Revolutions in Evolutionary Thought: Darwin and After

Renee Borges

Renee M Borges studies the evolution of interactions between species at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore. She currently works on ant-plants, ant-mimicking spiders, crab spiders, figs and fig wasps, and carpenter bees. Her major interests are in the visual and chemical mediation of behavioural ecology and evolution.

Darwin is as much a household name today as he was a century and a half ago. Phrases such as Universal Darwinism, Social Darwinism, The New Science of Darwinian Medicine, Darwin Machines, Darwin's Dangerous Idea, The Universal Acid of Darwinism, Neo-Darwinism, Darwin is Dead – Long Live Darwin ... . are in common usage today. Darwin stands out as a colossus – a giant among giants. A progression of great thinkers led to Darwin. Who were these revolutionaries and what are the frontiers of modern evolutionary thought? Some of these questions are addressed in this article.

Essentialism

Let us begin with a little history. The early pre-Socratic philosophers believed that all life was generated spontaneously from inorganic elements like fire and water. For them, life forms were constituted without a predetermined goal, without a teleological[1] purpose. Evolutionary thought may have made significant progress under these philosopher-scientists but for Plato who has been described by the evolutionist Ernst Mayr as the "great anti-hero of evolution". Plato's essentialism implied that the world was composed of fixed, immutable entities. Aristotle followed Plato and Aristotle's world too was eternal and unchanging. Origins by creation, yes, but evolution, no!

[1] The study of evidence for end-directed design in nature.

Keywords
Darwin, theory of evolution, natural selection, sexual selection, levels of selection.

The Age of Reason and Enlightenment

The rise and spread of Christianity with its biblical chronologies for world events provided a powerful

intellectual strait-jacket. The hegemony of creationism was firmly established; all else was blasphemy, a situation made worse by the fundamentalism of the Reformation. Major cracks in this worldview began to appear by the 16th century. The Copernican revolution (1543) toppled the Ptolemaic view of the earth as the centre of the planetary universe. Galileo (1610) looked out into the heavens and saw new stars and new moons and thus stretched the limits of known space. The Newtonian revolution at the end of the 17th century gave a mechanistic approach to nature and suggested that the universe was working according to natural physical laws. During the Age of Reason and Enlightenment in the 17th and 18th centuries, free thinkers began to stress the need for rational explanations for natural phenomena. 'Profane' literature started to appear. Fontenelle (1686) postulated the existence of living beings on other planets in his '*Conversations on the Plurality of Worlds*'. He proposed the infinity of the solar system and the infinity of time and space. Even the great German philosopher Immanuel Kant (1755) devised the Nebula Theory in which the galaxies, sun and planets were supposed to have been formed out of a chaotic nebula. Scientists and philosophers were seeking ultimate truths and were not satisfied with religious revelations. Thinkers were divided into theists, deists and atheists. The theists were those who believed that God set the universe in motion and then intervenes, performing divine acts to create species. The deists believed that although God set the universe in motion, the divine being only created natural laws; God does not subsequently intervene but allows the universe to function according to these laws. The atheists deny the existence of God.

During the Age of Reason and Enlightenment in the 17th and 18th centuries, free thinkers began to stress the need for rational explanations for natural phenomena.

Scientists and philosophers were seeking ultimate truths and were not satisfied with religious revelations.

Evolution in France

Many revolutions in evolutionary thought occurred in France in the 17th and 18th centuries. The great French naturalist Comte de Buffon was impressed by Newtonian

Many revolutions in evolutionary thought occurred in France in the 17th and 18th centuries.

ideas of natural law and was the first to clearly articulate the concept of common descent – some species looked similar probably because they descended from common ancestors. He speculated that just as men and apes could have had a common origin, so could various species of domestic livestock be related to wild forms. He also privately believed, contrary to biblical dogma, that the earth was at least half a million years old. As a Christian, however, he was intimidated by the authority of creationism and, even in his writings, chastised himself for such speculations. For his radically new perspectives, Buffon is considered to be the Father of Evolutionism.

Buffon was followed by Lamarck. Jean Baptiste de Monet, Chevalier de Lamarck, was the curator of invertebrates in the Natural History Museum at Paris. He could see numerous examples of the extinction of species in the fossil record. Yet he could not reconcile extinction with the established concept of a 'perfect' God – surely such a God would not annihilate His own creations? Lamarck attempted to resolve this dilemma and explain the disappearance of species by proposing that species do not go "extinct"; they are merely "transformed" in response to changing environments. A new environment would create a need for a new body function or would make an older body function superfluous. Certain "subtle fluids" would migrate to parts of the body needing modification and would form new organs: the redundant organs would wither away by disuse. New or modified body parts thus acquired during the lifetime of an organism would be passed on to its progeny. Lamarck didn't know exactly how these changes were inherited, but he postulated that all life forms from the simplest to the most complex were linked by such transformations leading to increasingly greater perfection and culminating in man. Although there were several critics of Lamarckism, evolution by the inheritance of acquired characters

For his radically new perspectives, Buffon is considered to be the Father of Evolutionism.

was the only theory of evolution when Darwin appeared on the intellectual scene in Victorian England.

