentials to positive potentials as discovered in the early 1900s), however, the original terms are retained to the continuing confusion of innumerable high school students and university students. On the other hand, the meanings of terms in a discipline often evolve with various practitioners redefining the terms in the literature according to their own interpretations and this process may lead to confusion (Fallon & Smyth 2009), and employing a term with a changed meaning.

To illustrate this principle, an example is borrowed from the discipline of sedimentology. Sedimentologists have employed an adjectival term “sedimentary”, to refer to unconsolidated geological material (e.g., sedimentary deposit), but the adjective has also been incorrectly applied to the study of rocks derived from sedimentary materials resulting in the oxymoron “sedimentary petrology”. Consider the etymological evolution of the adjective “sedimentary”; it has changed in its use in referring to a sediment, to a sedimentary deposit, to a sedimentary rock (change in the strict meaning of “sedimentary”), to sedimentary petrology (another change in the strict meaning of “sedimentary”), in that petrology cannot be “sedimentary”), to sedimentary
research, e.g., The Journal of Sedimentary Research (where it is implied that the phrase "sedimentary research" conveys the meaning of "research into sedimentary materials, and rocks deriving from sediments, and the petrology of those sediments and sedimentary rocks"). The meaning embedded in the adjective "sedimentary" in "sedimentary research" is very different from that in "sedimentary deposit".

Critique of terms in biological evolution

This brings us to the confusing and sometimes unfortunate terms existing in the area of biological evolution. There are many commonly misused, misleading, misunderstood, inappropriate or not well conceptualised terms extant in the biological evolutionary literature and a selection of these is presented in Table 1. Several problematical terms are discussed in detail below.

Darwin himself has the distinction of proposing one of the most misleading terms in the concepts of biological evolution, viz., "natural selection". It was a term that Darwin came to regret, as shown in a letter to his friend Charles Lyell in 1860, where Darwin wrote "Talking of 'Natural Selection', if I had to commence de novo, I would have used 'natural preservation'; for I find men like Harvey of Dublin cannot understand me" (Burkhardt et al. 1993).

Later, in a letter to the Irish botanist W H Harvey, Darwin replied in part "The term 'Selection' I see deceives many persons; though I see no more reason why it should than elective affinity, as used by the old chemists. If I had to rewrite my book, I would use 'natural preservation' or 'naturally preserved'" (Burkhardt et al. 1993).

The problem with "natural selection" is that embedded in the word "selection" is the implication of choice by a living agent. The act of selection does not apply to inanimate processes, which is a problem since the process of differential survival and reproduction of organisms (termed as "natural selection") is an inanimate, deterministic occurrence, viz., the action of

<table>
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<th>Table 1</th>
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<tr>
<td>Examples of terms employed in the area of biological evolution which are either often misunderstood and consequently misapplied, or poorly designed as conceptual explanatory terms.</td>
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<tr>
<td>Adapt: &quot;to fit&quot;; should be used only for species/populations, not individuals, and only in the intransitive sense e.g. &quot;animals have become adapted to their environment&quot;, not &quot;the animal adapts to its environment&quot; or &quot;the animal learns to [physically] adapt&quot;</td>
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<td>Biological evolution: a term that should be used instead of &quot;evolutionary biology&quot; where the main topic, &quot;evolution&quot;, has been transformed into a descriptor</td>
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<td>Design: a word that should not be applied to a deterministic process such as biological evolution which evidences a variety of states that range from poorly organised to complex</td>
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<td>Darwinism: philosophy based on Charles Darwin's ideas; the word has no place in a scientific discussion of biological evolution where &quot;Charles Darwin's concept of evolution&quot; would be more appropriate; one does not see the words &quot;Newtonism&quot; or &quot;Einsteinism&quot; employed in scientific writing</td>
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<td>Evo-devo: an unscientific abbreviation of the phrase &quot;evolutionary development biology&quot;; ontogenological phylogeny would more accurately describe this area of study</td>
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<td>Evolution: &quot;unrolling&quot; or gradual development; the word has become synonymous with biological evolution, whereas there is evolution of landscape, magmas, societies, language, amongst others; a natural process that should never be personified</td>
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<td>Fitness: the success of an organism in surviving in its environment and reproducing its genetic material into the next generation; mistakenly perceived as only physical strength as in &quot;Survival of the Fittest&quot;= survival of the strongest or most aggressive, which is not always the case (cf. biological altruism)</td>
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<td>Gene: a sequence of nucleotides coding for a protein; by definition, a &quot;non-coding gene&quot; is an oxymoron; exclusive focus by scientists on genes has resulted in a public perception that genes comprise the total genetic material of an organism whereas in reality, genes form only ~ 2% of the DNA (in humans)</td>
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<td>Junk DNA: a somewhat short-sighted term for non-coding DNA which comprises 98% of human genetic material. Now found to have important regulatory functions in gene expression</td>
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<td>Natural Selection: Darwin acknowledged that this phrase had unintended connotations (the concept of a &quot;Selector&quot;); often personified as in &quot;Natural selection chooses...&quot;; an alternative phrase such as &quot;environment-constrained differential phenotype survival&quot; might be more accurate</td>
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<td>Orthogenesis: hypothesis that biological evolution is an intrinsic drive towards perfection; confusing and discredited term</td>
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<td>Primitive characters: misleading term for antecedent characters in a lineage; these characters may be quite complex</td>
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<tr>
<td>Random mutation: change in the DNA that is unpredictable by current scientific models; often conflated with biological evolution, ignoring environment-constrained differential phenotype survival (natural selection) which is deterministic, NOT random</td>
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environmental pressures on variable organisms. It is understandable as to why Darwin chose the term "natural selection". However, the fact that the "Great Chain of Being" idea has persisted throughout history in various guises (Lovejoy 1936; Bynum 1975) supports the idea of an anthropocentric bias in human perceptual frameworks. That is, Lovejoy's unit ideas of "plentitude, continuity and gradation" reflects genetic behaviours involved in survival such as obtaining food, reproduction and social hierarchy. This tendency for the human condition to be reflected in the perception of natural order has been noted previously (Durkheim & Mauss 1903).

The terms "primitive" and "advanced" as applied to the more appropriately termed antecedent or derivative, respectively, characters in an organism's lineage are misleading as the word "primitive" is usually equated with "simple" and a primitive character may actually be very complex. Chloroplasts, for example, are considered a primitive character of vascular plants, although, in fact, these organelles are relatively complex. The word "character" also is confusing and poorly defined, as it can refer to a range of features from molecular to morphological, to behavioural, and to be applied to a range of levels from individual to species, to clades. That is, the term "character" has different meanings in different disciplines, and even different meanings within the same discipline. Use of this term, therefore, does not convey explicit meaning.

