Checklist

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☑ Ample margins left for marker’s comments
☑ Correct use of paragraphs
☑ Use of subheadings to indicate changes of topic
☑ Strict observance to chronology of scientific understanding

Figures
☑ Inclusion of title and legend for each figure
☑ Reference to figures in the text

References
☑ Avoidance of only Internet sources
☑ More than 100 references
☑ Many references to primary literature
☑ Correct citation of journal reference:
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Developing ideas in “The Origin of Species”

Methodology
Critical review of science history and comparison with contemporary knowledge

Abstract
In interpreting the background to this project I noticed three key themes, these are: criticism from contemporaries, Darwin’s amendments to the Origin of Species and, effectively, ‘who was right’. In other words, I researched all the changes between all the editions of the Origin of Species and all the contemporary criticisms to find relationships between the two. I then included sections describing the relevant knowledge of today, and by today’s understanding, how much could have been improved. The whole dissertation is arranged in chronological order.

Introduction
The Origin of Species is one of the most famous, influential and notorious books in human history. More frequently cited than read and more often read than understood, it was once estimated that 90% of biology degree students had not read the Origin. Until work on this project began, I myself was one of the 90%. I understood the concepts it included, but had no idea how Darwin conceived and developed these concepts. Since Darwinian evolution forms the cornerstone of modern biology it is therefore of great importance that we understand how this theory evolved.

The aim of this dissertation is to examine Darwin’s ideas and how they developed in response to the criticism he received from his contemporaries. The ‘development’ took the form of five editions subsequent to the first, published between 1859 and 1872. Of the 3,878 sentences in the First Edition, nearly 3,000 (approximately 75%) were rewritten from one to five times each. Over 1,500 sentences were added and 325 were omitted. In terms of added sentences, the Sixth Edition is nearly a third longer than the first.

In considering the issues raised by Darwin and his critics, it is imperative that we keep in mind that they lived during the Victorian Era and that the First Edition of On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life is almost 150 years old. As such we must be prepared for a scientific understanding far more rudimentary than today. However, it is a testament to Darwin’s theory that it still forms the foundation of the biological sciences in the Twenty First Century.

Pre Publication

Born in Shrewsbury on the 12th February 1809, Charles Robert Darwin was the fifth of six children to wealthy doctor Robert and his wife Susannah Darwin (née Wedgwood – daughter of Josiah Wedgwood). Charles Darwin had an upper class, upbringing and his interest in natural history started at a very
young age; in his autobiography he recalls: “By the time I went to this day-
school my taste for natural history, and more especially for collecting, was
well developed”⁸⁶. Darwin’s father was constantly disappointed in Charles’s
lacklustre academic performance, famously claiming: “You care for nothing
but shooting, dogs and rat catching, and you will be a disgrace to yourself and
all your family”¹¹⁹. In 1825 he attended the University of Edinburgh to study
medicine, mainly to please his father as he, himself, was still more interested
in natural history. However, unsurprisingly, during his time at Edinburgh, he
neglected his studies but joined the Plinian Natural History Society where he
became a pupil of Robert Edmund Grant; a proponent of Jean-Baptiste
Lamarck’s theory of evolution.
Displeased with his lack of progress in medicine, Darwin’s father enrolled him
in Christ’s College Cambridge intending him to train as a clergyman. At
Cambridge, Darwin joined the Reverend John Stevens Henslow’s natural
history course. Darwin was particularly interested in the writings of William
Paley, especially the argument for divine design in nature. Despite Darwin’s
unrelenting indifference to his studies, he managed to scrape a pass mark
and acquire his degree in divinity.
On the 27th December 1831, HMS Beagle with the 23 year old Charles Darwin
on board left England. The primary aim of the voyage was to carry out a
‘hydrographic survey’ of the coasts of South America. The captain, Robert
FitzRoy, also intended to seek evidence for the literal biblical interpretation of
creation. Had FitzRoy known what his shipmate would go on to propose
twenty eight years later (namely the theory of evolution) then he would have,
most certainly, not allowed him aboard. Darwin’s presence aboard the Beagle
seems rather odd; he was to be FitzRoy’s gentleman companion. However,
Darwin’s main role was to prevent FitzRoy committing suicide, as had the
previous captain of the Beagle and many members of FitzRoy’s family. Upon
leaving England, FitzRoy gave Darwin a copy of Charles Lyell’s Principles of
Geology, which explained landforms as the outcome of gradual processes
over huge periods of time, which Darwin studies intently. Most of the five year
long voyage, Darwin spent on land collecting and recording specimens and
observing geological features⁵. In Chile he survived an earthquake and
discovered a new species of dolphin, which he named Delphinus fizroyi. In
South America, Darwin found, excavated and identified many fossils (including the finest *Megatherium* found to date); upon Darwin’s return Richard Owen showed that several of his finds were closely related to living creatures exclusively found in the Americas. On the Galápagos Islands, Darwin collected mockingbirds and tortoises and noted that they differed depending on which island they originated. Contrary to popular belief, Darwin did not propound the theory of evolution during his time on the voyage, evolution, as a concept was already decades old (his own grandfather, Erasmus Darwin had published a poem hinting at evolutionary principles).

When compiling his notes on the journey back to England in 1836, Darwin wrote that if his growing suspicions about the mockingbirds and tortoises were correct, “such facts undermine the stability of Species” He later wrote that ‘such facts’ “seemed to me to throw some light on the origin of species”. In 1837 Darwin moved to London and married his cousin, Emma Wedgwood. In 1839 he became Secretary of the Geological Society wherein he witnessed Richard Owen destroy the reputation of Robert Grant by discrediting the Lamarckian theory of evolution.

In 1842 Darwin started work on his theory of natural selection largely based upon observation from his voyage on the Beagle. It was Darwin’s friend John Gould that realised the significance of the Galápagos finches in Darwin’s collection of specimens. He saw that each bird had a different ‘talent’ (specifically beak shape) depending upon which island it originated. In order to strengthen the evidence for natural selection Darwin consulted animal husbanders and carried out extensive experiments with plants, trying to find evidence to answer all the arguments he anticipated when his theory was made public. Also in 1842, Darwin (who had now moved to Downe House in Kent) contacted the famous biologist Charles Lyell upon who’s book, *Principles of Geology*, Darwin’s geological knowledge was based. Lyell did not agree with Darwin’s ideas, noting that: “Darwin denies seeing a beginning to each crop of species”⁴. By this, Lyell is inferring that Darwin is a transmutationist⁵, someone who believes in the capacity of species to change. Lyell believed the opposite, specifically the immutability of species and the theory that would later become Quantum Evolution (as devised by
George Gaylord Simpson) – the rapid emergence of higher taxonomic groups.

Darwin mainly worked in secret; he aimed to perfect his theory and create counter arguments to the criticisms he anticipated before publishing. Although it is documented that Darwin was susceptible to criticism; Lyell’s opposing views did nothing to deter Darwin’s resolve and the two scientists even became good friends.

In 1844 Darwin wrote to his friend, the botanist Joseph Hooker who supported his theories, claiming that: “There might have been a gradual change of species”.

In the same year, Darwin completed his 230 page ‘rough sketch’ which contained the rudiments of his theory. Then, for almost fifteen years, Darwin neglected his notes on the theory and busied himself with other matters; he fathered ten children and conducted an eight year long study on barnacles, supposedly remarking at the end: “I hate a barnacle as no man ever did before”. It was during this time that he became ill; some sources claim from Chaga’s disease, a South American tropical disease contracted from the bite of the Bechuga beetle, the result of this was some pretty debilitating symptoms and the inability to concentrate on work for periods longer than twenty minutes.

In 1844 Robert Chambers anonymously published his work Vestiges of the Natural History of Creation in which he suggested that humans might have evolved from lesser primates, the book was unsurprisingly attacked by the religious community, and by some of the scientific including T. H. Huxley (who, himself, believed in evolution). In light of this reception, with ten children to look after and afflicted by debilitating illness, Darwin may never have published his manuscript. The event that convinced him was Alfred Russel Wallace’s draft of a paper On the Tendency of Varieties to Depart Indefinitely from the Original Type. Wallace was a young naturalist working on the theory in Borneo; his paper was uncannily similar to Darwin’s sketch that he had neglected years ago. Darwin did not want Wallace to gain all the credit for a theory that he (Darwin) had independently proposed and had been working on, intermittently, for almost two decades. However, Darwin intended to step aside and let Wallace publish his theory because his son Charles was
critically ill with scarlet fever. Darwin wrote to Lyell and Hooker offering to step aside but they came up with a compromise, Darwin and Wallace should produce a summary of their combined ideas and present it to the Linnean Society.

In 1858, they presented their works which were entitled: *On the Tendency of Species to form Varieties* (Wallace) and *on the Perpetuation of Varieties and Species by Natural Means of Selection* (Darwin). Neither author was present, however, as Wallace was still in the distant east and Darwin and Emma were burying their son who had succumbed to the scarlet fever. The papers met with little response.

Later the same year, Darwin produced an abstract of the paper and Lyell and Hooker pressured him into publication. Darwin originally titled the work: *An abstract of an Essay on the Origin of Species and Varieties Through natural selection*. Upon criticism from the publisher, John Murray, the title was changed to: *On the Origin of Species* with the ‘subtitle’: *by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*.

Darwin’s developing ideas were little shaped by the criticisms he received in the decades spent working on his theories before publication, mostly he received constructive criticism from his friends who generally agreed with the theories proposed. All this was about to change as Darwin published his work and unleashed the most hotly contested scientific theory in history.