The Orthodoxy in England Shaken

The hallowed universities of Oxford and Cambridge were the strongholds of the clergy and aristocracy and attempted to control seditious thought. Blasphemy was an offence punishable by imprisonment. Yet, conformism to creationist views and literal interpretations of the Bible could barely be disciplined. Geologists were finding that the earth had great antiquity, many hundreds of millions of years compared to the 4004 BC date ordained by Archbishop Ussher for the creation of the earth. The evidence for species extinction was mounting. There was the problem of providing a biblical explanation for disjunct distributions of the same or similar species across the globe. Sea voyages and explorations were bringing in vast numbers of life forms, including reports of types of human beings, never mentioned in the Bible. If God created man in His own image, how could the diversity of human groups be accounted for? How could one explain homologous body structures which appeared to indicate common shared origins such as the wings of birds and bats and the limbs of mammals? The number of issues on which the credibility of the biblical account of nature was being questioned kept growing. This was also the time of the industrial revolution when belief in the universal applicability of Newtonian physics and in mechanistic processes was increasing. The deists were gaining ground. The strong nexus between science and religion controlled by the Anglican Church was being threatened.

If God created man in His own image, how could the diversity of human groups be accounted for?

How could one explain homologous body structures which appeared to indicate common shared origins such as the wings of birds and bats and the limbs of mammals?

Church leaders, royalty, and the aristocracy in Victorian England were also afraid of what had happened only a few decades ago across the Channel in France – the French Revolution of 1789 had abolished hierarchical privileges. The demands for democracy, equal rights

and universal suffrage were in the air, and were even the cause of civil unrest and riots. The foundations of orthodoxy were being weakened.

Darwin entered holy orders but was not ordained a clergyman – somehow doubts were nagging.

The Age of Darwin

Into such an atmosphere came Darwin (1809-1882), born into a progressive family of Whigs and Unitarians, to a deist grandfather and a free-thinking father who was an atheist in private life. In college in Edinburgh, Darwin was exposed to many debates on unorthodox scientific, religious and social issues and had even witnessed the gaoling of fellow blasphemers. The major argument being made for creationism against the so-called scientific rabble-rousers was the 'Argument from Design' whose chief proponent was the Reverend William Paley. As a student in Cambridge, Darwin was required to read Paley's *Natural theology: or evidences of the existence and attributes of the Deity collected from the appearances of nature*. Paley argued that just as something as efficient and prefect as a watch could only have been designed by a watchmaker, something as marvelous as the eye could only have been designed by a perfect deity. Paley saw evidences of divinity in the perfectly adapted forms in nature. Darwin entered holy orders but was not ordained a clergyman – somehow doubts were nagging.

Darwin went on the epic five-year voyage on the *Beagle*, and returned in 1836, full of experiences and more doubts.

Darwin went on the epic five-year voyage on the *Beagle*, and returned in 1836, full of experiences and more doubts. He was especially struck by the island-to-island differences he had seen in tortoises, mockingbirds and finches in the volcanic islands of the Galapagos off the western coast of South America. He was also impressed by the similarity of the mockingbirds and finches to counterparts on the South American mainland. Species in different geographical locations were sufficiently similar to be recognized as the same type and yet sufficiently different to be considered as varieties of the same species or even as different species. Darwin's belief in

the constancy of species, and even in the clear delimitation of species in nature as ordained by the essentialists and creationists, was shaken.

The Malthusian Paradigm

In 1838, Darwin read the sixth edition of Malthus' *An Essay on the Principle of Population as it Affects the Future Improvement of Society* and crystallized his theory of evolution by Natural Selection (*Box* 1).

Darwin had always been an admirer of rigorous, mathematical science. He was impressed by the logical and mathematical approach of Malthus. Resources can only increase arithmetically but populations increase geometrically. Some resources, such as space, remain constant. Demand would very soon outstrip supply. In the struggle for existence only those individuals who were better adapted to the existing conditions would survive and reproduce. Darwin realized that if there was variation between individuals then the selection process which

Box 1. Rev. Thomas Robert Malthus (1766–1834)