An example of how the meaning of terms can evolve is shown in the history of the term "orthogenesis". Orthogenesis was a popular idea in the 19th and early 20th Centuries, and originally represented the hypothesis of an intrinsic lateral direction in the development of life, and later became conflated with teleological ideas where evolution was unidirectional towards a perfect goal as in "progressive evolution" (e.g., the increasing complexity of organisms from simple prokaroytes to complex eukaryotes culminates in the superior complexity of humans [Bonner 1988]). Orthogenetic ideas became discredited by palaeontological evidence of non-linearity in the fossil record. However, some modern researchers now employ the term "orthogenetic" to describe a local linear trend in the evolution of a trait within a species (Jacobs et al. 1993), thus changing its meaning yet again.

Regardless of the discrediting of the orthogenesis idea, the impression of direction and progress in biological evolution still persists among the general public (Scott 1999). This is in spite of the fossil evidence. Additionally, there are many examples of extant lineages producing less complex organisms from complex ancestors (non-linear biological evolution) as, for example, in mites (Walter & Proctor 1999) and parasitic flatworms (Poulin 2006). Other evidence against orthogenesis includes: 1) the vast bulk of life on Earth consists of prokaroytes (and if "progressive" biological evolution has been occurring for ~ 4 billion years, then life on Earth should be dominated by complex forms); 2) there exist prokaroytes and eukaryotes with a range of structural complexity from a microscopic bacterium to a macroscopic cetacean, all concurrently undergoing the processes of biological evolution with the result that a modern prokaryote is often more complex than an ancestral prokaryote (biological evolution should only be occurring in the most "progressive" stage if a linear progression is true); 3) many organisms (e.g., the rice plant, Oryza sativa) have
more complex genomes than that of humans, and 4) cross-species or horizontal gene transfer (Syvanen 1985; Rumpho et al. 2008) occurs, thereby eliminating the idea of a unidirectional linear progression of genetic material. As a denouement of the orthogenetic hypothesis and challenging the teleological and anthropocentric idea that humans, as the most complex organism on Earth (due to their complex brain), are the final goal of biological evolution, recent research has shown that humans have an invertebrate rival for neuronal complexity in coleoid cephalopods (Wollesen et al. 2009).

The fact that the idea of “progressive” biological evolution persists, despite the overwhelming evidence against it, is interesting as this phenomenon illustrates more about the cognitive behaviour of humans than any empirical reality of the idea. A possible explanation for persistence of erroneous ideas in the face of empirical evidence is that humans may have cognitive filters in pattern recognition (Van Essen et al. 1991) or cognitive frameworks in reasoning (Stenning & van Lambalgen 2008) that predicate them towards deriving false correlations from natural data. In the case of “progressive” evolution, the logic proceeds as follows: eukaryotes biologically evolved from prokaryote organisms (true), and multi-celled organisms are structurally more complex than single-celled organisms (true), and therefore biological evolution is directed towards increasing complexity (false).

One of the most misunderstood words in biological evolution is “random” as in “random genetic mutation”. Since events occur axiomatically in a deterministic fashion, nothing is “random”, not even genetic mutations – there is just not enough information currently available to predict their occurrence. French astronomer and mathematician Pierre-Simon Laplace was confident that the universe is not random (Laplace 1814) when he wrote the following words:

We ought to then regard the present state of the universe as the effect of its anterior state and as the cause of the one which is to follow. Given for one instant an intelligence which could comprehend all the forces by which nature is animated and the respective situation of the beings who compose it – an intelligence sufficiently vast to submit these data to analysis – it would embrace in the same formula the movements of the greatest bodies of the universe and those of the lightest atom; for it, nothing would be uncertain and the future, as the past, would be present to its eyes. (Translation from Truscott & Emory 1902)

Thus “random” as employed in biological evolution refers to a causal event that is unpredictable as to its occurrence in time and place. The word “random” is often equated with the word “chance” to mean an unpredictable event of unknown cause.

A common misunderstanding of biological evolution is that complex anatomical structures (such as complex eyes) develop entirely by chance, which seems impossible. However, chance does not operate in isolation. Complex anatomical structures are a resultant of a cumulative two-stage process: 1) random (chance) genetic mutations in individuals producing variant phenotypes; and 2) differential survival and reproductive success of these phenotypes. Where are the terms that accurately describe and encapsulate this process? Why in the 150 years since Darwin put forward the self-acknowledged inadequate term “natural selection” have no researchers advanced more appropriate terms? An explanation may be that humans generally comprehend simple events better than complex abstract and long term processes, and have neurological systems that cope with either routine common events or novel events (Stimikova, Holecomb & Kuperberg 2008). Examples abound where scientists and engineers reduce complex, non-linear, and interacting phenomena to simple models in order to cope with understanding them. Perception of biological evolutionary processes has not been necessary for human survival or reproductive success, unlike as for example, perception of the ecological process of predation or the process of reproduction, for which humans have genetic behaviours, and hence I suggest that there is not the genetic “hard wiring” to adequately address the complexities of biological evolution.

“Junk” DNA (Ohno 1972) illustrates an important principle in how terms and words are misapplied, and how there is (potential) creation of misperceptions with ramifications for future research directions. Without fully understanding the function of “junk” DNA, supposedly “non-coding” DNA regions were interpreted to be non-functional genetic relics, and this interpretation led to molecular biologists focusing on only the 5% of DNA which coded for proteins and ignoring 95% of the entire human genome for almost 40 years! A term should have been utilised that was objectively descriptive, and that would survive acquisition of additional information, since the use of the adjective “junk” now has to be abandoned, as more information on the functionality of this “junk” DNA has been obtained. Sections of “junk DNA” termed transposable elements, comprising ~50% of the human genome (Smit 1999) have been recognised (retrospectively in some cases), to have a regulatory effect in gene expression (McClintock 1965; Thorneburg et al. 2006) and cell differentiation (Britten & Davidson 1969), so perhaps the “junk” term will be relegated to the trash bin.

Conclusions

The abstract concepts embodied in biological evolution are difficult for most people to comprehend, since the processes involved occur either over long time-scales or at the microscopic genetic level. As discussed above, humans are not genetically endowed with the cognitive mechanisms to directly perceive biological evolutionary events and must deal with them in a culturally derived intellectual manner. This can lead to inaccurate, misapplied, and poorly conceived terms, and to the inappropriate changing of meanings of established terms. The coining and continued use of inaccurate, misapplied, and poorly conceived terms has only added to the problem of understanding biological evolution. While the scientific discipline of biological evolution is not unique in having a proliferation of confusing or misleading terms (Barrass 1979), more effort than shown in the past should be made by authors when coining new terms or applying existing terms. Terms should be descriptive and
not genetic, such that the meaning of the word can be “unpacked.” Other considerations involved in coining a new term include consideration of the relevant scientific history and possible future directions of the research (whether the new term has older connotations, or whether the term is “fashionable” and likely therefore to become out-dated), and consideration of the cognitive impact of the term (i.e., will the term fit into human language/perception schema, or be invisible in that people will not understand and will ignore it). By not addressing these issues of terms and meanings, future research may go in unproductive directions and resources may be wasted, thus delaying attainment of a better understanding of the mechanisms of biological evolution.