**The First Edition**

Finally, on the 24th of November 1859, John Murray of London published 1250 copies of: *On the Origin of Species by Means of Natural Selection, or the*
Preservation of Favoured Races in the Struggle for Life. All of the 1170 copies available for purchase were sold within the first day. The volume took the form of an octavo, was 502 pages in length and cost fifteen shillings. Darwin describes the structure of the book as “one long argument” of detailed observations, inferences and consideration of anticipated objections\textsuperscript{122}. The only allusion to human evolution was the understatement that “light will be thrown on the origin of man and his history”\textsuperscript{123}. The term evolution was not included as it was controversial at the time; however, Darwin concludes the work with the paragraph: “endless forms most beautiful and most wonderful have been, and are being, evolved.”\textsuperscript{124}

\textit{Darwin’s Theory}

In order to better comprehend some of the ideas dealt with in this dissertation, I think it necessary to first explain the theories as proposed by Darwin in the First Edition. Darwin’s theory is based on the following key observations and inferences drawn from them\textsuperscript{88}.

- Species have great fertility (which Darwin referred to as superfecundity) i.e. they make more offspring than can grow to adulthood.
- Populations remain roughly the same size, with modest fluctuations.
- Food resources are limited, but are relatively stable over time.
- An implicit struggle for survival ensues.
- In sexually reproducing species, generally no two individuals are identical.
- Some of these variations directly impact the ability of an individual to survive in a given environment.
- Much of this variation is inheritable.
- Individuals less suited to the environment are less likely to survive and less likely to reproduce, while individuals more suited to the environment are more likely to survive and more likely to reproduce.
- The individuals that survive are most likely to leave their inheritable traits to future generations.
This slowly effected process results in populations that adapt to the environment over time, and ultimately, after interminable generations, the creations of new varieties, and ultimately, new species.

There had been mechanisms of the process of evolution proposed before Darwin but Darwin’s theory was revolutionary in the idea that heritable variations in species were preserved and ‘extrapolated’ if they proved advantageous in the struggle for life – this is the idea of natural selection.

We now believe Darwin to be mostly correct in his description of the mechanism of evolution by natural selection. In the early years of the twentieth century the theory underwent a revolution, with the discovery of chromosomes by Weismann, the importance of Gregor Mendel’s theory of genetics as the basis for biological inheritance was realised (largely by William Bateson). Variation was attributed to random genetic mutation. This integrated theory was named Neo-Darwinism (also called: new synthesis, modern synthesis, evolutionary synthesis or neo-Darwinian synthesis). The interesting thing is that Mendel’s work was published in 1866, predating the last three editions of Origin of Species but very few people at the time read Mendel’s paper and no one realised its importance. Pangenesis was Charles Darwin’s hypothetical mechanism for heredity – a mechanism now known to be deeply flawed; the theory states that body cells shed ‘buds’ called gemmules, which collect in the reproductive organs prior to fertilization. Supposedly every cell in the body has a ‘vote’ in the constitution of the offspring. Atavisms (reoccurring traits that disappeared generations ago) arise due to the awaking of long-dormant gemmules while limbs regenerate due to the activation of gemmules from the missing limb circulating in the main part of the body. This theory was described by Darwin in his 1871 volume: The Descent of Man. If Darwin had understood the implications of Mendelian inheritance and applied them to his theory of evolution then one of the weak points in his argument could have been removed to the satisfaction of all (see page ???).
Shortly after publication, the Athenaeum Magazine extrapolated the implication of “monkeys into men” – this notion, although nothing new (see page), filled the minds of the generally non-scientific public and clergy who did not fully understand the ideas proposed. Outraged by the implications of the theory; the Athenaeum critic of the day, Gerald Massey, remarked that: Darwin should be tried in the Divinity Hall, the College, the Lecture Room and the Museum. Darwin’s theories were to be “tried” in due course but there was little time for scientific criticism of the First Edition as a second edition was already imminent.

The Second Edition

Published on the 7th of January 1860, less than two months after the First Edition, the Second Edition, consisting of a run of 3000 copies, was barely more than a re-print of the first organised by John Murray in order to meet the demand for the book. The ideas in the book remained the same but, having been pressured into what he considered premature publication by Lyell and Hooker, Darwin took the opportunity to alter aspects of the phraseology and punctuation to clarify his argument. Darwin did make a very few changes to the content, the most interesting being the addition of “by the Creator” into the closing paragraph, at the point here marked *: “There is grandeur in this view of life, with its several powers, having been originally breathed * into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved”. This ‘clause’ was probably added by Darwin in order to absolve himself from future religious objections.
On the 31st of March 1861, the Third Edition of the *Origin of Species* was published by Murray. More than a year had passed since the publication of the Second Edition, during which time the *Origin of Species* received heavy criticism. However, aside from the many people who took opposition to Darwin’s theories and to Darwin himself, there were many people who agreed with and supported him, people such as Thomas Huxley, Charles Lyell, Joseph Hooker, John Tyndall and, in America, Asa Gray.

At least one of the published critiques was the result of professional envy; Darwin’s old friend and instructor Richard Owen submitted a malicious article to the Edinburgh Review in 1860, in which he criticised many aspects of the origin, he questioned: “Are all the recognised organic forms of the present date, so differentiated, so complex, so superior to conceivable primordial simplicity of form and structure, as to testify to the effects of Natural Selection continuously operating through untold time? Unquestionably not”\(^1\). Owen was in league with St George Jackson Mivart (we will see more of him later); together they attacked Darwin’s theories, seeking to supplant them with their own view that a divine plan was clearly visible in the laws of evolution. However, their criticism initially had little impact, Peter Bowler (*in Evolution; The History of an Idea 1983*) attributes this to “the clumsiness of their tactics”, he is referring to the personal criticisms they made of Darwin and his ‘followers’. Mivart would go on to raise some very serious criticisms of the *Origin* but they were not addressed by Darwin until the Sixth Edition (*SEE PAGE*). The criticisms put forward in Owens’ article proved so unfounded that
Darwin responded by claiming: “I could have written a much more damming criticism myself”\(^2\).

Much of the criticism of the *Origin* met with a similar response to Owens’, Darwin’s supporters and friends especially Thomas Huxley (termed: ‘Darwin’s Bulldog’) engaged in endless debate with critics of the theory. Famously, in 1860, in the debate between Thomas Huxley and the Lord Bishop of Oxford Samuel Wilberforce, at the British Association for the Advancement of Science in Oxford; the following exchange allegedly took place (although both religious and scientific accounts of the time claim victory in the debate and there are many different interpretations): Samuel Wilberforce: “Is it on your grandfather’s or your grandmother’s side that you claim descent from a monkey?”\(^6\). Upon momentary contemplation of this rhetorical snub, Huxley (allegedly) muttered to himself: “The Lord has delivered him into my hands”\(^6\). Huxley’s subsequent reply was as follows: “I would rather be descended from an ape than from a cultivated man who used his gifts of culture and eloquence in the service of prejudice and falsehood”\(^6\). One account of the debate claims this retort was of such contention that it caused a lady there present to faint. There are also reports of Captain FitzRoy (there to present a paper on storms) walking across the hall holding a Bible aloft and exclaiming “believe in God not science”\(^110\).

The Third Edition was a full thirty six pages longer than the Second Edition and included so many revisions and corrections that Darwin tabulated the main ones “for the convenience of those interested in the subject, who possess only the earlier editions”\(^8\). For the convenience of those reading this dissertation without the Third Edition to hand I have included all his tables of revisions and corrections as appendices.

From the table of corrections, one of the first entries we see is the phrase: “On the improbability of the occurrence of sudden and great modifications of form”\(^125\). Darwin is referring to his refutation of ‘saltations’ as a credible driver of speciation. In the next section we will examine this aspect in detail.

*Saltationism*
An article appeared in *The Gardener’s Chronicle* on the 18th of February 1860 by a Professor W. H. Harvey entitled: *A case of monstrous Begonia*. In the article, Harvey criticised Darwin on his theory of gradual change resulting in the creation of separate species. Harvey instead proposed that speciation could be effected by jumps or ‘saltations’ (saltation, from the Latin, *saltus*, meaning ‘leap’, is a sudden change from one generation to the next, that is large, in comparison with the usual variation of an organism)\(^9\). He claimed that: “The jumps between generations are so extremely large and divergent that speciation could be effected in a single leap”\(^10\).

As a result of this criticism, Darwin included in the Third Edition the following retort: “It may perhaps be doubted whether monstrosities, or such sudden and great deviations of structure as we occasionally see in our domestic productions, more especially with plants, are ever permanently propagated in a state of nature. Monsters are very apt to be sterile; and almost every part of every organic being, at least with animals, is so beautifully related to its complex conditions of life that it seems as improbable that any part should have been suddenly produced perfect, as that a complex machine should have been invented by man in a perfect state”\(^11\).

In this paragraph, Darwin is rejecting the idea of saltations resulting in the creation of new species arguing that the “monsters” produced are likely to be sterile and the probability of their spontaneous generation in a viable state is “improbable” (this idea is explored further, 125 years later, in *The Blind Watchmaker* by Richard Dawkins\(^12\) see page ???).