Who was Malthus – the man considered to be largely responsible for the Darwinian revolution? The Reverend T R Malthus was an economist for the East India Company. He had witnessed the population explosions especially of the poorer classes around industrial towns in England during the industrial revolution. He realized that populations could not increase indefinitely without over-consumption of resources. This would lead to starvation, greater poverty, disease and death. He advocated that the poorer classes be denied welfare benefits as this would only encourage them to reproduce resulting in cycles of population explosions and crashes. A staunch Whig, Malthus was a believer in open competition, denounced charity as a social evil, and predicted that in the struggle for survival only the most competitive individuals would win. Darwin was familiar with Malthusian theory even before he had actually read Malthus because the social impact of Malthusian ideas was being felt in the reformed Poor Laws in which relief for all but the most destitute was ended. Moreover, Malthus had been popularized by Harriet Martineau, whose novels were read avidly by Darwin's sisters. They wrote often about Martineau to Darwin while he was on the *Beagle*. In the sixth edition of his famous Essay, Malthus was advocating that the Crown ship the surplus populations of the poorer classes to colonies like Australia. Emigration was perceived as an answer to overpopulation.

Darwin realized that if there was variation between individuals then the selection process which consisted of "preservation of favourable variations and rejection of injurious variations" could lead to the establishment of new forms and new varieties.

consisted of "preservation of favourable variations and rejection of injurious variations" could lead to the establishment of new forms and new varieties. Darwin called this process of the development of new more-adapted organisms 'Evolution by Natural Selection'. Thanks to Malthus, Darwin's revolutionary theory was ready in its basic form by 1838, only two years after his return from the voyage.

Darwin had also developed considerable experience with pigeon breeding. In pigeons and dogs, he realized the power of artificial selection in creating new forms and varieties. This strengthened his belief in natural selection. Darwin also began to realize, like Buffon before him, that all organisms, even man, must have descended from common ancestors. By providing a plausible mechanism for common descent, Darwin dethroned man from the privileged position assigned to him in the *Bible*.

Wallace Converges on Darwin

Darwin's ideas were heretical yet understandable given the social and intellectual milieu. In 1844, *Vestiges of the Natural History of Creation* was anonymously published. In this book, the author (who was subsequently discovered to be Robert Chambers) tried to use natural phenomena to explain the origin of "creation" of all life. He explored connections between life forms in the fossil record and similarities in the embryological development of groups of animals. Although not a scientist, he was a science-writer and *Vestiges* was a popular book that went into twelve anonymous editions – a "must" in Victorian drawing-room conversations. Darwin was aware that the author of *Vestiges* wished to remain anonymous for fear of being ostracized. Darwin had earlier seen how the establishment had dealt with dissenters. And so he brooded quietly over his theory of evolution for twenty long years, until 1858. He may have continued to brood, even settling for posthumous publication of his theory,

By providing a plausible mechanism for common descent, Darwin dethroned man from the privileged position assigned to him in the *Bible*.

were it not for the independent discovery of the same theory by Alfred Russel Wallace (1823–1913). Wallace, a naturalist who had collected specimens in Amazonia and in the Malayan archipelago, had also been impressed by *Vestiges* and by Malthus' Essay and came to the same general conclusions about the development of new forms[2]. Darwin's friends prevailed upon him to write up his twenty-year old manuscript and to establish primacy over the concept of natural selection. The ideas of Wallace and Darwin were jointly presented before the Linnean Society in 1858, and in 1859, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggles for Life* by Charles Darwin appeared in print. The year 1859 marks the crossing of a major frontier in evolutionary thought.

[2] See *Resonance*, Vol.13, March 2008.

Darwin and Sexual Selection

Darwin also realized that the theory of evolution by natural selection not only applied to the struggle for survival between individuals of the same species but also to males competing for access to females (intra-sexual selection) and to females who must select the fittest male (inter-sexual selection). Sexual selection, as defined by Darwin, is now acknowledged to be a major evolutionary force responsible for such characters as the magnificent antlers of the stag and the shimmering beauty of the peacock's tail.

Gradualism

While several people such as Thomas Henry Huxley initially thought that evolution occurred in big leaps or saltations, Darwin could not understand how intricate, supposedly perfectly adapted structures like the eye could arise by saltation. How would the organisms, with the intermediate structures produced by saltation, survive before the appropriately adapted stage was achieved? He proposed, therefore, that evolution could only occur by gradual, incremental changes.

The year 1859 marks the crossing of a major frontier in evolutionary thought.

Although Darwin knew that variation between individuals was the cornerstone of the selection theory, yet he did not know how variations came into existence.

Pangenesis

Although Darwin knew that variation between individuals was the cornerstone of the selection theory, yet he did not know how variations came into existence. He also did not know how the 'favourable' variations were passed on from one generation to another. Darwin was still Lamarckian in his ideas about inheritance and he therefore proposed the 'Theory of Pangenesis' in which each type of body cell produced tiny particles called 'gemmules'. These collected together in the reproductive organs and, during mating, combined with gemmules of the opposite sex to produce offspring with the modifications in body structures acquired by the parents prior to mating. This theory provided the link between body cells and sex cells needed for Lamarck's theory of the inheritance of acquired characters. Since gemmules were supposed to blend and combine at mating, in order to account for atavisms[3] Darwin proposed that gemmules sometimes remained dormant in the sex cells without being expressed.