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1 The term “genetic” is used in the sense of origin, and does not refer to the discipline of genetics. Terms and classification systems may be descriptive, e.g., the phrase “quartz sandstone” is comprised of descriptive terms, and simply provides a description of what is at hand. Alternatively, terms may be genetic, referring to how an author interprets something has formed, e.g., the term “aeolianite”, implying that the material has been deposited or formed by aeolian processes. In the latter case, if the origin of the material eventually is re-interpreted as non-aeolian then the term “aeolianite” has to be revised. It is therefore preferable to have non-genetic, descriptive terms and classification systems, rather than genetic terms.


Evolution for undergraduates: fostering critical thinkers

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Abstract

The process of evolution underpins all in biology, directs research and provides a unifying explanation for the history and diversity of life. The study of evolutionary biology draws on many disciplines (from molecular biology to ecology to palaeontology), and has applications in numerous areas, such as medicine, conservation, and agriculture. How then do we use evolution to train university undergraduates in a meaningful way, and what do we want them to learn? There are many aspects of evolution that could be taught at the undergraduate level, and content will vary depending on the course-context. Some basic components include the evidence for evolution, microevolution, speciation and macroevolution. However, teaching evolution offers exciting opportunities to convey more than just content. Evolutionary biology immerses students in the process of science and should encourage them to think critically and to carefully analyse concepts, problems and evidence. It offers students nearing graduation the opportunity to draw together their learning across different areas in biology, asking them to synthesize their thinking and appreciate how problems in evolution can be analysed with multidisciplinary tools. In this paper we argue the importance of teaching evolution and justify its place in the teaching curriculum by providing examples of its wide applications, and by using case studies to illustrate the value of inquiry learning in teaching evolution at all undergraduate levels.

Keywords: evolution, evolutionary biology, inquiry based learning, scientific method

Introduction

According to Murdock (1945, as cited in Wilson 1998), all human cultures studied have accounts of the origin of biodiversity. Modern biologists are in overwhelming agreement that the best explanation of how existing biodiversity arose is evolution, in which all living species are descendants of the earlier ones and share a single common ancestor. From the early 18th century onwards evidence has accumulated steadily to support the evolutionary viewpoint, with an explosive increase of convincing molecular evidence during the late 20th and early 21st centuries (see, for example, Nardi et al. 2003; Tarlinton et al. 2006; Endicott et al. 2009).

Given the natural human curiosity about the mechanisms behind the origin and diversity of life, as well as the agreement of almost all biologists that the explanation lies in evolution, we believe that it follows naturally that evolution should be an important part of teaching biology at all levels of our education system. It may therefore come as a surprise to some that evolution is a recent addition to the curricula in some Western countries (Chinsamy & Plagányi 2008; Sanders & Nkxola 2009), or that in some cases there are strong campaigns to remove evolution from biology curricula (Bleckmann 2006).

We believe that researchers and teachers in the biological sciences should always look critically at the subject matter they present to ensure that it remains factually accurate, up-to-date and relevant to the needs of students in contemporary society. Knowledge is expanding at a rapid rate, yet University degrees remain fixed at three-year lengths, so there is great competition for space in a crowded curriculum. It is helpful if material in the curriculum performs multiple functions to facilitate the breadth of objectives that students need to achieve within the short time of their degrees. Justifying the teaching of evolution within this scenario requires answers to three important questions. They are:

1. Why teach evolution? – how do we justify the teaching time when so many exciting biological developments are jostling for a share of students’ time?
2. What should we teach? – exactly what parts of a dynamic and expanding discipline should be selected for the undergraduate curriculum at its different levels?
3. How should we teach it? – what examples and pedagogical techniques are appropriate to make the subject relevant and interesting for modern students?

In this paper we give our answers to all these questions, in the hope of providing resources to colleagues teaching evolutionary biology for the first time and giving important background to educational researchers wishing to use the teaching of evolution as a case study. Given the breadth of evolutionary biology, we are unable to explain all background biology and evolutionary theory for each example that we present. However, we feel that a wide breadth of examples is critical to illustrate the breadth and the diversity available for teaching. Therefore while our descriptions
are often short, we do provide primary and secondary references so that interested readers may follow up topics in greater depth. We also present some examples as more detailed case studies, to illustrate the teaching elements within them. Our examples are necessarily selective and inclined toward our personal interests in evolutionary ecology rather than other equally important areas such as palaeontology.

**Why teach evolution?**

*The theory of evolution unifies modern biology*

Undergraduate students studying biology or related disciplines will study the diversity of life on Earth, looking in detail at the different taxonomic groups, and comparing how they live and function in their specific environment. This taxonomic understanding is very important for all biologists. However, knowing what biodiversity is out there is only one level of understanding of the biological world; delving into questions about why that biodiversity exists, takes scientific minds to the next level. Studying evolution attempts to answer some of the most fundamental questions that humans can ask about the natural world, including:

*Where did all the diversity come from?* — as Samways (1994) points out, we know many physical constants in the natural world with great certainty, yet we cannot state confidently how many different species of life are on Earth. We do know, though, that there are a great many and have a good idea of the relative abundances of different groups. How was all this diversity formed?

*Why are organisms like they are?* — why, for example, do cetaceans breathe air when they live exclusively in aquatic environments, whereas most other aquatic vertebrates use gills?

*Why do they do what they do?* — in many mammals, males compete for access to females. In contrast, in Mormon crickets females compete for access to males (Gwynne 1981). Why should this be?

As Dobzhansky (1973) observed ("Nothing in biology makes sense except in the light of evolution"), evolution unifies all biology in answering these questions. It can be thought of as a play unfolding within a theatre of ecology in which human beings themselves are included in the cast (Groom et al. 2006). The theory of evolution explains a great array of seemingly otherwise unrelated facts, from the universality of the DNA code amongst all living things, through to changes in the genetic make-up of populations over time, the similar biogeographic distributions of similar organisms, and the order of appearance of animal taxa, such as fish, amphibians, reptiles and mammals, in the fossil record. In that way, it provides a cohesive and unifying foundation for all of the life sciences.

As a result, evolution is studied using multidisciplinary tools, such as molecular biology, population genetics, population ecology, embryology and development, taxonomy and phylogeny, biogeography, palaeontology and studies in speciation, comparative anatomy, behaviour, physiology and biochemistry. Undergraduate units in evolution cannot attempt to offer technical training in each of these specialist areas, although they may offer training in one or two, if these are of common relevance to the student cohort. Ultimately evolution provides a framework to synthesize students’ previous knowledge and provides an understanding of how each field of study can be applied to answer universal questions in biology.

**Evolution exemplifies the scientific method**

A further reason for teaching evolution is to illustrate the scientific method in action through inquiry-based learning, by which students discover knowledge for themselves by applying scientific methods rather than being shown passively (Finn et al. 2002). Alters & Nelson (2002) observed that this type of approach "...presents science as a process of critical thinking that provides a model for critical thinking elsewhere in the student’s life.”

In particular, studies in evolutionary biology require both observational and experimental approaches. Studies of comparative anatomy or of a series of fossils represent very good examples of observational science because there is no experimental manipulation, no control and no independent replication. However, predictions can be made on the basis of theory and tested through structured observations. Biogeography and the fossil record provide good examples of this approach in action (see, for example, the discussion of Antarctic paleoecology in Coyne 2009, pp. 102-103).