Despite this initial refutation of Harvey’s ideas, some scientists and literary historians believe that Darwin was not as sure of his theories as he seemed. The following passage comes from the March 1981 edition of *Acta Biotheoretica*:

Darwin had rejected monstrosities and saltations as a means of generating variation in earlier editions. However, Vorzimmer pointed out (in his 1972 volume entitled: *Charles Darwin The Years of Controversy*) that Harvey’s criticism caused Darwin to became somewhat wider in his definition of individual differences (which Darwin had introduced as the tool of natural selection)\(^13\).
The supporting quote the article gives is from page 100 of the Third Edition of the *Origin*, just 54 pages since Darwin’s outright rejection of Harvey’s theory: “Natural selection can act only by the preservation and accumulation of small inherited modifications, each profitable to the preserved being; and as modern geology has almost banished such views as the excavation of a great valley by a single diluvial wave, so will natural selection, if it be a true principle, banish the belief of the continued creation of new organic beings, or of any great and sudden modification in their structure” 14.

The quote is still clearly a defence of his theories but Darwin’s language does seem vaguer – he appeals to future discoveries to ‘banish the belief’ of his critic.

A major contributor to the criticism and ambiguity surrounding the *Origin of Species* was that Darwin gave no clear definition of a “species”. He mostly seems to have thought that there was no distinction between varieties and species. This was important because he devoted much attention to showing how new varieties could be produced by man. If varieties were really species, constancy of species clearly wasn’t an issue. This becomes relevant in the consideration of Harvey’s criticism that a new species could be produced in a single leap. We know today that this is not true; the situation is, as Darwin correctly assumed, that: firstly the probability of a viable ‘monster’ is very slight, secondly the monster is unlikely to be favoured by natural selection and lastly monsters are often sterile. Statistical biologist R. A. Fisher gives the analogy of a microscope almost in focus with macromutations represented by large adjustments to the focus, he says: “It is sufficiently obvious that any large derangement will have a very small probability of improving the adjustment”, Fisher’s full argument is described in *The Blind Watchmaker* on page 231. With progress in the field of genetics in the twentieth century, the term ‘monster’ was replaced by ‘mutant’ and the nature of its conception was understood (i.e. replication errors in its DNA) 92.

This is where much of the confusion comes in; mutations are important in generating variation in Neo-Darwinism, as in the well known example of the melanic *carbonaria* morph of the peppered moth *Biston betularia* out-
competing the lighter coloured *typica* morph (during the English Industrial Revolution that darkened the trunks of many woodland trees)\(^9\).

*Figure 7. Biston betularia typica and carbonaria morphs*

Figure 7. The two moths are completely different in appearance due to their polymorphism but, by the modern definition of a species (by phenetics etc), they remain the same species.

Saltationists believe that the gradualist nature of natural selection is insufficient to explain the “bridgeless gaps” in the fossil record (see page ???) and that speciation by mutation is the only explanation. Saltation is a theory little subscribed-to nowadays but it was very popular shortly after the rise of genetics, many scientists, the most famous of whom was Richard Goldschmidt, attempted to explore possible genetic mechanisms that, if slightly altered would result in a large phenotypic change – Goldschmidt called these “controlling genes” and the resulting large-scale mutations “macromutations”. As a result of its biological novelty, the macromutant (created in a single generation) might enjoy a selective advantage under changing environmental conditions. He called the macromutants ‘hopeful monsters’ i.e. random mutation effected such large scale change that the progeny was a separate species to its parents and then environmental conditions would decide if the monster would be better or worse adapted for life than its parents.
The Age of the Earth

Another obvious nuance in the Third Edition is that “The computation of time required for the denudation of the Weald is omitted” (see appendix). Darwin based the calculation on the rate of wave attrition upon the specific rock type of the Weald of Kent; from this, Darwin offered a time scale of “306, 662, 400 years since the latter part of the Secondary Period”. The calculation was initially included in order to give an idea of the lapse of time in years available for the action of natural selection to accumulate small gradual changes providing greatly modified structures. In the table of corrections we also find the reason for the omission, Darwin claims: “I have been convinced of its inaccuracy in several respects by an excellent article in the ‘Saturday Review,’ Dec. 24, 1859”. Copies of the ‘Saturday Review’ from Christmas Eve 1859 have proved elusive but, in this exert from a correspondence between Darwin and Hooker on the 3rd of January 1860, Darwin describes the argument of “the reviewer”: “The hostile arguments of the reviewer are geological, and he deals especially with the denudation of the Weald. The reviewer remarks that, “if a million of centuries, more or less, is needed for any part of his argument, he [Darwin] feels no scruple in taking them to suit his purpose”. In the same letter to Hooker, Darwin admits ‘defeat’; conceding that the Earth was not as old as his calculations suggested: “Some of the remarks about the lapse of years are very good, and the reviewer gives me some good and well-deserved raps – confound it. I am sorry to confess the truth: but it does not at all concern the main argument”.

Despite the omission of the calculation, Darwin still includes the paragraph: “It is highly important for us to gain some notion, however imperfect, of the lapse of time. During each year, over the whole world, the land and the water have been peopled by hosts of living forms. What an infinite number of generations, which the mind cannot grasp, must have succeeded each other in the long roll of years!”.
In *Charles Darwin; The Years of Controversy* (1972), Peter Vorzimmer proposes that the reason for the substitution was possibly because Darwin was “being too daring in his biblical denouncement”\(^{20}\). At the time of the publication of the *Origin of Species*, much of the populace (especially the clergy) still believed the Earth was created in 4004 BC according to Bishop Ussher’s ‘calculation’. Opinion was changing on the age of the Earth as scientific attempts to establish its age were well underway and promised an age far greater than six thousand years (although the ultimate age calculated would cause Darwin problems in editions to come see page ???).

The problem caused for Darwin arising from the criticisms of his calculation from both fronts, namely the Saturday Review and the Church, were the same – Darwin had no proof beyond that of scientific guesswork and extrapolation over a huge range. Not even Huxley, ‘Darwin’s Bulldog’, could argue without evidence so, in the Third Edition, the calculation of the age of the Weald was omitted. However, Darwin remained sure that the denouncement of his geological calculation “does not at all concern the main argument”\(^{16}\).

The problem of geological time, especially regarding the immense timescale the theory of evolution by natural selection required, would cause Darwin some of his most damaging criticism which he would respond to in the Fifth and Sixth Editions of the *Origin* (see page ???).

*The Advancement of Organisation*

Towards the end of Chapter IX, the problem of natural selection acting in favour of the advancement of organisation is addressed. Although admitting that different naturalists have different concepts of the term ‘advance in organisation’\(^{26}\) Darwin stresses the fallacy of the Lamarckian premise of an inherent tendency to advancement and perfection and accounts for the presence of ‘lowly’ animals amongst those classified as higher in organisation on his Natural Selection theory\(^{27}\):
“On my theory the present existence of lowly organised productions offers no difficulty; for natural selection includes no necessary and universal law of advancement or development – it only takes advantage of such variations as arise and are beneficial to each creature under its complex relations of life.”

This passage was included to refute the progressionist view of Ernst Haeckel in which lower animals were merely stages in nature’s ascent toward the fully mature form of human species. Haeckel’s theories of an almost linear tree of life (see Figure 5.) were based upon ontogenetical (embryological) evidence, today we see why Darwin was right – he correctly summarises that variations are only beneficial in the context of the creature’s ecological niche – organisms do not aspire to become more complex – natural selection “chooses” the individuals that are better adapted to their environment.

The Fourth Edition

The Fourth Edition of the Origin of Species was extensively revised until publication on the 31st of December 1866. Almost six years had passed since the Third Edition. The controversy the book had caused had abated little; this well known caricature from the Hornet Magazine was published shortly after the emergence of the Fourth Edition:
An important structural change involved the addition of a number of new subheadings within the chapters (for example the title “Individual Differences” added on page 4829). The changes however merely seem to increase the clarity of the arguments by further segregating the “one long argument” of the book. Also new in the Fourth Edition there are the many additional examples quoted from other authors in order to corroborate Darwin’s theories, for instance: “Sir J. Lubbock on a diving Hymenopterous insect”106.

**Hybrid Sterility**

At one point in the Fourth Edition, Darwin corrects his previous thought that hybrid sterility is a result of natural selection19 and gives reasons to suppose that it must merely be the result of incompatible reproductive organs: “remembering that species which have never coexisted in the same country, and which therefore could not have profited by having been rendered mutually infertile, yet are sterile when crossed; and bearing in mind that in reciprocal crosses between the same two species there is sometimes the widest difference in the resulting degrees of sterility, we must give up the belief that natural selection has come into play; and we are driven to our former proposition, that the sterility of first crosses, and indirectly of hybrids, is simply incidental on unknown differences in the reproductive systems of the parent-species”30. In this instance, Darwin was right the first time – with our current knowledge of genetics we can explain why: if one species is separated from another and they evolve independently, an individual born without the genetic characteristics necessary for successful reproduction (e.g. the same karyotype) with a member of the other species will not be selected against by natural selection.
The genetic make up of the two species will diverge to a point, that, if they do procreate, the offspring produced are likely to be sickly or sterile (like a mule)\textsuperscript{107}. So natural selection penalises any predilection, on the part of individuals on either side, towards hybridizing with the other species\textsuperscript{66} (see Figure 6.).

Darwin had a particular interest in this subject since he fathered ten children by his own cousin.