[3] Atavistic traits are those that seem to skip generations; they are present in grandparents or great-grandparents and in children but are absent from the parents.

The Discovery of Mendel

In 1866, seven years after the *Origin* appeared in print, Gregor Mendel published a solution to the problems inherent with pangenesis in the obscure Austrian Journal of the Brno Natural History Society. Darwin didn't read Mendel: In fact, Mendel lay unknown till his work was rediscovered by Hugo de Vries, Carl Correns and Erich von Tschermak in 1900. Working mainly with pea plants, Mendel found that each trait or character is represented in a fertilized egg by two particles – one paternally derived, the other maternally. The paired particles always remained discrete, without fusing. Dominance or recessiveness and the independent inheritance of particles from generation to generation could explain atavisms and variable trait expression depending on which two forms of the particles came together in the

fertilized egg. The probability of a particular type of trait appearing depended on the number of existing variant forms of each particle controlling each trait. Mendel derived laws of inheritance which enabled precise predictions about the inheritance of traits. Still, no one knew how the variant forms of the particles (or genes) were produced.

Mendel derived laws of inheritance which enabled precise predictions about the inheritance of traits.

Hugo de Vries arrived independently at the same conclusions as Mendel and was naturally devastated at having been preempted by Mendel. However, de Vries made his own mark on evolutionary history by emphasizing the production of genetic variation by a process called mutation (de Vries' Die Mutations theory, 1901). In his studies of breeding in the evening primrose, he once found two plants in an abandoned potato field in Holland which were greatly different from all the other individuals whose traits he had recorded for many generations. He realised that a new variety had been suddenly generated. Although he still did not know how the new variants had arisen, he was prescient and even proposed that subjecting germ cells to "Roentgen rays or those of Curie" could cause changes in the hereditary particles. He also found that the mutability of traits differed and aroused great interest in the causes and rates of mutation.

Dethroning Lamarck

There were other concomitant discoveries which had great bearing on the understanding of evolution. There was still the problem of reconciling Lamarck's theory of the inheritance of acquired characters with the mainstream of evolutionary thought. Darwin had attempted to include Lamarckism in his pangenesis theory by proposing a feedback loop between body cells and sex cells via the migration of gemmules from the body to the reproductive organs. However, many experiments were showing the opposite results. Importantly, offspring of parents

Any changes in offspring could only occur if these occurred in the germ cells of the parents and not in their body cells.

with amputated limbs were born with limbs that were perfectly formed. Such observations were beginning to dethrone Lamarck. It was in 1883 when August Weismann showed that germ cells (sex cells) were completely separated from somatic cells (body cells) and did not communicate with each other, that the case against Lamarckism appeared to be closed. Any changes in offspring could only occur if these occurred in the germ cells of the parents and not in their body cells. Change was directed from sex cells to body cells and not vice versa.

Mutations versus Selection

Towards the end of the 19th century, there was an increased understanding of the structure of chromosomes and their role in inheritance. T H Morgan at Columbia University described and recorded scores of mutations in fruitflies in the early 20th century and earned for the fruitfly an important place in the evolutionary Hall of Fame. In the 1920s, H J Muller found that as predicted by de Vries, bombardment of fruitflies with X-rays caused a 100-fold increase in mutation rates compared to the rate of spontaneous mutations reported by Morgan's group. This also provided insights into the chemical structure of the gene (a term coined by W L Johannsen in 1909 as a short form for pangene, the earlier de Vriesian name for the units of inheritance). The first quarter of the 20th century was busy with genetic research centred around mutation. This preoccupation with mutations coupled with the excitement over the discovery of Mendel's laws resulted in the widespread view that Darwinism was dead. Evolution driven rapidly by mutations could replace evolution by natural selection, which was predicted to be an inherently gradual process.

Towards the end of the 19th century, there was an increased understanding of the structure of chromosomes and their role in inheritance.

Neo-Darwinism

Was Darwinism really dead? The tensions between the mutationists and the selectionists were resolved when the 'holy trinity' of J B S Haldane[4], R A Fisher[5] and Sewall Wright[6] became the principal architects of Neo-Darwinism or the 'Modern' Synthesis of the 1930s and 1940s. Neo-Darwinism is basically a marriage of genetics and the Darwinian theory of evolution. According to the synthesis, small mutations or micromutations were the ultimate source of variation. Most mutations were believed to have negative or deleterious effects. Evolution was considered to be a process whereby different forms of a gene (alleles) arising by mutation, changed in frequency from one generation to another within a population largely under the effect of natural selection – the favoured alleles increasing relative to the others. Gene frequency changes due to random processes of genetic drift were also considered. The major difficulty of reconciling the slow process of evolution by natural selection with the drastic changes in character brought about by mutation was ultimately resolved by the discovery that many complex traits involved multiple genes. These genes, acting concertedly, could create a spectrum of phenotypes on which selection could operate.