Evolutionary biology also provides numerous opportunities to illustrate the principles of experimental methods to test hypotheses. The classic textbook example has long been the case of industrial melanism in the moth *Biston betularia* in the United Kingdom. In Kettlewell’s (1973) original experiments, dark and light morphs were exposed on different backgrounds. Their differing vulnerability to predation by birds in terms of their contrast to the background was demonstrated (for a review of more recent developments in this example, see Ridley 2004). Variations of this exercise are still practised with high school and undergraduate students using both field based (Barker 1983) and computer based activities (Gendron & Staddon 1984; Calver & Woolier 1998).

A key point that should be noted in the example above is that the work begins with a hypothesis, requires experimental and control treatments (given by characteristics of the backgrounds and the objects or shapes displayed against them) and needs adequate replication in the sampling to allow convincing tests of the original hypothesis. If desired, statistical analysis can also be taught in such exercises when students process their data. At the very least, students can also practise presentation techniques by using tables and graphs in written reports describing their experiments.

**Understanding evolution has many practical applications**

Any teacher of modern students is familiar with the catch cry: ‘what is this all good for?’

Fortunately, evolutionary thinking applies to many different fields. For example, students of conservation biology should be aware that long-term conservation of biodiversity requires that we also conserve the process that renews it: evolution. This requires, amongst other
A major phylogeographic break is evident between the Indo-Pacific and Atlantic Ocean, indicating two separate ESUs, within which are multiple management units. Figure reproduced from Moritz (1994), with permission from Elsevier. Numbers in brackets indicate sample sizes (number of nests).

Figure 1. Evolutionarily significant units (ESUs) in the green turtle Chelonia mydas. UPGMA dendogram of mtDNA analysed from 15 rookeries in green turtles (study by Bowen et al. 1992). A major phylogeographic break is evident between the Indo-Pacific and Atlantic Ocean, indicating two separate ESUs, within which are multiple management units. Figure reproduced from Moritz (1994), with permission from Elsevier. Numbers in brackets indicate sample sizes (number of nests).

What should we teach?

Teachers of evolution are inevitably confronted with the difficult question of selecting which aspects of evolution to teach in introductory and specialist biology units. We argue that the difference between the introductory and the specialist units is one of breadth rather than depth, so the major themes of evolution should be at least touched on for beginning students. We also argue that all material should be presented in the context of scientific method, so that science is understood as a process rather than a body of knowledge to be memorised, and that practical examples should be used wherever possible of the topic’s relevance to contemporary life. Content might vary depending on the course-context in which evolution is taught, but there are some basic principles that should be covered and can be found in the chapter headings of any good evolutionary text.

Evidence for evolution

First and foremost should be a clear understanding of the evidence for evolution. A range of evidence from different disciplines and on different scales can show that (i) populations within species show evolutionary change in heritable traits (population studies of microevolution, breeding of domesticated plants and animals), (ii) this within-species change can lead to the evolution of new species (biogeography of ring species, transitional forms in the fossil record, genetics of polyploidy in plants), (iii) all life on earth shares a common ancestry (lineages within the fossil record, comparative anatomy and embryology, molecular biology and genetics, vestigial traits in morphology, development and genetics). This material can be made contemporary and exciting by including recent examples of all these characteristics (see Coyne 2009, especially chapters 2 and 3). The text books by Freeman & Herron (2007) and Ridley (2004) present insightful and scientifically rigorous chapters reviewing the evidence for evolution, and see Irwin (2001) for a review of ring species.

Microevolution – small scale changes in gene frequencies within populations

Students should also gain a clear understanding of microevolution, its four contributing processes (natural selection, mutation, gene flow and genetic drift) and how they contribute to gene frequency change in populations. There are good Australian examples of microevolution. One is the response of snake species to the introduction of the cane toad Bufo marinus to Australia. The cane toad was introduced in 1935 to control insect pests, principally of the cane beetle, but was ineffective in its primary role. Nevertheless, it thrived under Australian conditions and spread from its original introduction sites in Queensland across much of northern Australia. While native snakes prey on the cane toads, far from controlling toad numbers snakes were often killed by the toad’s venom. Snakes with large heads relative to their body size can eat larger toads and therefore ingest more venom. However, if the snake is heavy it can tolerate more poisoning by cane toads, show that both species have evolved smaller heads and heavier bodies (Phillips & Shine 2004).
Other examples of microevolution include: the evolution of beak shape in Galápagos finches (see Peter and Rosemary Grant and colleagues, Freeman & Herron 2007); adaptive divergence in body size in sockeye salmon (Hendry 2001); evolution of life-history traits in guppies (Roznick et al. 1997); and the evolution of beak length in soapberry bugs (Carroll & Boyd 1992; Carroll et al. 1997; Carroll et al. 2001; Carroll et al. 2005; for an overview see Freeman & Herron 2007). All these examples are particularly useful as sound examples of microevolution, because rather than just illustrating phenotypic change, they have also explicitly tested the criterion that the traits involved are genetically based and therefore heritable: a key component of the microevolutionary process.

Studies of natural selection can be used to test each of Darwin’s four postulates about populations that inevitably lead to natural selection (Darwin 1859). Darwin’s four postulates, which Freeman & Herron (2007) illustrate with examples of snapdragons and Galápagos finches, are:

(i) Individuals within populations are variable
(ii) The variations among individuals are, at least in part, passed from parents to offspring
(iii) In every generation, some individuals are more successful at surviving and reproducing than others, and
(iv) The survival and reproduction of individuals are not random; instead they are tied to the variation among individuals. The individuals with the most favourable variations, those who are better at surviving and reproducing, are naturally selected.

As a consequence, individuals with characteristics well-suited to their environment increase in the population (Freeman & Herron 2007).

Speciation
Integral to understanding evolution is the study of how speciation occurs. Students should appreciate how species are defined, and the difficulties of reaching a consensus species concept. Different modes of speciation should also be explored, including how speciation may occur in space (such as allopatric or sympatric speciation), and what mechanism/s might be involved (such as natural selection, genetic drift, sexual selection or more sudden karyotypic changes) (Freeman & Herron 2007).

Macroevolution – large scale change beyond speciation
The final essential component in general undergraduate studies of evolution is an understanding of the difference between microevolution and macroevolution, and an appreciation of macroevolutionary patterns. Students should gain an overview of the history of life on earth, an appreciation of the fossil record and how it contributes to our understanding of the relationships of organisms, as well as our understanding of patterns and processes (sensu McNamara 2009), and an overview of patterns of extinction and radiation. It is impossible to gain a detailed understanding of the fossil record and how it can be studied in a general evolutionary unit, however, some key topics can be studied in detail to gain the depth of thinking required from advanced students. During detailed reading about the evolution of Cambrian fossil fauna, for example, students can encounter both fossil and molecular evidence which contributes to scientific understanding of whether this truly was an ‘explosive’ evolutionary event (Mapstone & Mapstone 2003; Peterson et al. 2005). Students can then be encouraged to critically evaluate what these two disciplines tell us about how and when the Cambrian fauna evolved. They can also integrate their ecological knowledge when they encounter discussions on the role of ecological triggers in Cambrian evolution.