*Figure 6.* A mule hard at work on the South American island of Tierra del Fuego

The predilection of mating with each other would not be favoured in wild horse and donkey populations

*Perpetuation of Variation*
Darwin had previously stated that variations, having once arisen, were reproduced in the same manner as normal characters. Yet in various scattered parts of the First Edition of the *Origin*, one finds implied something more than the mere heritability of a new character. Darwin alluded to the fact that variations, when inherited, had a tendency to result in further variation, claiming that: “descendants would probably inherit a tendency to a similar slight deviation of structure”, indicating that the character itself need not be passed on, for “the tendency to variability is in itself hereditary, consequently they will tend to vary and generally to vary in nearly the same manner as their parents varied.”

The theory then says that the variations produce all the requisite forms which, in their continued variation produced all the requisite variation and then, after having been ‘fixed’ as established forms at each stage, produced all the intermediate forms all the way up to, and including, new species. This concept was helpful in defence of the theory against critics claiming that variation would eventually reach a limit and could not result in speciation. However, the concept of continued variability did receive criticism...

In October 1862, Darwin read Hugh Falconer’s manuscript on fossil elephants which was, in part, a criticism of his theory. Two matters seemed to trouble Falconer, these were, first, the lack of variation in certain specific types; and second, the way in which variability could coexist alongside persistence of type. These remarks came at just the time Darwin was working on the subject. He had seen that the tendency to continued variability was a definite asset to the selective process. Yet it appeared that this phenomenon, which assured the continued variation within the already improved forms, would prevent that equally important goal of persistency of type.

In recognition of Falconer’s remarks, Darwin added in the Fourth *Origin of Species* Edition the idea: “that the periods during which species have been undergoing modification, though very long as measured by years, have probably been short in comparison with the periods during which these same species remained without undergoing change.” In other words, while individual variability might itself continue; actual modification of the species took place only at widely spaced intervals. During these intervals, variations which had
arisen previously became assimilated into the population, increased in numbers and fixed into a new form. This was Darwin’s way of incorporating variation leading to speciation with persistence of type. We now believe that an individual, showing considerable variation has no increased predilection for further variation over an individual that has varied only slightly. It demonstrates Darwin’s ignorance of genetics that he assumes that a variation, which we now know to be a result of differing DNA, must become ‘fixed’ before it becomes heritable. If Darwin had an understanding of genetics at the time he was working on his theory then he would not have proposed that the tendency toward variation was, in itself, inheritable.

Absence of Intermediate Types in the Fossil Record

Darwin was ready to be challenged on the lack of evidence for evolution by natural selection based upon the fossil record. He included a chapter in the First Edition (and all subsequent editions) entitled: “On the Imperfection of the Fossil Record”. The following passage from *The Blind Watchmaker* (Dawkins 1991) summarises the argument and implications of the chapter: “Darwin’s view was that a complete fossil record, if only we had one, would show gentle rather than jerky change. But since fossilization is such a chancy business, and finding such fossils as there are is scarcely less chancy, it is as though we had a cine film with frames missing. We can, to be sure, see movement of a kind when we project our film of fossils, but it is more jerky than Charlie Chaplin, for even the oldest and scratchiest Charlie Chaplin film hasn’t completely lost nine-tenths of its frames.” In the chapter, Darwin justifies his view that the incomplete nature of the fossil record is the reason why we do not observe a gradual process of intermediate forms: “Now let us
turn to our richest geological museums, and what a paltry display we behold! That our collections are very imperfect is admitted by every one. The remark of that admirable palaeontologist, Edward Forbes, should not be forgotten, namely, that numbers of our fossil species are known and named from single and often broken specimens, or from a few specimens collected on some one spot. Only a small portion of the surface of the earth has been geologically explored, and no part with sufficient care, as the important discoveries made every year in Europe prove. No organism wholly soft can be preserved. Shells and bones will decay and disappear when left on the bottom of the sea, where sediment is not accumulating. From this quote Darwin was clearly confident that subsequent research would restore the lost episodes and that the continuity of the record would eventually be restored.

Darwin experienced a partial victory in regards to this last belief; the first fossilized Archaeopteryx lithographica was found in Germany in 1861. Archaeopteryx was a primitive bird that lived 150-155 million years ago during the Jurassic Period. It had feathers similar in structure and design to modern-day birds but it also had many theropod dinosaur characteristics. Unlike modern birds, Archaeopteryx had small teeth, as well as a long bony tail and features which it shared with other dinosaurs of the time (see Figure 1.).

*Figure 1. Archaeopteryx lithographica*
Figure 1. A reproduction of the Archaeopteryx lithographica fossil found near Solnhofen in Germany in 1861 in which you can clearly discern the unfused wing feathers along with the lizard-like tail

It was an impressive and helpful find – a supposed missing link between dinosaurs and birds, its significance was much debated, but a single discovery could hardly be considered conclusive\textsuperscript{101}.

Darwin also included the following passage in all of the six editions regarding the absence of intermediate types in the fossil record: "The case at present must remain inexplicable; and may be truly urged as a valid argument against the views here entertained"\textsuperscript{93}. As a tentative explanation Darwin did (incorrectly) speculate that the Precambrian seas had been too clear to lay down sediments and had therefore preserved no fossils\textsuperscript{93}. Despite Darwin's pre-emptive defence of the lack of fossil evidence, which he considered "probably the gravest and most obvious of all the many objections which may be urged against my views"\textsuperscript{58}, many of the criticisms of the \textit{Origin} were focused upon the lack of fossil evidence. This weak point in Darwin's theory, completely unsupported by evidence, led many to propose alternate theories to explain evolution, the most influential of these were saltationism (see page ???) and catastrophism:

\textit{Catastrophism}

It was believed by many, in both scientific and religious spheres, at the time, that the world had been created by a series of immense catastrophes. This idea, known as catastrophism, was in opposition to uniformitarianism – the theory developed by James Hutton and later Charles Lyell that stated that; fundamentally the same geological processes that operate today also operated in the distant past\textsuperscript{59}. Darwin's theories describing the processes behind evolution were reliant upon gradual change (both geological and biological); this is unsurprising when we consider that Darwin gained much of his geological knowledge from Charles Lyell. The fashionable theory of catastrophism was championed at the time by the French anatomist and palaeontologist Georges Cuvier. Catastrophism was often used as supporting evidence for intelligent design i.e. the Creator would introduce new hoards of
birds and beasts to the world after obliterating of their predecessors. Cuvier, however, never made any reference to the Noachian flood or to divine creation as the mechanism by which repopulation occurred following the extinction event. In fact, Cuvier influenced by the ideas of the Enlightenment and the intellectual climate of the French revolution, avoided religious or metaphysical speculation in his scientific writings Cuvier also believed that the stratigraphic record indicated that there had been several revolutions, which he viewed as recurring natural events, amid long intervals of stability during the history of life on earth. Although the religious angle of Cuvier's theory of catastrophism was greatly expanded (and altered!) by English geologists William Buckland and Robert Jameson in *The Theory of the Earth*, a student of Cuvier, Louis Agassiz, would see the scientific merit in Cuvier's ideas. Agassiz criticised the gradualist nature of Darwin's theory in defence of catastrophism, using the lack of intermediate types in the fossil record in corroboration: “Between two successive geological periods, changes have taken place among plants and animals. But none of those primordial forms of life which naturalists call species are known to have changed during any of these periods. It cannot be denied that the species of different successive periods are supposed by some naturalists to derive their distinguishing features from changes which have taken place in those of preceding ages, but this is a mere supposition, supported neither by physiological nor by geological evidence; and the assumption that animals and plants may change in a similar manner during one and the same manner is equally gratuitous.”

Saltationism

The gaps in the fossil record were also accordant with the theory of saltationism that states that speciation “could be effected in a single leap” (see page ???). Huxley was an advocate of saltationism based upon fossil evidence and opposed Darwin’s staunch support of gradualism, exclaiming:
“Charles! If you go on overstressing the importance of imperceptible change and insisting on the gradual transition from one type to the next, you’ll be digging your own grave!”

The strong and growing influence of catastrophism, advocated by eminent scientists like Agassiz, even when combined with Huxley’s opposition did not convince Darwin to change his ideas about the gradual nature of evolution. But was Darwin right to ignore the voices of his critics and maintain that imperceptible change was responsible for evolution?

Now, 148 years later, a great deal more is known about the fossil record and many transitional forms have been found, such as the intermediates in the evolution of the sperm whale (see Figure 2.), from which we can see how the leg bones became vestigial features: Figure 2. The well-documented evolutionary history of the sperm whale based upon fossil evidence

*Ambulocetus* (literally: Walking Whale) – 49, million years ago, 3m long
Basilosaurus – 36 million years ago, 18m long, the hind limbs are greatly reduced compared to those of Ambulocetus

Modern Sperm Whale (Physeter macrocephalus) – the hind limbs are now vestigial features. Interestingly, the whales that possess genes for longer extremities develop miniature legs (this is an atavism)