Neo-Darwinism or the 'Modern' Synthesis of the 1930s and 1940s is basically a marriage of genetics and the Darwinian theory of evolution.

[4] *Resonance*, Vol.3, No.12, 1998.
[5] *Resonance*, Vol.2, No.9, 1997.
[6] *Resonance*, Vol.4, No.12,1999.

Macromutations and Neutral Evolution

Cracks in the Neo-Darwinian doctrine soon began to appear. Macromutations were being documented; sometimes bits of chromosomes were broken off and lost or were added to other chromosomes during the process of sex-cell formation. Whole sets of chromosomes were duplicated in some new plant species. Therefore, gradual changes via micromutations were not necessarily the norm. In the 1960s and 1970s, it was also discovered that many mutations had neutral effects; i.e., they did not affect the functionality of the proteins coded for by the genes. Natural selection is "blind" or insensitive to

Evolution was considered to be a process whereby different forms of a gene (alleles) arising by mutation, changed in frequency from one generation to another within a population largely under the effect of natural selection.

The neutral theory of evolution, in which selectively neutral genetic changes formed the major force of evolution, was proposed by Motoo Kimura in 1968 and helped to explain many aspects of molecular evolution.

such neutral mutations and they could persist in populations or even be fixed within populations by the random processes of genetic drift. The neutral theory of evolution, in which selectively neutral genetic changes formed the major force of evolution, was proposed by Motoo Kimura in 1968 and helped to explain many aspects of molecular evolution.

The Myth of Panmixia

Many of the predictions made by Neo-Darwinists, with regard to changes in gene frequencies in populations under the direction of natural selection, were based on the fundamental premise of panmixia – a situation in which all individuals within a population select mates freely throughout the population. However, population geneticists and ecologists of the 1950s and 1960s began to realise that plants and animals with large geographically continuous populations are not necessarily panmictic. Most usually, such plant and animal populations are sub-divided into smaller local neighbourhoods or sub-populations called 'demes' within which breeding occurs. It also came to be realised that in a large, freely mixing population, the genetic composition of descendents represents only a sample of all possible genetic combinations. If the demes are small, then the effects of random genetic drift can be quite pronounced, and certain genetic combinations may become more common in populations, not necessarily because of the selective advantages of these combinations but because of the limited number of genetic combinations possible within a smaller population with limited genetic variability. Such a population could also be undergoing a "random walk" in evolutionary space.

Evolutionists were being forced to look more closely at population sub-structures.

Evolutionists were now being forced to look more closely at population sub-structures. The experimentalists began to put fluorescent dyes on pollen grains in flowers to follow their transport by pollinators, and to affix radio

collars on animals, to actually estimate sizes of plant and animal demes. There was beginning to be a synthesis between ecology, behaviour, population biology, genetics and evolution. Evolutionists were coming to appreciate the strong effects of genetic drift in the evolution of new varieties or even new species especially when populations were reduced to a few individuals. Severe population bottle-necks can occur due to disease or when the initial population itself is small as when a few founding individuals arrive on uninhabited, newly created volcanic islands such as the Galapagos. Geographic isolation between demes, type and rate of mutation within demes, deme sizes, rates of genetic drift, natural selection – all these were being viewed as important components of evolution. A pluralistic view of evolution began to emerge.

There was beginning to be a synthesis between ecology, behaviour, population biology, genetics and evolution.

Levels of Selection

Until the 1960s, it was considered dogma that natural selection acted at the level of the individual – it was the individual with the relatively better or worse genetic combination that won or lost the evolutionary race. In the 1960s, another revolutionary idea emerged whose importance and validity is being debated even today. V C Wynne-Edwards proposed the idea of group selection according to which natural selection should favour those groups of individuals that regulated their population size to match available resources so that demand kept pace with supply. Groups that breed indiscriminately so that they outstripped resources would not be favoured by natural selection. Prudence would be favoured over profligacy. The group selection theory incited fierce intellectual debates. Today, although the group selection controversy has not been fully resolved, there is a realization that natural selection can act at levels above the individual. Consider what happened 65 million years ago. The dinosaurs succumbed to a natural disaster; tiny shrew-like mammals survived and a

Wynne-Edwards proposed the idea of group selection according to which natural selection should favour those groups of individuals that regulated their population size to match available resources so that demand kept pace with supply.