New directions in evolutionary research
Evolution for advanced students should not just stay on steady ground, but should also explore the frontiers of evolutionary science. Students should be readily aware that there are many questions still unanswered, with differing viewpoints and models currently being tested (McBride et al. 2009). Delving into some of these issues, for example the importance of genetic drift versus natural selection in driving molecular evolution (see Freeman & Herron 2007 for an overview), provides insight into how research can be used to evaluate different hypotheses, and provides another stimulus for critical thinking.

How should we teach it?
Here we explore specific case studies in more detail to illustrate the teaching elements within them, and thus show how evolution can be taught as inquiry learning, in which students focus on the process of science rather than learning content by rote (Finn et al. 2002).

Evolution as a stimulus for teaching critical thinking skills
Developing critical thinking and analysis skills should be central in teaching evolution. In particular, advanced undergraduates can synthesize their learning to solve problems, thereby developing their analytical thinking skills.

The availability of information by electronic sources means that the role of the university teacher has shifted somewhat from disseminating information, to facilitating access to the most accurate, useful and relevant types of information. It is useful for students to reflect on just how accurate some of the ‘fast information’ they access might be. One way to stimulate critical reflection is to have students read an online news article from a mainstream news outlet which reports on the findings of evolutionary research. The article could be reporting on bacterial conjugation, human evolution, population genetics or any topic with an evolutionary slant (see Table 1 for a listing of useful online news sites). Students should read with a critical eye, looking at whether there are significant compromises in how the scientific principles are explained for a mainstream audience. The students’ job is then to find the published research article on which the news story is based (using clues given in the news story, such as authors and date). They should also read around the topic to gain a deeper understanding of the original research before writing a
critique examining how accurately and effectively the news story reports the research from the scientific paper. It can help for students to have small-group discussions, facilitated by the tutor/lecturer, where they examine the research and any oversimplifications made in the news story, and explore some of the reasons why these oversimplifications might be there. Through the critique process they should gain an understanding of just how superficial scientific information is when it comes from these 'fast' sources. There is no substitute for finding the original research and reading it critically.

The Honey Possum – a showcase for developing hypotheses and testing them with structured observations

Sex is a sure subject for sparking interest amongst undergraduate students as well as being a highly relevant topic to explore from the perspective of evolution. One sexual athlete worthy of attention is the Australian honey possum *Tarsipes rostratus*. Honey possums are endemic to the south-west corner of Western Australia, and feed exclusively on nectar and pollen (Wooller *et al.* 1984; Wooller *et al.* 2004). Although tiny and weighing 6–9 g, males of this species produce the longest sperm recorded for any mammal (Cummins & Woodall 1985). Their testes represent approximately 4.2% of their total body weight (Renfree *et al.* 1984), making them much larger than those of any other marsupial, most of whom have a relative testes mass of less than 1% (Taggart *et al.* 1998), and amongst the largest recorded for eutherian mammals (Kenagy & Trombulak 1986; Breed & Taylor 2000).

In our own teaching, the honey possum example becomes a case study in sexual selection. Sexual selection arises due to asymmetries in reproductive success within and between the sexes (Freeman & Herron 2007). One form of sexual selection is sperm competition, which occurs as a consequence of female multiple mating, where the gametes of two or more males compete to fertilize a given set of ova (Birkhead & Möller 1998; Parker 1998; Anderson & Dixon 2002). Before using this example students should be familiar with the basics of sperm competition and the characteristics it selects for in males. Extensive research has found that in species where females mate with more than one male in a single reproductive event (multiple mating), the relative testes mass is greater than in species where females mate with a single male (Gomendio *et al.* 1998). Larger testes indicate a larger investment in spermatogenesis (Harvey & Harcourt 1984; Möller 1988; 1989). This observation is seen across a range of taxa including primates, ungulates, other eutherian mammals, marsupials, birds, fish, frogs, and butterflies (Birkhead & Möller 1998, chapters and references therein). This *observational* evidence is tested by *experimental evolution* in the laboratory, where testes mass has been shown to increase in response to polyandrous mating (e.g., see Hosken & Ward 2001). It is further used to *predict* the direction of evolution, as in feathertail gliders, where testes mass was used to predict sperm competition (Taggart *et al.* 1998); a fact later confirmed using genetic studies (Parrott *et al.* 2002).

Thus, using this research as a springboard, the large relative testes size in the honey possum (but not necessarily sperm length, see Gomendio & Roldan 1991; Gomendio *et al.* 1998; Gage & Freckleton 2003) predicts that this species has sperm competition and multiple mating. In addition the students will also discover that there are other intriguing features about the honey possum that indicate sexual selection, such as a strong skew in the operational sex ratio (sensu Emlen & Oring 1977; Reynolds 1996). At any one time more males than females are ready to breed because males can produce sperm in all months, while females in the population are asynchronous in their timing of oestrus, due to continuous year-round breeding, embryonic diapause and a brief oestrus duration (Bryant 2004). This creates competition amongst males: another flag to students that sexual selection is at work.

The case study can be further developed by exploring the genetic research on whether there is sperm competition in the honey possum. Female honey possums and the 2–4 pouch-young they were carrying, were genotyped at four highly polymorphic microsatellite loci using fluorescently labelled DNA primers (Bryant 2004; Bryant unpublished data). Offspring genotypes were compared to the maternal genotype, and paternal alleles were identified (see Figure 2) to distinguish multiply sired litters (multiple paternity). In all mammals, all ova are released simultaneously, thus multiple paternity provides unquestionable evidence of sperm competition (Gomendio *et al.* 1998).

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**Table 1**

Examples of news websites and popular magazine sites that publish stories reporting on research in science. The stories on these sites focus on particular research studies and are just some of the sites that are useful sources of evolution stories for undergraduate students to research and critique.

<table>
<thead>
<tr>
<th>Website</th>
<th>URL</th>
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<tbody>
<tr>
<td>BBC News (Science and Environment)</td>
<td><a href="http://news.bbc.co.uk/2/hi/science/nature/default.stm">http://news.bbc.co.uk/2/hi/science/nature/default.stm</a></td>
</tr>
<tr>
<td>New Scientist</td>
<td><a href="http://www.newscientist.com/">http://www.newscientist.com/</a></td>
</tr>
<tr>
<td>Cosmos</td>
<td><a href="http://www.cosmosmagazine.com/">http://www.cosmosmagazine.com/</a></td>
</tr>
</tbody>
</table>
and evidence that evolution is a dynamic process, not only observed over geological timescales, but also happening in the bush just outside one's backdoor. We have also found that our own students respond well to hearing what their own faculty are researching. However, other case studies could be substituted here with the same effect, exploiting students' inherent interest in 'home industry'.