The number of intermediate types known, however, seems too small for us to claim that the gaps in the fossil record have been filled; something else is clearly going on. It no longer seems to be an artefact of ‘chancy’ preservation that we see little change in species for long periods, followed by extinctions, followed by rapid radiations (the most famous of these being the rise of mammals after the extinction of the dinosaurs). What then was causing the gaps? Catastrophism? Saltations? The answer, as believed by scientists (many creationists still use the idea to support the theory of serial creation) today, is described by the theory of punctuated equilibrium. Proposed by American palaeontologists Niles Eldridge and Stephen Jay Gould in 1972, the theory of punctuated equilibrium states that the gaps in the fossil record are a true reflection of what really happened, rather than being the annoying but inevitable consequences. The reason the ‘transition’ from ancestral species to descendant species appears to be abrupt and jerky is simply that, when we look at a series of fossils from any one place, we are probably not looking at an evolutionary event at all: we are looking at a migrational event, the arrival of a new species from another geographical area. Certainly there were
evolutionary events, and one species did evolve, probably gradually, from another. But in order to see the evolutionary transition documented in fossils we should have to dig elsewhere. The theory claims that brief episodes of rapid gradual change are separated by long periods of evolutionary stagnation. This sounds awfully familiar because it was previously proposed by Darwin himself, in the Fourth Edition you will recall Darwin wrote, in response to Falconer’s criticism (see page ???), that: “the periods during which species have been undergoing modification, though very long as measured by years, have probably been short in comparison with the periods during which these same species remained without undergoing any change.” Punctuated equilibrium theory does not infer that this is the only explanation for the gaps in the fossil record; most biologists agree that certain gaps, most obviously the lack of fossils from the Precambrian period, are due to other factors (one of these being the possible abundance of organisms with ‘wholly soft’ bodies). The upshot of this is that Darwin was indeed right not to subscribe to the theories of Catastrophism and Saltationism as many transitional forms have subsequently been found and he was clearly right about the imperfection of the fossil record. However, Darwin was not proven right in his assumption that a complete fossil record would show a gradual, and very pronounced, transition from one form to the next. I believe this is because he did not think that isolation was of importance in evolution by natural selection (see page ???). If Darwin had understood the role of allopatric speciation earlier then it is very probable he would have been able to propose the basic concept of punctuated equilibrium 100 years before Eldridge and Gould.
The Fifth Edition

Published by Murray in August 1869; ten years after the First Edition, the Fifth Edition contained extensive revisions.

Survival of the Fittest

The most famous inclusion in the Fifth Edition is the, often quoted phrase “survival of the fittest” (page 72) in the following context: “I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, in order to mark its relation to man’s power of selection. But the expression often used by Mr. Herbert Spencer of the Survival of the Fittest is more accurate, and is sometimes equally convenient. We have seen that man by selection can certainly produce great results, and can adapt organic beings to his own uses, through the accumulation of slight but useful variations, given to him by the hand of Nature. But Natural Selection, as we shall hereafter see, is a power incessantly ready for action, and is as immeasurably superior to mans feeble efforts, as the works of Nature are to those of Art.” Interestingly this phrase which is synonymous with Darwin and his works in the public understanding was not proposed by Darwin himself. Derbyshire born philosopher and prominent classic-liberal political theorist Herbert Spencer originally coined the phrase “Survival of the Fittest” (although he disagreed with Darwin, believing in Lamarckian evolution instead).

The Fifth Edition is regarded by many literary historians as the edition that marked the turning point in the development of Darwin’s theory. The previous editions show little development of Darwin’s theories, the changes Darwin made served mainly to clarify his position and improve the quality of the
language. The change the historians refer to is a reversion to Lamarckian principals and the subversion of natural selection as the only cause of evolution, by the theory of unconscious selection. Also important is Darwin’s changing view regarding the importance of isolation on speciation – in prior editions he maintained that it was of no importance but now admits that it could aid speciation. The literary historians believe that the turning point came about (almost) exclusively as a result of the criticism from Fleeming Jenkin. The following section describes Jenkin’s criticism and Darwin’s response.

**Blending Inheritance and Isolation**

In the Fifth Edition Darwin inserts a large amount of material on how the conditions of life affect an organism and its offspring, based upon his study on native weeds, Darwin claimed the following: “The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species...Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought seem to be the most effective of all checks.”

Darwin assumes that the conditions act in two ways, directly on the whole organism and indirectly via the reproductive system, the actual modifying effect on the offspring being determined by the nature of the organism. An important point is that this theory, allowing for many offspring to become modified in the same way, is Darwin’s answer to Fleeming Jenkin’s objection. In June 1867, Fleeming Jenkin published his Review of the Fourth Edition of *The Origin of Species* in *The North British Review*. Jenkin’s argument can be divided into two distinct halves. First, Jenkin dispatched individual differences by asserting that they could never be selectively accumulated to pass beyond the confines of a definite “sphere” of variation. There was, he said, a point or “norm” around which individual types could vary. They could vary in every direction from this norm but not beyond a certain limit in any one direction; they were like oscillations about a fixed point. This fixed point represented an essentially specific character so that at best, dogs could be improved as dogs and rabbits as rabbits, but little else could be effected. Continued selection could avail nothing because the limit
of this type of variation was reached well before even a new subspecies could be produced. In the article, Jenkin questions: “if man’s selection cannot double, treble, quadruple, centuple any special divergence from a parent stock, why should we imagine that natural selection should have that power?” In pointing this out, Jenkin felt he had shown the impossibility of employing individual differences as a source of evolutionary material. He then turned his attention to the obvious alternative, saltations. In the second half of his argument Jenkin began by citing all the usual difficulties encountered with saltations: they occurred rarely and singly, they were too freakish – too great a departure from the normal form and were therefore usually sterile. Secondly, and on the supposition that there might occur some less drastically anomalous types of saltation, he invoked the swamping effect, claiming “it is impossible that any sport or accidental variation in a single individual, however favourable to life, should be preserved and transmitted by Natural Selection”. Jenkin goes on to describe blending and points out that, in terms of whole populations; “the advantage, whatever it may be, is utterly outbalanced by numerical inferiority” and the variation would be swamped. He also gave the following example “A highly-favoured white cannot blanch a nation of negroes”. In summing up the first chapter of the Fifth Edition, Darwin shifts the cause of variation from natural selection as the main one, to a collection of factors, stressing the role of external conditions, habit, use and disuse, inheritance and reversion and correlation of growth, emphasizing a Lamarckian tone: “Variability is governed by many unknown laws, more especially by that of correlation. Something may be attributed to the definite action of the conditions of life, but how much we do not know. Something must be attributed to use and disuse. The final result is thus rendered infinitely complex.” The full force of Jenkin’s argument is seen in Chapter IV and is the section referred to as the turning point by many reviewers of the theory. Darwin admits that he did not appreciate how rarely single variations, whether slight or strongly-marked, could be perpetuated until he had read Jenkin’s article in *North British Review* in 1867. Darwin then uses two arguments to overcome the blending inheritance or ‘swamping effect’ problem; he stresses that a number of offspring within the population could have the same slight variation: “The conditions might indeed act in so energetic and definite a
manner as to lead to the same modification in all the individuals of the species without the aid of selection." He also defended his theory by supposing that isolation would allow a variation in a small number of individuals to become established; "it should be borne in mind that most animals and plants keep to their proper homes, and do not needlessly wander about." Consequently each newly formed variety would generally be at first local; so that similarly modified individuals would soon exist in a small body together, and would often breed together. If the new variety were successful in its battle for life, it would slowly spread from a central spot, competing with and conquering the unchanged individuals on the margins of an ever increasing circle. The two fundamentally important points can be seen here – that a non-selective process of change is becoming important and that isolation (which Darwin had previously denied as a necessary condition for speciation) was now being used as a necessity to prevent blending from removing small variations. But Darwin was conscious of the ‘swamping’ influence of blending prior to the First Edition of the Origin and had presented an alternative: unconscious selection, which actually utilised blending: “I believe that during the slow process of modification the individuals of the species will have been kept nearly uniform by intercrossing; so that many individuals will have gone on simultaneously changing, and the whole amount of modification will not have been due, at each stage, to descent from a single parent.” But it seems that Jenkin committed Darwin more fully to the use of unconscious selection: “I saw the great importance of individual differences, and this led me fully to discuss the results of unconscious selection by man.” A dichotomy had therefore developed in Darwin’s theory. Modification could be caused in two ways: nonselectively via direct action of the conditions of life and if via natural selection, either avoiding blending by isolation or incorporating it in unconscious selection. Blending selection, as the basis of unconscious selection implied that superior variant forms were more likely to spread their ‘qualities’ within the general population and therefore blend with them. Modification of the population would follow from the continued appearance and reappearance of the variation, blending thus ensuring the equal and widespread distribution of the advantageous quality through the whole population.
accumulation of slight gradual changes by natural selection to modify and ‘perfect’ organs\textsuperscript{52} and that the same ends can be reached by various means, i.e. that different accumulated changes could yield the same modification\textsuperscript{53}.

Having just examined the objections raised by Jenkin and Darwin’s response to them, we will now examine who is correct according to the accepted science of today.

\textit{Isolation}

Fleeming Jenkin believed in variation within species and that natural selection could modify a species, but only to a certain limit, it could not result in speciation as Darwin proposed. In his thinking, Jenkin was right, up to a point; natural selection would not normally result in the creation of a new species, as he correctly assumed – the rest of the gene pool would attenuate the effects of the advantageous variation. We now realise the importance of isolation in speciation – populations within a species have to be separated in some way for them to result in evolution in different directions to the point where they can no longer reproduce with the other population (see hybrid sterility \textsuperscript{PAGE}).

This separation is mostly geographic i.e. allopatric, peripatric or parapatric, or in some instances, such as the case of polyploidy in \textit{Xenopus laevis}, species can diverge in the same place – this is sympatric speciation. Darwin did not attribute much significance to the role that isolation could play in speciation before Jenkin’s criticism. In all the previous editions of the \textit{Origin} Darwin regarded isolation as a useful situation for speciation rather than a condition for it.