Evolutionists began to acknowledge a hierarchical process in evolution – selection among individuals, demes, populations, species, and even above the species.

mammalian radiation occurred. Climate changes, predation, disease – these are all agents of natural selection which can also act at levels higher than the individual. Yet, at the time of the dinosaur extinction, there must surely also have been individual variation among the shrews – only the better adapted shrews survived the disaster to become the ancestors of the great mammalian diversity. Evolutionists began to acknowledge a hierarchical process in evolution – selection among individuals, demes, populations, species, and even above the species.

Kin Selection

Evolutionists were also being forced to find explanations for breeding systems that seemed to defy the premise of selection at the individual level. In honey bees, as in many insect societies, only a few individuals (the queens and drones) reproduce. The sterile female worker bees are seemingly altruistic in aiding the reproduction of the queen and giving up their own changes for reproduction. W D Hamilton's Theory of Kin Selection (1964) and concept of Inclusive Fitness was initially thought adequate to explain this phenomenon. Fitness is a term that quantifies reproduction. An individual's fitness is the number of offspring it has produced. At the level of the gene, however, the fitness of an individual who shares the same genes with another individual would actually include the numbers of copies of the same genes transferred into the next generation. The inclusive fitness of an individual would, therefore, not only include the number of offspring it produced but also the number of related individuals or kin, such as sisters, uncles, and cousins, who share the same genes, and who could also pass on these genes to the next generation.

The inclusive fitness of an individual would, therefore, not only include the number of offspring it produced but also the number of related individuals or kin.

The honey bee female has two sets of chromosomes – one set obtained from her mother and the other from her father – she is said to be diploid. Male drone bees

have only a single set of chromosomes derived from their mothers; males are haploid. Honey bees therefore have a haplodiploid type of sexual system. When a queen produces daughters, she fertilizes her eggs with sperm obtained by mating with a drone; when she produces sons, she lays unfertilized eggs which bear only a single set of her own chromosomes. When a queen transmits any one of her paired chromosomes to her daughter or her son, she could transmit either her paternal or maternal chromosome for each chromosome pair. Therefore, queens and daughters share 50% of their genes. Similarly, a queen shares 50% of her genes with her sons. Daughters, however share between themselves, not only maternal genes but also paternal genes whereas sons only share maternal genes. This means that sisters are more closely related to each other (sharing 75% of their genes) than they are to either their mother or their brothers. Therefore, according to Hamilton, by the concept of inclusive fitness, it should pay daughters to raise more sisters than to raise their own offspring. This could then explain the sterility of the workers and the 'altruistic' behaviour of the worker bees, and was found to be compatible with selection at the level of the individual.

Although kin selection has been invaluable in the interpretation of altruistic behaviours, recently its role in altruism in some insect societies has been questioned.

Although kin selection has been invaluable in the interpretation of altruistic behaviours, recently its role in altruism in some insect societies has been questioned. Using DNA fingerprinting, studies of genetic relatedness between members of these societies have shown that to produce daughters, the queen could be using sperm from multiple matings with several unrelated males. Daughters of the same queen could have different fathers and could therefore actually be half-sisters. This could cause a reduction in the percentage of genes shared between some sisters to a level equal to that shared between mother and daughters or sisters and brothers. The origin and maintenance of many insect societies is therefore still a difficult problem in evolutionary biology.

The origin and maintenance of many insect societies is still a difficult problem in evolutionary biology.

Theoreticians who make mathematical models of cooperative strategies have concluded that a TIT FOR TAT strategy is one of the most stable evolutionary strategies for interactants to adopt.

Reciprocal Altruism

If Hamilton's kin selection theory can explain altruism only between relatives, how can one explain situations in which altruistic acts occur between unrelated individuals? In 1971, Robert Trivers, inspired by the musings of Darwin in *Descent of Man* (1871) and those of the great evolutionary biologist George C Williams in 1966, proposed the Theory of Reciprocal Altruism. This theory says that even unrelated individuals may perform altruistic acts that might seem to reduce their own fitness if by doing so they can be assured of receiving reciprocal treatment when needed. Is there any empirical evidence for such a theory? Surprisingly, the evidence is mounting. Vampire bats feed on the blood of wild and domestic animals at night. These bats lose a considerable percentage of their body weight each night in the process of burning body fuel to keep warm. All bats are not successful in feeding each night. Bats which do not obtain a blood meal have reduced chances of surviving the night. In a bachelor colony of unrelated males, Gerald Wilkinson observed that full males would regurgitate blood to feed hungry males. By marking individual bats and following their behaviour closely, Wilkinson showed that males who received regurgitated blood from a particular individual were more likely to return the favour and regurgitate blood to the same individual when needed. Reciprocal altruism was working. Theoreticians who make mathematical models of cooperative strategies have concluded that a TIT FOR TAT strategy is one of the most stable evolutionary strategies for interactants to adopt. Of course, such a strategy could only persist if individuals remembered both the identities of the interactants and whether the interaction was good or bad, thus ensuring that cheats would not be rewarded. This has profound implications for the origin, evolution and maintenance of cooperation within animal (and human) societies.