**Trinidad guppies – developing hypotheses and testing them with manipulative experiments**

The next example, the Trinidadian Guppy, is also studied following scientific methods. Once again, students begin with an observation and make a prediction, but in this case the prediction is put to an experimental test. Thus, this example illustrates good principles of experimentation in illustrating evolutionary phenomena.

The Trinidad Guppy *Poecilia reticulata* is a wild freshwater fish found in mountain streams in the tropical forests of north-eastern South America and adjacent islands (Endler 1980). Generally, guppies living under high predation conditions are found downstream of waterfalls, together with the pike cichlid *Crenichichla alta* and other species of cichlids that prey on large, mature guppies (Roznick et al. 1997). Guppies living under low predation conditions are found upstream where large predators cannot traverse up waterfalls or rapids. In these populations guppies are found with *Rivulus hartii*, an omnivore that sometimes preys on juvenile guppies.

Endler's (1980) classic experiments on the guppies investigated natural selection on the colouration patterns (bright spots and patches of colour) found on adult male guppies. The colour genes are not expressed in females. Endler (1980) hypothesized that males in streams with cichlid fishes had fewer spots due to selection pressure from predation, and he tested this in two ways. Firstly, he created a mixed guppy population from a variety of streams, divided these fish randomly amongst artificial ponds, and to each pond added either a cichlid fish, *Rivulus*, or no other fish. Over 19 months the guppies in the control ponds and *Rivulus* ponds exhibited an increase in the average number of spots due to sexual selection, whereas the guppies in the cichlid ponds exhibited a decrease in the average number of spots associated with predation (Endler 1980). Secondly, Endler tested this effect in the wild in the Aripo river in Trinidad. He translocated guppies from a stream where guppies were already living with cichlids, to a stream with *Rivulus*, but no guppies, and compared them to a control stream where guppies were already living with *Rivulus*. After about two years, the average number of spots in the translocated guppy population had increased to become similar to the *Rivulus*-only guppies, diverging from the lower number of spots found in the cichlid-stream guppies.

Evobeaker® (SimBio Virtual Labs 2010) provides a computer simulation 'How the guppy got its spots' (SimBio Virtual Labs 2009) which allows students to investigate guppy spot brightness first hand, rather than just reading about the Endler experiments. It is useful if students are not exposed to the Endler experiments until after they have done at least some initial hypothesis building and experimentation of their own. Using Evobeaker® software, students can design and carry out
experiments to test their hypotheses in a complex environment with a range of streams, artificial ponds and predators. Under the simulation, spot brightness decreases under predation from cichlids, in comparison to controls, similar to the findings of Endler's (1980) experiments. There are opportunities for the more advanced and motivated students to refine their experimentation, after a few initial experiments, and include testing, for example, for the impact of different types of cichlids, different abundances of cichlids, the impact of *Rivulus*, and the impact of different stream environments, and to record the observation that spot brightness increases when predation pressure is released (due in the wild to sexual selection, Endler 1980). This allows depth in the learning of both the process of natural selection and the research skills needed to study it. The approach used in the guppy exercise is constructivist: where a problem is proposed, alternatives are put forward, and evidence is gathered to address the problem, and this type of approach is thought to increase learning and retention (Alters & Nelson 2002).

The guppy work also provides linkages to learning about life history evolution. Reznick and co-workers (1987; 1990; 1997) have investigated predation pressure as a driver of life history evolution by performing translocation experiments. The work started with observations by these workers and others (Reznick et al. 1997 and references therein) that guppies from high predation populations have a higher mortality rate and ‘faster’ life history strategy than guppies from low predation populations (Reznick & Endler 1982; Reznick et al. 1997). They mature earlier, at a smaller size, and they reproduce more frequently, with each litter containing more young of a smaller size than low-predation guppies, as predicted under life-history theory (Reznick & Endler 1982). These differences have a genetic basis (Reznick 1982).

The descendants of guppies that were translocated from high to low predation, matured at a later age and larger size than those in the control population under high predation (Table 2), and produced fewer, larger offspring (Reznick & Bryga 1987; Reznick et al. 1990; Reznick et al. 1997). This response was measured after 11 years in the Aripo River and at both 4 and 7.5 years in the El Cedro River, with a slower response in the female traits than in the male traits, likely due to a lower heritability (Reznick et al. 1997). Thus the differences in life history traits observed in high and low predation populations of guppies were shown through experimental evidence to be a consequence of these high and low predation environments. The primary selection force is thought to be predation, along with a role from selection based on differences in resource availability in high and low predation communities (see Reznick et al. 2001).

The research undertaken in this case study exemplifies how observations can be taken through to experimentation to test the actual drivers of natural selection on gene frequencies in populations, and how they have shaped life histories in the past. Students can also reflect on experimental design, especially the use of controls, to develop their critical thinking skills (Alters & Nelson 2002). It also provides a clear example of natural selection occurring rapidly over ecological timescales (albeit through selection imposed by experimental means), dispelling the misconceptions that evolution only happens extremely slowly over geological timescales (which probably arises due to problems with use of the term ‘gradual’ in descriptions of natural selection; it can refer purely to the process as being incremental rather than the rate being constant; see Ridley 2004, box 21.1), and that only events at the speciation level and above count as true evolution (for a student-friendly article see Holmes 2005). Addressing student misconceptions is a key part of the learning process (Alters & Nelson 2002). Finally, for advanced students, this example can be used in discussions about the processes of micro- versus macroevolution. Reznick et al. (1997) use this example to show that selection among individuals within populations can occur rapidly enough to account for the periods of rapid change observed in the fossil record, and thus contribute to the debate on whether the pattern of punctuated equilibrium must be explained using different processes to those of microevolution (see also Svensson 1997).

**Student background: an important issue**

In choosing examples to be presented, it is important to be aware of students’ backgrounds. For example, many topics in evolution can be explored using sophisticated mathematical models. We have presented none of these, because in our experience many students lack the mathematical background necessary to fully appreciate these examples. However, instructors whose students are not restricted in this way may prefer to develop some of the mathematical approaches. This could include, for example, statistical analyses of the results of experiments (Ruxton & Colegrave 2006) or

<table>
<thead>
<tr>
<th><strong>Table 2</strong></th>
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| Measurements of male and female age and size at maturity for low predation (experimental) sites and high-predation (control) sites of guppies *Poecilia reticulata* in a translocation experiment by Reznick et al. (1997). These are measurements from second generation laboratory-reared descendents of the guppies from the wild populations. Measurements are least squares means adjusted for covariates and unequal samples sizes and * indicates statistical significance (see details in Reznick et al. 1997).