However, before publication of the Fifth Edition, Jenkin’s criticism was not the only one to force Darwin to rethink his ideas regarding isolation. The German naturalist Moritz Wagner had been greatly impressed by the blending arguments against Darwin’s theory\textsuperscript{126}. Wagner concluded that isolation must be the only solution to the problem of swamping. On March 7\textsuperscript{th} 1868 Wagner published his criticism of Darwin, proposing instead his ‘theory of separation’ (that assigned isolation its rightful importance in speciation). Darwin’s response to Wagner’s criticism in the Fifth Edition is as follows: “Isolation is an important element in the changes effected through natural selection. In a
confined or isolated area, if not very large, the organic and inorganic conditions of life will generally be almost uniform; so that natural selection will tend to modify all the varying individuals of the same species in the same manner. Intercrossing with the inhabitants of the surrounding districts will, also, be prevented. Moritz Wagner has lately published an interesting essay on this subject, and has shown that the service rendered by isolation in preventing crosses between newly formed varieties is probably greater even than I have supposed. But I can by no means agree with this naturalist, that migration and isolation are necessary for the formation of new species. The importance of isolation is likewise great in preventing, after any physical change in the conditions, such as of climate, elevation of the land, &c., the immigration of better adapted organisms; and thus new places in the natural economy of the district are left open for the old inhabitants to struggle for and become adapted to. Isolation will give time for a new variety to be slowly improved; and this may sometimes be of importance in the production of new species. If, however, an isolated area be very small, either from being surrounded by barriers, or from having very peculiar physical conditions, the total number of the inhabitants will be small; and this will retard the production of new species through natural selection, by decreasing the chances of the appearance of favourable individual differences. Darwin claims that if there exists a small isolated population then the probability of an individual favoured by natural selection occurring is low. Modern studies of populations tend to consider the whole population of a species rather than isolated groups. Based upon this view it is easy to see why Darwin was wrong – variations have no lesser chance of occurring if the population is segregated rather than in one place.

Mendel and the Swamping Effect

As for Jenkin’s second major objection, you will remember he criticised natural selection on the basis that; saltation could not effect speciation because of the drastic, and therefore lethal (or sterilizing), changes that would result. He then claimed that; if a less drastically anomalous ‘sport’ (read mutation) occurred that was advantageous, blending this trait with the rest of the population would diminish its influence by one half each generation, the
belief at the time was that offspring were a mixture of their parent’s traits. Darwin responded to this by laying stress on the conditions of life as a cause of variation, this provided a mechanism by which multiple individuals could acquire the same modification (because they inhabit the same environment). This Lamarckian view was consistent with his theory of *Pangenesis* – in which each parental cell supposedly had a ‘vote’ in the construction of the offspring via ‘buds’ that he termed ‘gemmules’. So the modifications to the individual resulting from the conditions of life (including use / disuse of organs) could be inherited by the progeny. Variation was caused by the mixing (or blending) of the parent’s gemmules in sexual reproduction; further variation could be effected by the disturbing influence of a changed environment on the reproductive system, by ‘reproductive system’ Darwin is referring here to the totality of the mechanisms involved producing young. In his Lamarckian view, Darwin was incorrect; with the advent of genetics, it is easy to see why the inheritance of acquired characteristics is impossible, although current research seems to indicate that certain specific aspects of the immune system acquired in life may be heritable, but I digress, the fact is that there is no mechanism to ‘translate’ the variations acquired in life into genetic code and include that code into the genome. In fact, we now know that, all the female ova are set aside at birth. So what was going on, if it was not, as Darwin proposed, the environmental conditions modifying several individuals simultaneously? The answer lies with Czech monk Gregor Mendel. Despite many accounts that portrayed Mendel as a simple but observant provincial monk, Mendel was a trained scientist, he had a degree in maths and physics from the University of Vienna and the monastery at Brno where he lived was a learned institution with a library of over twenty thousand books. During his eight year long study, accompanied by his two assigned helpers; Mendel repeatedly bred and cross-bred hybrids from thirty thousand pea plants. By choosing a very distinct variation, namely, height (in his pea plant variety), Mendel showed that tall crossed with short always resulted in tall offspring, upon breeding these hybrids he observed a one in four chance of a short plant produced. What he established was that every seed contained two ‘factors’ or *Elemente* as he called them – a dominant and a recessive one, and that these factors when combined, produced predictable patterns of
inheritance. He proved that we don’t blend our inheritance from our two parents. We receive our inheritance in discrete particles. As far as each particle is concerned, we either inherit it or we don’t. R. A. Fisher pointed out that the fact of particulate inheritance has always been staring us in the face, every time we think about sex. He claimed that: we inherit attributes from a male and female parent, but each of us is either male or female, not hermaphrodite\textsuperscript{108}.

So Jenkin was wrong because of the very limited knowledge of genetics at the time – blending inheritance would render evolution by natural selection impossible (without isolation) but blending inheritance is a flawed concept. Darwin was wrong to deduce that acquired characteristics results in further variation but right in his supposition that some sort of isolation was needed to effect speciation (in most cases).

\begin{quote}
Unconscious Selection
\end{quote}

The alternative theory Darwin proposed in response to the blending argument came in the First Edition, it was the idea of unconscious selection. The theory is based upon the axiom that: the individuals best adapted for life will pass on their successful genes and blend them with the rest of the population thus resulting in the ‘unconscious’ modification of the whole species. Darwin describes the idea as being similar to artificial selection in which the farmer chooses the best animals to breed. While we know this to be true today, we also know that it is not enough, in itself, to cause speciation; some form of isolation is needed. Darwin did not change his idea regarding unconscious selection between the editions; he merely laid more stress on the theory in response to Jenkin’s criticism.

From the evidence presented, it may be pertinent to assume that Jenkin’s criticism was responsible for Darwin’s changing ideas, but was this the case?

Garrett Hardin describes the impact of Jenkin’s criticism on Darwin’s theory: “Jenkin had put his finger on a critically weak point in Darwinian theory – its dependence on a mistaken theory of heredity. The unanswerableness of the criticisms led Darwin to make one of the strangest about-faces in the progress
of science. Darwin, a long-time anti-Lamarckian, became an unwilling and unavowed convert. Despite the numerous commentators that share Hardin’s view; Vorzimmer (1972) disagrees, proposing that: “There is no “turning point” in Darwin’s evolutionary thought.” Vorzimmer goes on to say: “studying the post-Origin period, one sees that these assumptions are incorrect; for all these historical deductions hinge upon a mistaken impression of the nature of Darwin’s post-Origin “change”…What unrolls before us in the twenty-three years after the Origin is a gradual but progressive modification. Vorzimmer also implies that Darwin started to modify the Origin before the First Edition had gone on sale and that “the seeds of nearly all the significant changes can be seen in the first edition.” Sure enough, we find plenty of quotes to support this hypothesis in the First Edition: “Some slight amount of change may, I think, be attributed to the direct action of the conditions of life – as in some cases, increased size from amount of food, colour from particular kinds of food and from light, and perhaps the thickness of fur from climate.” However, Darwin remained extremely doubtful about the amount of change that could be effected by direct action: “Instances could be given of the same variety being produced under conditions of life as different as can well be conceived; and, on the other hand, of different varities being produced from the same species under the same conditions.” In the First Edition Darwin recognised both modes of environmental action, he inclined toward indirect action as the most frequent cause of the two.

Loren Eiseley implied, in his 1958 work Darwin’s Century: Evolution and the men who discovered it, that Jenkin’s review destroyed Darwin’s confidence in the selection theory and led him to abandon it in favour of Lamarckism. There is no evidence, however, to support the theory that Darwin ‘abandoned’ natural selection. Vorzimmer maintains that the timing of Jenkins review is coincidental to the subsequent changes in the Fifth Edition of the Origin. I believe that the answer lies between the two – Jenkin forced Darwin to think seriously about the mechanism of natural selection, whereupon he incorrectly laid stress on the inheritance of acquired characteristics (in the absence of Mendelian genetics). I do not believe that the changes following shortly after
the review are coincidence; nor do I believe that the review caused Darwin to ‘abandon natural selection’.