The Selfish Gene

The discovery of the structure of DNA in 1953 by James Watson and Francis Crick led to a greater understanding of the relationship between the evolutionary history of an organism as stored in its genes and the function of these genes when translated into proteins. In his famous book *The Selfish Gene*, Richard Dawkins in 1976 eloquently made a case for considering individual cells containing genes, and bodies made up of cells, merely as vehicles to promote the propagation of their genes. Through the selfish gene concept, Dawkins provided a powerful metaphor for natural selection acting at levels, such as the gene level, that are lower than the individual level. If genes are selfish and are only concerned with their own propagation, what is to prevent individual genes from taking over cell machinery and making multiple copies of themselves within a single cell? But this is exactly what is known to happen. We now know that there are some genes that exist in multiple copies in cells; there are jumping genes called transposons that hop between chromosomes and leave copies of themselves behind. Some forms of genes "kill" or suppress the transfer of other forms of the gene to the developing egg or sperm cell. We know about 'selfish' chromosomes that 'drive' cell division processes so that only one particular type of chromosome is transmitted. What prevents total anarchy among the genes – a few genes from taking over? According to the evolutionary biologist Egbert Leigh, it is the "parliament of genes" which prevents any one gene or a few genes from multiplying indiscriminately. Leigh believes that for every wayward, rebellious gene that starts to multiply within a cell, there will be a sufficient number of suppressor genes to counteract the runaway process. If cells and bodies are considered vehicles of genes without which genes cannot multiply indefinitely, then the survival and successful multiplication of cells and bodies is also vital

Through the selfish gene concept, Dawkins provided a powerful metaphor for natural selection acting at levels, such as the gene level, that are lower than the individual level.

If cells and bodies are considered vehicles of genes without which genes cannot multiply indefinitely, then the survival and successful multiplication of cells and bodies is also vital to the survival of the genes.

If individuals are merely vehicles of their genes and need only to ensure successful propagation of their genes, why don't individuals reproduce exact copies of all their genes by cloning?

to the survival of the genes. This probably explains why the incidence of wayward genes is relatively low in normally functioning cells. Selection and fine-tuning is occurring at the level of the genes and the 'parliament of genes' actually works.

Why Sex?

When diploid individuals reproduce sexually, each individual transmits only half its genetic material to the embryo – an egg or sperm has only one set of chromosomes. Fertilisation restores diploidy to the embryo. If a diploid individual were to reproduce asexually by cloning, it would transfer all its genetic material to the embryo. This two-fold reduction in genes transferred by an individual to its offspring as a result of sex has been termed the Cost of Sex. If genes are merely to play a numbers game and if individuals are merely vehicles of their genes and need only to ensure successful propagation of their genes, why don't individuals reproduce exact copies of all their genes by cloning? Why has sex evolved? Even those species that are mostly asexual usually have one or more sexual phases at some stage in their life cycle. There are only very few species in which males have not been found. One of the popular explanations for the ubiquitous presence of sex is the 1975 lottery ticket idea of George C Williams – not having sex and producing clones with the same genetic composition is like having hundreds of lottery tickets all with the same number. It is believed that the more varied the genetic make-up of the individual offspring, the better their chances of surviving short-term unpredictable changes in the environment.

Not having sex and producing clones with the same genetic composition is like having hundreds of lottery tickets all with the same number.

Sex and the Red Queen

For many years the 'environment' of the individual was largely focused on abiotic elements such as climate. However, in recent years, more attention is being paid to the

relation between sex and Leigh Van Valen's Red Queen Hypothesis. This hypothesis gets its name from the Red Queen in Lewis Carroll's *Through the Looking Glass* in which the Red Queen is always running as fast as she can to stay in the same place. From an examination of the fossil record Van Valen found that there appeared to be a constant rate of species extinction such that the average time between emergence and extinction of a species remains the same; thus organisms must keep evolving constantly not only because the abiotic environment changes but because other organisms around them are also evolving. Sex is viewed as an essential weapon in the co-evolutionary arms race between predator and prey, host and parasite. As fast as the predator gets swift, the prey must get swifter if it is to survive. As fast as the parasite evolves a method of eating into the host's tissues, the host has to develop methods of sealing off the parasite, killing it or blocking its entry. Sex, with its ability to combine genetic materials to form new genetic combinations, is a vital ingredient for survival in the evolutionary game. In freshwater topminnow fish in Mexico, asexual clones were found to be more heavily parasitised than individuals from sexual populations. Moreover, when genetic variation in the sexual population was reduced by inbreeding, the parasitism level in the sexual forms increased. And when new genetic variation into the sexual population was introduced via fish from different stocks, the sexual forms once more became more resistant to the parasites compared to the asexual clones. These results show the Red Queen in action.