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Control</th>
<th>Experimental</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aripo river</strong> (11 years/18.1 generations)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male age (days)</td>
<td>48.6</td>
<td>58.2*</td>
</tr>
<tr>
<td>Male size (mg)</td>
<td>67.5</td>
<td>76.1*</td>
</tr>
<tr>
<td>Female age (days)</td>
<td>85.6</td>
<td>93.5*</td>
</tr>
<tr>
<td>Female size (mg)</td>
<td>162.3</td>
<td>189.2*</td>
</tr>
<tr>
<td><strong>El Cedro River</strong> (4 years/6.9 generations)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male age (days)</td>
<td>60.6</td>
<td>72.7*</td>
</tr>
<tr>
<td>Male size (mg)</td>
<td>56.0</td>
<td>62.4*</td>
</tr>
<tr>
<td>Female age (days)</td>
<td>94.1</td>
<td>95.5</td>
</tr>
<tr>
<td>Female size (mg)</td>
<td>116.5</td>
<td>118.9</td>
</tr>
<tr>
<td><strong>El Cedro River</strong> (7.5 years/12.7 generations)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male age (days)</td>
<td>47.3</td>
<td>52.5</td>
</tr>
<tr>
<td>Male size (mg)</td>
<td>71.5</td>
<td>74.4*</td>
</tr>
<tr>
<td>Female age (days)</td>
<td>75.8</td>
<td>80.4</td>
</tr>
<tr>
<td>Female size (mg)</td>
<td>141.8</td>
<td>152.1*</td>
</tr>
</tbody>
</table>

Data from Reznick et al. 1997
introductions to mathematical modelling (Calver & Wooler 1998), and a detailed treatment of quantitative concepts in population genetics (Ridley 2004).

Instructors need to assess the cultural appropriateness of examples too. Many hereditary human diseases are interesting teaching examples, but some students may be particularly sensitive about these matters. Similarly, while our honey possum example is interesting to our Australian students, we can well imagine why it would be an inappropriate example in other cultural contexts.

Religious perspectives and beliefs are a sensitive issue. We are not advocating discussion of creation science or intelligent design alongside evolution, but some students come to classes prejudiced against evolution (Chinsamy & Plaganyi 2008; Sanders & Ngxola 2009) and we agree with Slingsby (2009) that these prejudices should be treated with ‘philosophical neutrality’. Anticipating these views is as much a part of preparation as mastering the subject matter or dealing with students’ poor backgrounds in mathematics or English. Excellent suggestions on responding to students fearful or hostile to studying evolution are discussed with sensitivity from a range of cultural perspectives in Jones & Reiss (2007). Instructors may also find value in Dobzhansky (1973), who argues the compatibility of evolution and religion.

After the classroom

We would hope that students introduced to some of the processes and ideas that we described above will appreciate that evolution does not simply equal speciation. Rather, we hope that they will understand that it is a dynamic process occurring at generational as well as geological timescales. Using examples in teaching that can contribute to a range of areas in evolutionary thinking, helps to encourage synthetic and critical thinking in our students. They should also have a clearer idea of scientific evidence and scientific process, especially developing predictions from hypotheses and experimental tests. Students should be able to apply their critical thinking, powers of synthesis and logic not only to evolutionary problems, but to other issues that they encounter in all areas of life.

References


Harvey P H & Harcourt A H 1984 Sperm competition, testes size, and breeding systems in primates. In: R I Smith (ed),
Throughout Human history there have been events and discoveries that have changed the thinking, consciousness, perspectives and life styles in Western Society. Leaving aside theological considerations, a time-axis has been provided of what I consider to be some of the major scientific and philosophical events and discoveries between 500 BC and the present that have impacted on Society and Science (Figure 1); these are associated with Socrates, Galileo, Newton, Maxwell, and Darwin.

Newton, “The Father of Modern Physics”, stands significantly in the history of Science. His discoveries at the time of the English Scientific Renaissance were readily accepted by the Scientific establishment; his equations of motion, developing the mathematics behind planetary orbits, and his investigation of light were profound. Impressed by Newton’s contributions, Alexander Pope (later) wrote: “Nature and nature’s laws lay hid in night; God said ‘Let Newton be’ and all was light”.

Of course, there were a number of significant scientific discoveries prior to Newton, such as those by Copernicus, Galileo, and Kepler, and many more afterwards resulting, for example, in formulation of the Laws of Thermodynamics, formulation of the Theory of Quantum Mechanics, the discovery of subatomic particles, and the discovery of DNA structure which, while significant in advancing Science, arguably did not have such a profound effect on Society at large. From this latter group, Maxwell has been chosen as typical of a scientist contributing to knowledge as part of a larger Scientific Community. By solving the equations of electromagnetic waves, he paved the way for the development of radio communication and the other uses of electromagnetic waves, the Theory of Relativity, and much of the technology of today.

In contrast to Socrates, Galileo and Darwin, the research of Maxwell did not lead to a negative reaction from Society, Church, and Scientists, and regardless of who one might choose to fit the role of major contributing scientist in the place of Maxwell along the time-line of Figure 1 (be they Banks, Bohr, or Planck, amongst others), their work, generally, did not offend Society, Church and Scientists (though their work and results did have some Sociological effects, and there were conflicts and disagreement amongst the scientists). Many of the discoveries in the History of Science, in fact, have been directly beneficial to Society and, in time, useful to the development of an understanding of the world and how it operates, or resulting in knowledge and technology leading to such benefits as better navigation, or radio communication, or improvement in Human health. Western Society has welcomed such adventures in that they aided, enriched and helped the Human lot. But most of such discoveries were external, i.e., not focused on “the nature of Man”, nor his place in the Universe, e.g., discovering the nature of light, or its speed, did not challenge the teachings of the Church.

Focusing on Socrates, Galileo and Darwin: these three were controversial and had impacts on Society, the Church and Scientists. One can see that their thinking and results appeared to displace Man from his perceived privileged position. Socrates, “The Father of Western Philosophy”, transgressed Society with his style, ideas and logic, effectively showing Humanity their fuzzy logic. He was condemned to death, and drank hemlock.
Galileo, "The Father of Astronomy", removed Earth, and implicitly Mankind, from the centre of the Universe, offending the Church. Though he escaped burning at the stake for heresy, he was placed under a life-long house arrest. Darwin, considered to be "The Father of the Theory of Evolution", displaced Man as the pinnacle of Creation, thus offending Society, Church, and Scientists. One could be a fuzzy thinker, and one could dwell on a planet that was not at the centre of the Universe, but it was unpalatable that Humankind was not the quintessence of Creation and the epiphany of Evolution (if it existed as a process). The impact of Darwin's Theory was enormous, and inadvertently had drawn attention to the Nature of Man. Implicit, though not necessarily intended, was the conclusion that Man was just another cog in an unscripted history of Life on Earth. As such, I have made Darwin's Theory of Evolution (notwithstanding that I agree with Stefan Revets that it should be the Darwin-Wallace Theory of Evolution), as presented in "On the Origin of Species", the largest impact, along this time axis because the effects were manifold: it struck at the core of Human self-perception, and spawned a range of studies that continue to today. The reactions and fall-out to Darwin's Theory of Evolution, at that time, and leading to the present, can be summarised in the following ideas, notions, conclusions, and outcomes:

1. Man is a monkey
2. Man may not be the pinnacle of evolution
3. the Theory provided a unifying framework to Biology
4. the Theory provided a unifying framework to Palaeontology
5. Church and Science were in collision (again)
6. scientists were in disagreement over the Theory
7. prove it! — spawns hosts of scientific studies
8. good Theory! — spawns hosts of other scientific studies
9. as a Theory, it spills over to Sociology
10. as a Theory, it influenced how scientists now dealt with Biology, Palaeontology, Genetics, and Biochemistry, amongst other disciplines
11. as a phenomenon, because of its ramifications, it even spills over to other disciplines such as History, the History of ideas, Philosophy, and Theology
12. as a phenomenon, it spills over directly into Society, with commentary from learned scholars, editors, social commentators, and cartoonists, amongst others — in other words, it was not ignored.