The Age of the Earth

The leading physicist of the day, William Thompson (later known as Lord Kelvin – the title was bestowed upon him in honour of his achievements, and named after the River Kelvin, which flowed past his university in Glasgow), was disturbed by the religious implications of Darwin’s theory. Kelvin was an old friend of Fleeming Jenkin (they met in 1859 during work on the Atlantic cable – Thompson a physicist with an interest in engineering and Jenkin an engineer with an interest in physics), he agreed with Jenkin’s idea of blending inheritance resulting in the swamping of advantageous traits but Kelvin’s criticism did not doubt the biological process of natural selection, it was instead a more fundamental and damaging objection based upon his recent calculation of the age of the earth. His work on thermodynamics offered an indirect way of attacking Darwin because it could be used to undermine Lyell’s estimates for the vast age of the earth on which Darwin’s theory depended. Darwin assumed natural selection was an immensely slow process, he therefore required a long timescale for his theory of evolution. You will recall, in the First and Second Editions of the *Origin*; Darwin included an estimate of the length of time required for the denudation of the Weald of Kent based upon erosion rates. The estimate was inspired by Lyell’s steady state view of earth history. Kelvin believed that the laws of thermodynamics operated from the start of the universe and envisaged a dynamic process that saw the organisation and evolution of the solar system and other structures, followed by gradual “heat death”. He developed the view that the Earth had once been too hot to support life and combined this with his view of gradualism (that conditions had remained constant since the indefinite past) to come to the conclusion that “This earth, certainly a moderate number of millions of years ago, was a red-hot globe”. Using his concept of the conservation of energy, Kelvin knew that the earth must be cooling down – it could not maintain itself in a geologically active state indefinitely. Kelvin then estimated the time it would take for the planet to cool from a molten state, concluding that the total age might only be one
hundred million years. This clear contradiction of Lyell’s theory of the geological formation of the earth, on which Darwin’s theory of natural selection relied, drew Kelvin into public disagreement with Darwin's supporters John Tyndall and Thomas Huxley. In his response to Huxley’s address to the Geological Society in London in 1868 Lord Kelvin presented his address “Of Geological Dynamics” in 1869 which set back the scientific acceptance that the earth must be of very great age. Darwin’s responds to the threat to his theory directly, by adding this passage into the Fifth Edition: “before the lowest Silurian or Cambrian stratum was deposited long periods elapsed, as long as, or probably far longer than, the whole interval from the Cambrian age to the present day; and that during these vast periods the world swarmed with living creatures. Here we encounter a formidable objection; for it seems doubtful whether the earth in a fit state for the habitation of living creatures has lasted long enough. Sir W. Thompson concludes that the consolidation of the crust can hardly have occurred less than 20 or more than 400 million years ago, but probably not less than 98 or more than 200 million years. These very wide limits show how doubtful the data are; and other elements may have to be introduced into the problem.72 Darwin discredits Lord Kelvin’s data on the basis that they are too wide ranging, despite this objection to Kelvin’s calculations; Darwin was seriously worried by the growing impact of Kelvin’s attack for the rest of his life.73 However, Darwin suspected that Kelvin’s calculations would turn out to be erroneous.74 The last point made in the above paragraph is interesting – Darwin infers that he believes ‘other elements’ are responsible; if he (and Kelvin) had lived slightly longer they would have seen Darwin proven right. In 1896 the French chemist Henri Becquerel discovered radioactivity. In 1898, two other French researchers, Marie and Pierre Curie, discovered the radioactive elements polonium and radium. Geologists quickly realized that the discovery of radioactivity upset the assumptions on which most calculations of the age of the earth were based. Kelvin’s calculations assumed that the Earth and Sun had been created at some time in the past and had been steadily cooling since that time. George Darwin (Charles’ second son), in 1903, was one of the first to discover that radioactivity provided a process that generated heat. Today’s accepted age of the Earth of 4.567 billion years was determined by
Clair Patterson using Uranium-Lead dating on fragments of the Canyon Diablo meteorite and published in 1956. The current estimate for the age of life on this planet is 3.5 billion years. When faced with this inconceivably immense timescale, it is hard to argue against natural selection on the basis that it is too slow to have acted in the 3,500,000 millennia during which the earth has supported life.

The Sixth Edition

On the 31\textsuperscript{st} of March 1872 the sixth and final edition was published. The very first observable difference is the omission if the word “On” from the title, which, to this day reads: *The Origin of Species by means of natural selection, or the preservation of favoured races in the struggle for life* (although almost ubiquitously simply referred to as simply *The Origin of Species*). The ideas put forward in this edition marks Darwin’s final standpoint regarding the theory of the *Origin of Species*.

*Inheritance of Acquired Characteristics*

In the three years since the Fifth Edition, Darwin did not change his mind about the importance of acquired variation. In the Sixth Edition he increases the importance of the inheritance of acquired characteristics, one of the additions to corroborate this point simply states: “Changed habits produce an inherited effect”\textsuperscript{16}. Also, newly added in the Sixth Edition, Darwin categorically states that acquired variation is important as an alternative to
natural selection: “variability in many cases, be the simple result of the nature of the organism and of the different physical conditions to which it has long been exposed; but with respect to the more important and adaptive characters, the passage from one stage of difference to another, may be safely attributed to the cumulative action of natural selection, hereafter to be explained, and to the effects of the increased use or disuse of parts”117.

The Age of the Earth
Despite Darwin’s dismissal of Lord Kelvin’s calculation of the age of the earth as being too wide ranging in the Fifth Edition, in the Sixth Edition Darwin gives in to the mounting pressure of Kelvin and his supporters. He includes a compensatory statement, to allow for the great amount of modification which must therefore take place in a shorter time span76: “It is, however, probable, as Sir William Thompson insists, that the world at a very early period was subjected to more rapid and violent changes in its physical conditions than those now occurring; and such changes would have tended to induce changes at a corresponding rate in the organisms which then existed”77. Darwin’s argument is based upon the axiom: the earth underwent more rapid and violent changes therefore evolution occurred at a faster rate. This explanation is very much a shoehorning of Darwin’s idea to make it fit in with Kelvin’s estimation of a much younger earth. In my opinion, Darwin is assuming natural selection to be fact in his defence of natural selection i.e. he is saying; since we know natural selection has occurred and that we now know the world is not as old as first thought; natural selection must have occurred at a greater rate. Despite Darwin’s dubious defence of his theory; modern day calculations resolve the dispute between Darwin and Kelvin, setting the age of the earth at over 4.5 billion years supports Darwin’s theory (which is consistent with Lyell’s view of uniformitarianism).
The Incipient Stages of Useful Structures

In 1871, English biologist George Jackson Mivart (initially a supporter of natural selection) published a collection of objections against Darwin’s theory in a work entitled *Genesis of Species*. Darwin describes the situation in the Sixth Edition as follows: “A distinguished zoologist, Mr. St. George Mivart, has recently collected all the objections which have ever been advanced by myself and others against the theory of natural selection, as propounded by Mr. Wallace and myself, and has illustrated them with admirable art and force. When thus marshalled, they make a formidable array.” Many attributed the force and clarity of Mivart’s criticism to his previous legal training. It is evident that Darwin took Mivart’s criticisms seriously by the fact that he devoted over thirteen thousand words (even longer than this dissertation) of the chapter he entitled Miscellaneous Objections to the Theory of Natural Selection, to the refutation of Mivart’s criticism. Mivart’s most famous criticism and the one that arguably did most to discredit Darwinian evolution in his lifetime (and after) states: “that natural selection is incompetent to account for the incipient stages of useful structures.” Darwin describes this criticism as “The one new point which appears to have struck many readers.” Darwin then goes on to present many examples to counter those put forward by Mivart. For the most part the counter took the form of laying stress on previous premises: “I have collected a greater number of well-established cases than can be found in any other work known to me. My judgment may not be trustworthy, but after reading with care Mr. Mivart’s book, and comparing each section with what I have said on the same head, I never before felt so strongly convinced of the general truth of the conclusions here arrived at, subject, of course, in so intricate a subject, to much partial error.” An example of such a ‘case’ is Darwin’s address of Mivart’s scepticism of natural selection as an adequate mechanism to explain the incipient stages of the evolution of the fine detailing of insects that mimic inanimate objects to avoid predators: “I cannot see any force in Mr. Mivart’s difficulty with respect to “the last touches of perfection in
the mimicry;” as in the case given by Mr. Wallace, of a walking stick insect (*Ceroxylus laceratus*), which resembles “a stick grown over by a creeping moss or jungermannia.” So close was this resemblance, that a native Dyak maintained that the foliaceous excrescences were really moss. Insects are preyed on by birds and other enemies, whose sight is probably sharper than ours, and every grade in resemblance which aided an insect to escape notice or detection, would tend towards its preservation; and the more perfect the resemblance so much the better for the insect.

Although Darwin recognised the force of Mivart’s argument, it did little to change his ideas.

We now believe Darwin to be right in his insistence that intermediate structures confer some sort of use and that the variation is not ‘seeking to evolve’ into the structure it ultimately becomes.

A favourite example of evolutionists today to support this theory is the African black heron *Egretta ardesiaca*. The African black heron is a wading bird with well developed wings, perfectly capable of flight buts its wings more commonly serve a different purpose; the heron uses them as a sun shade over the water in order to better observe its prey, namely fish and tadpoles (see Figure 4.).

*Figure 4. The African black heron, Egretta ardesiaca*
Figure 4. Photograph of the African black heron taken in The Gambia portraying the heron’s primary use of its wings as a sun shade

Flight has become the wings secondary function. The argument is that many species ‘make do’ with existing structures for a different purpose and that, if most other birds should become extinct, people may look at the black heron and conclude that flight was a stage in the evolution of its ‘sun shades’. People believe that feathers may have originally evolved as a form of heat insulation and that the species they belonged to spent much of its time in the trees, the individuals with more developed feathers could jump slightly further to the next tree etc until the possibility of flight was realised. Never that the feather evolved with a view to becoming a wing in millions of years to come.

Post Sixth Edition

The Sixth Edition was the last revised edition but it did not mark the end of publication of the Origin, a run of 2000 copies was commissioned less than a year later and the Origin of Species has never since been out of print. It was translated into Danish, Dutch, French, German, Italian, Polish, Russian and Swedish in Darwin’s lifetime and into ten further languages since.

The criticisms continued after publication and Darwin’s supporters continued to argue in favour of evolution by natural selection but the Sixth Edition marked Darwin’s final standpoint.

Darwin continued to work on the theory as well as his other avenues of interest; alongside the six editions of the Origin of Species he published dozens of other books and articles, the most influential of these being The Descent of Man.