Organisms must keep evolving constantly not only because the abiotic environment changes but because other organisms around them are also evolving.

Sex, with its ability to combine genetic materials to form new genetic combinations, is a vital ingredient for survival in the evolutionary game.

Beyond the Gene?

Although Darwin knew nothing about genes, the role of these units as specifiers and carriers of information vital to the life and reproduction of organisms has been entrenched over the last century. The gene and more specifically DNA have been considered the sole repository

Gene expression is now considered to be greatly influenced by the intracellular, intercellular, extracellular, and even external environment of the organism.

of hereditary information. This view is now being supplanted by the new perspective of epigenetics according to which heritable changes in an organism's phenotype may be caused by factors other than direct changes in gene sequences. For example, methylation of DNA resulting in genomic imprinting can cause heritable changes in gene expression. Furthermore, gene expression is now considered to be greatly influenced by the intracellular, intercellular, extracellular, and even external environment of the organism. Thus genetic determinism is scarcely tenable for many traits, especially complex ones. Looking for genes "for" a trait is no longer considered a practical exercise except in special cases. Thus the emphasis has shifted from a genomic view of life and evolution to a more holistic view that also includes the interaction of genes with their environment.

A Long Way Since Darwin

Evolution has come a long way since Darwin. Many revolutionary theorists and experimentalists have contributed to this journey. And yet, Darwin's central idea of Evolution by Natural Selection is still the grand unifying theory of biology. Despite this, we must acknowledge that even natural selection cannot perform miracles. It can only act on the existing variation. This means that all species, all individuals, all structures, are not necessarily perfectly adapted. There will be a time lag between the origin of new variation, the action of natural selection on the variation, and the establishment of the better adapted form in the population. The next time you curse an aching back, remember it is a legacy from your quadrupedal ancestors, the apes. Proto-humans and humans walk upright despite a spinal architecture better suited for walking on all-fours!

The emphasis has shifted from a genomic view of life and evolution to a more holistic view that also includes the interaction of genes with their environment.

Darwin's ideas were born of the Encantadas – the Enchanted Islands of the Galapagos. It is benefiting, then, that two Darwinian disciples should continue to produce

revelations about the origin of new species at the Galapagos even as we read these words. Since 1973, Peter and Rosemary Grant have been working in the Galapagos on several species of Darwin's finches. On a few islands, they have individually marked entire populations of these birds and have followed their population sizes, and the changes in the sizes of their beaks depending on the availability of seeds of certain types. They have watched the larger-beaked species or larger-beaked individuals within smaller-beaked species become more common when only large seeds are available. The smaller-beaked species and smaller-beaked individuals were disadvantaged and not favoured by natural selection. They have watched reversals of these trends when only small seeds become available. They have seen species hybridise and are recording the fate and reproductive success of the hybrids. Is a new species about to form?

The Grants are studying evolution in action. They may witness a speciation – an event that has occurred and is occurring silently all around us and even within us all the time; Darwin machines inexorably at work. How appropriate then the words of Immanuel Kant (1755) in *A General History of Nature and a Theory of Heavens* – "The Creation is never over. It had a beginning but it has no end. Creation is always busy, moulding new scenes, new things, and new worlds".

Address for Correspondence
Renee M Borges
Centre for Ecological Sciences
Indian Institute of Science
Bangalore 560 012, India.
Email:
renee@ces.iisc.ernet.in

Suggested Reading

[1] **Richard Dawkins, *The Blind Watchmaker*, W W Norton, New York, 1986.**

[2] **Richard Dawkins, *The Selfish Gene*, Second edition, Oxford University Press. New York, 1989.**

[3] **William Irvine, *Apes, Angels, and Victorians*, McGraw-Hill, New York, 1955.**

[4] **John Maynard Smith, *The Theory of Evolution*, Reprint, Third edition (1975), Canto edition, Cambridge University Press, Cambridge, 1995**

[5] **Ernst Mayr, *The Growth of Biological Thought. Diversity, Evolution and Inheritance,* Belknap Press, Cambridge, Massachusetts, 1982.**

[6] **Matt Ridley, *The Red Queen. Sex and the Evolution of Human Nature*, Viking (Penguin), London, 1993.**

[7] **Jonathan Weiner, *The Beak of the Finch. A Story of Evolution in Our Time*, Vintage Books, New York, 1995.**