For these reasons, in Figure 1, Darwin's Theory of Evolution is treated as a major phenomenon in the history of Science.

The effect of Darwin's Theory of Evolution continues to the present (Figure 2). At this Symposium, we have seen that the Science and other disciplines deriving from and influenced by the Theory of Evolution radiate and diversify. Science dealing with evolution has been approached from a wide range of perspectives, and even those within the same discipline, such as palaeontology, or genetics, have very different approaches and levels of detail. The Theory of Evolution, thus, more than most scientific endeavours, has spawned a host of studies and disciplines. Since it is core to so many disciplines, it holds scope to be a unifying theme, not only for different aspects of Biology, but also to bring together disparate sciences and to forge multi-disciplinary approaches. As Kate Bryant has pointed out at the Symposium on "Evolution for undergraduates — fostering critical thinkers", the Theory of Evolution can be a galvanising framework for students to learn the process of science.

Many disciplines are inter-related and can be assembled under a unifying banner of the Theory of Evolution; they are: Taxonomy, Terminology and classification, Autocology, Ecology and Palaeoecology, Genetics/Biochemistry/Molecular Biology, Palaeontology,
With the idea that the Theory of Evolution holds scope to bring together such disparate Sciences, and to forge multi-disciplinary approaches, let us apply the title of Stefan Revets' presentation: "No man is an island" (in which he refers to the fact that Darwin did not come to his conclusion in isolation nor without a rich personal history), to Science itself and say that: "No science should be an island". Multidisciplinary science is very important to obtaining an understanding of natural systems and how the World works. In this context, multi-disciplinary science is very important to obtaining an understanding of biological evolution.

Keith Oliver, the co-convenor for this Symposium, has suggested that we use this gathering as the first step to founding an interdisciplinary Society of Scientists for furthering the field of Evolution Studies. Such a Society would draw on scientists working in the field of Evolution from a range of disciplines. Like sub-groups in other Scientific Societies, this group for Evolution Studies may in fact be taken up as a sub-group, or section, under the banner of The Royal Society of Western Australia, a contingency already allowed for in the Constitution of The Royal Society of Western Australia. As a dedicated group, it would allow scientists from disparate fields to meet under the auspices of The Royal Society of Western Australia, and become enriched by information and insights from outside their immediate speciality.
Sitting here today, listening to such a variety of talks concerning evolution, I began to wonder what Charles Darwin would have thought about today’s presentations. Would he have felt an inner glow of pride that his ideas had permeated so many areas of science? Or would he have thought that perhaps people had been taking things a bit too far? I think the former, for I’m sure he would have been as impressed by the wide range of topics covered today, as I have been.

We have heard about areas about which he knew nothing, particularly those in genetics: the talks by Ted Steele, Keith Oliver and Kemanthi Nandesena, which highlighted the importance of transposable elements in the genome. Darwin would, I think, have been delighted by Ted Steele showing that natural selection operates even at the molecular and cellular levels. But I believe that he would have been equally as fascinated by the wide range of topics concerned, expertly reviewed by Kevin Thiele, not surprisingly, is supportive of the Tree of Life metaphor for the evolution of life, enunciated by Darwin in On the Origin of Species. Its subsequent use by Haeckel and Hennig and its continued use today would, I’m sure, have made Darwin very pleased, even if the tree at times appears to be more of a hedge, or a shrub, or, to quote Kevin Thiele “a bloody mess!”.

Darwin was very unsure about the fossil record. He felt that if there was one thing that could undermine his theory, that was it. “Geology”, wrote Darwin (The Origin of Species 1878, 6th Edition p.265) “...assuredly does not reveal any such finely-graduated organic chain; and this perhaps, is the most obvious objection which can be urged against this theory. The explanation lies...in the extreme imperfection of the fossil record.” He was equally dismissive of collections held in the country’s museums: “...our richest geological museums ...what a paltry display we behold!” (Darwin, The Origin of Species 1878, 6th Edition. p.270). But as Kate Trinajstic and my own presentation show, in fossil fishes and trilobites, respectively, Darwin can rest easy in the knowledge that not only does the fossil record support his ideas on evolution, but the museums now hold literally millions of specimens, each attesting to the veracity of evolution. My own presentation was about one of the areas much discussed by Darwin. Kate Trinajstic’s talk opened up a whole new fascinating world of evolution in the prokaryotes.

Despite what many people think, there was a world of evolution before Darwin, which he himself would readily have acknowledged, expertly reviewed by Kevin Thiele, Stefan Rivets and Alan Tapper. While Darwin may not have drawn on ideas from the ancient Greeks, he was no doubt influenced by more contemporary workers. As Stefan Rivets has shown, Darwin’s ideas have made us look back much more than we otherwise might have done to earlier philosophers’ attempts to understand and interpret the world around them. It is hard not to believe that Darwin could have ignored ideas, such as those promulgated in the 18th century by Georges-Louis Leclerc, Comte de Buffon, given his influence on Charles Darwin’s grandfather, Erasmus Darwin, and on Lamarck. Likewise, Darwin’s writing in On the Origin of Species on development and evolution, was very much influenced by embryologists on the continent, such as Karl Ernst von Baer in Germany and Etienne Serres in France, despite Serres having many objections to Darwin’s ideas on evolution.

Darwin would, I am sure, have been intrigued by Alan Tapper’s thoughts on how philosophers have viewed Darwinism, from the 100 years of indifference (a period of philosophical stasis, perhaps) to Popper’s criticism in the 20th century, to the enthusiastic and expansive phase of philosophers’ view on Darwinism in more recent times, and the philosophical realisation that the study of evolution may be scientific after all. As a botanist, Kevin Thiele, not surprisingly, is supportive of the Tree of Life metaphor for the evolution of life, enunciated by Darwin in On the Origin of Species. Its subsequent use by Haeckel and Hennig and its continued use today would, I’m sure, have made Darwin very pleased, even if the tree at times appears to be more of a hedge, or a shrub, or, to quote Kevin Thiele “a bloody mess!”.

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Lastly, Kate Bryant’s talk on the education of evolution stressed the importance of pointing out to students that evolution is happening all around us, not just on the Galapagos Islands. She showed the significance of using local examples. Given Darwin’s propensity for carrying out many experiments in his garden at Downe House, he would very much have appreciated this approach.

So had Charles Darwin been sitting in the audience with us today, I am sure he would have felt that publication of On the Origin of Species was well worth the many years of writing, and the long periods of anguish and self doubt that he experienced.
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