Charles Darwin died at Downe House on the 19th of April 1882. He had expected to be buried in St Mary’s churchyard at Downe, but at the request of Darwin’s colleagues, William Spottiswoode (President of the Royal Society) arranged for Darwin to be given a state funeral and buried in Westminster Abbey, close to Isaac Newton.
Conclusions

The Origin of Species was Charles Darwin’s life’s work; it took him 23 years to develop before publication. The volume proposed a theoretical mechanism to account for the evolution of specific forms. The mechanism was natural selection. The Origin also contained all the evidence to support the theory that Darwin had collected during his voyage on the Beagle and his subsequent studies on domestic organisms. Many corroborating examples from other biologists were included, especially in later editions. Darwin developed his ideas mostly in secret before publication, only revealing them to his closest professional friends Charles Lyell and Joseph Hooker. We can observe how Darwin’s ideas developed following publication of the First Edition because he subsequently published five more editions each containing revisions.

When Darwin’s theory went public, it received considerable criticism from some of the greatest scientists of the age, along with many criticisms on religious grounds.

The Second Edition was revised only slightly, mainly published to meet the demand for the book and because Darwin wished to alter aspects of the language and punctuation. All of the following editions, from three to six, contained sections detailing recent critiques of the theory and proposing counter arguments.

Some of the criticisms Darwin received resulted from professional envy and had little grounding in scientific fact, such as Richard Owen’s article in the Edinburgh Review. Many were based upon religious grounds such as Robert FitzRoy’s exclamation at the British Association for the Advancement of Science in 1860. However, much of the criticism was scientific, and some of it very damaging to public and scientific acceptance of the theory both during Darwin’s lifetime and up to the present day.
By modern understanding, Darwin was rightfully opposed to the theory of saltationism as a cause of speciation. He was also right to suspect that Lord Kelvin’s calculation of the age of the earth would turn out to be incorrect. Another major source of criticism was the lack of intermediate types in the fossil record. Darwin attributed the gaps to the imperfection of the fossil record and assumed that they would be filled following future discoveries. This has yet to happen. However, we do not believe that Darwin was wholly incorrect; we believe that the staccato fossil record is a true representation of events as explained by the theory of punctuated equilibrium.

Darwin was yet to concede and change his theory in response to the arguments of his critics. This might have remained the case had it not been for Fleeming Jenkin’s published review of the Fourth Edition.

In the editions prior to the review, Darwin considered that indirect variation was more important in modification than the inheritance of acquired characteristics and that isolation was not necessary for speciation. He was right in his first consideration but incorrect in his second; we now believe that acquired characters are not heritable and that some form of isolation is needed to effect speciation. Darwin did not vehemently insist these points. In the First Edition, he conceded that natural selection “has been the main but not the exclusive means of modification.” He also never believed that the effects of isolation on speciation were negligible; he simply believed isolation to be a favourable scenario rather than a condition for speciation.

Fleeming Jenkin’s criticism was two fold: first he claimed that natural selection could ‘improve a species about a fixed point’ but could not result in speciation, he then claimed that, should a saltation arise that was both fertile and better adapted to the environment, blending inheritance would ‘dilute’ the fortuitous trait within the population.

The arguments Darwin used to overcome the issues raised by Jenkin were as follows: he laid greater stress on the conditions of life acting to cause variety in organisms and that these variations could be inherited. In this way, he concluded, many individuals could become modified in the same manor and therefore negate the nullifying effects of blending. It is important to remember
that blending inheritance was the accepted mechanism of heredity in the Victorian Era and was not a creation of Fleeming Jenkin. If the significance of Mendelian genetics was realised at the time, then Jenkin’s argument would have been invalid, as Mendel was the first to prove that ‘hereditary particles’ (genes) were inherited in discrete units and were not blended together. The other argument Darwin proposed was that isolation could keep populations of the same species separate until they had independently evolved to a point were they were no longer the same species. We believe Darwin to be correct in this proposition. However, Darwin did not commit fully to the idea, claiming (in the same edition) that the segregation of a population would result in a lower probability of fortunate adaptations.

Jenkin’s criticism was the only one that caused Darwin to significantly develop his ideas. The absence of the science of genetics caused Darwin to come to the wrong conclusion regarding the inheritance of acquired characteristics. Many people claim that Jenkin’s criticism caused Darwin to admit that natural selection was incorrect in favour of Lamarckism. I believe that Jenkin forced Darwin to rethink his ideas regarding natural selection, eventually attributing greater significance to Lamarckian principles.

Despite the changes Darwin made to his theory in the latter editions, his ideas are still considered the foundation of modern biology when integrated with the science of genetics. Never originally conceived as a complete theory, developed in response to contemporary criticism and integrated into modern science; Darwin’s ideas “have been, and are being, evolved”\textsuperscript{123}.
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### Appendix – Additions and Corrections

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On deposition during subsidence partially modified—On the complete denudation of all the formations which must once have covered granitic areas.

On the slight modifications which the latest tertiary forms have apparently undergone.

On the nature of the links between past and present species, which geology has, and has not, revealed.

On early transitional links.

Case of fossil footsteps of birds in the United States, added in second edition in place of that of the whale, which is doubtful.

On the fallacy of great size or strength saving an animal from extinction.

On the degree of development of living forms compared with ancient forms, amplified.

Additional facts on former glacial action in the Cordillera of S. America.

On crossing keeping the birds of Madeira and Bermuda unmodified, added in second edition.

Passage added on the authority of Von Baer on the embryonic similarity of Vertebrate animals.

Distinction between nascent and rudimentary organs, indicated in the second edition.

On the theological bearing of the general argument, added in second and present editions.

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<td>The whole discussion on embryology and development has been considerably enlarged, chiefly from the writings of Fritz Müller and Sir J. Lubbock.</td>
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<td>xvii</td>
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<td>The account of Professor Owens views on Species corrected.</td>
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<td>Fritz Müller on the lancelet not competing with higher fishes.</td>
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<td>The views of Bronn and Nägeli on characters which are important under a morphological point of view, but are unimportant physiologically, not being acted on through natural selection.</td>
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<td>Additional cases of plants, which can be crossed by a distinct species, but are impotent with pollen from the same individual plant.</td>
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<td>331</td>
<td>Discussion on dimorphic and trimorphic plants corrected.</td>
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<td>327</td>
<td>333</td>
<td>Conclusions on the fertility of varieties when crossed, in contrast with species, corrected.</td>
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<td>330</td>
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<td>Infertility of varieties of Verbascum when crossed.</td>
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<td>On the rate of subaerial denudation, as measured by years, and on the probable rate of change of species.</td>
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<td>Absence of organic remains in certain great sedimentary formations</td>
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<td>Intermediate varieties within the same formation.</td>
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<td>On a monocotyledonous plant in the Cambrian formation.</td>
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<td>394</td>
<td>402</td>
<td>Gandry, Professor, on the intermediate character of the fossil mammals of Attica; and Professor Huxley on the connecting forms between birds and reptiles.</td>
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<td>Günther, Dr., on the large proportion of fishes in common on opposite sides of the isthmus of Panama.</td>
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<td>On a living seed in earth attached to a woodcocks leg.</td>
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<td>442</td>
<td>451 – 461</td>
<td>Mr. Croll on the alternate Glacial periods of the northern and southern hemispheres; and the bearing of this conclusion on geographical distribution.</td>
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Professor Häcked on phylogeny, or the lines of descent of all organic beings.

The whole discussion on embryology corrected, in small details.

Mr. G. H. Lewes on the functionless structure of the larva, of Salamandra atra. The whole discussion on rudimentary organs has been slightly modified.

Professor Weismann on the futility of the idea that rudiments complete the scheme of nature.

On the question whether one or many forms of life first appeared.
Influence of fortuitous destruction on natural selection.

On the convergence of specific forms.

Account of the Ground-Woodpecker of La Plata modified.

On the modification of the eye.

Transitions through the acceleration or retardation of the period of reproduction.

The account of the electric organ of fishes added to.

Analogical resemblance between the eyes of Cephalopods and Vertebrates.

Claparède on the analogical resemblance of the hair-claspers of the Acaridae.

The probable use of the rattle to the Rattle-snake.

Helmholtz on the imperfection of the human eye.

The first part of this new chapter consists of portions, in a much modified state, taken from chap. iv. of the former editions. The latter and larger part is new, and relates chiefly to the supposed incompetency of natural selection to account for the incipient stages of useful structures. There is also a discussion on the causes which prevent in many cases the acquisition through natural selection of useful structures. Lastly reasons are given for disbelieving in great and sudden modifications Gradations of character, often accompanied by changes of function, are likewise here incidentally considered.

The statement with respect to young cuckoos ejecting their foster-brothers confirmed.

On the cuckoo-like habits of the Molothrus.
68

307  240  On fertile hybrid moths.
The discussion on the fertility of hybrids not having been acquired through natural selection condensed and modified.

319  248  On the causes of sterility of hybrids, added to and corrected.

326  252  Pyrgoma found in the chalk.

377  284  Extinct forms serving to connect existing groups.

402  301  On earth adhering to the feet of migratory birds.

440  328  On the wide geographical range of a species of Galaxias, a fresh-water fish.

463  343  Discussion on analogical resemblances, enlarged and modified.

505  373  Homological structure of the feet of certain marsupial animals

516  382  On serial homologies, corrected.

518  384  Mr. E. Ray Lankester on morphology.

520  385  On the asexual reproduction of Chironomus.

521  387  On the origin of rudimentary parts, corrected.

541  401  Recapitulation on the absence of fossils beneath the Cambrian system, corrected.

552  409  Natural selection not the exclusive agency in the modification of species, as always maintained in this work.

568  421  The belief in the separate creation of species generally held by naturalists, until a recent period.