Natural Selection and Natural Processes: a philosophical examination of the processes of evolution

Colin Beckley (2012)

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Colin Beckley

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# Abstract

This thesis concerns evolution and how it is explained. The ambition here is to identify clearly the many aspects of evolution, and to evaluate past and present explanations of evolution for their coherence and validity. Historically natural selection has been taken to be the central and main explanans, with other explanations playing lesser roles. Here it will be argued that the sheer complexity and diversity within nature cannot be accounted for by any single explanatory mechanism and that a plurality of explanatory mechanisms is required. Loading natural selection with the main weight of explanation is an overburden which, far from strengthening its explanatory powers, actually renders it vacuous. A critical historical and philosophical examination of the concept of natural selection reveals that it has never received a formal scientific definition that commands universal respect. This has created a problem of demarcation between that which natural selection can legitimately be said to explain and that which it cannot. In fact, the ontology of natural selection is equivocal, giving rise to the many controversies that have plagued evolutionary biology. The disambiguation of the concept of natural selection is the principle aim of this thesis and guidelines on how this should be accomplished are provided. However, should these reforming guidelines fail to achieve a consensus then a more radical alternative is proposed. It is recommended that the selective terminology is replaced with the less anomalous and demanding principle of 'meeting the conditions of existence'. Moreover, talk of the evolution and origins by means of natural selection is to be replaced by talk of evolution and origins by means of natural processes. Finally, drawing from a 'Structuralist' alternative, it will be demonstrated that biological evolution should not be divorced from general or cosmological evolution. Rather, elucidation should be drawn more deeply from the fields of physics, chemistry, mathematics and topology, without the use of selection-tinted spectacles.

# Introduction

Within evolutionary biology and the accompanying theoretical and philosophical literature, there are several unresolved and contentious issues, none more so than those that arise from the use of the concept of natural selection. The main issue here is that the term covers too many different relationships and that little, if anything, is ruled out. Natural Selection was seen originally as an important distinction to theological explanation but it is identified here that we have outgrown the early concept. There are today so many uses ranging from early 'Malthusian natural selection', to 'positive selection', to 'negative selection' to 'balancing selection' and, far from least but most anomalously, to 'lifted or relaxed selection'. With such wide contrariness one must question the heuristic value of the concept and whether the application of natural selection or 'selection' is little more than a linguistic tick. Boundaries and parameters do matter and not exclusively for scientific purposes. During the 1920s, 1930s and 1940s natural selection was inappropriately applied to justify some obnoxious eugenic and socially racialist politics. It is justifiable and easy to condemn these applications as they transcended the intended usage. Unfortunately it is far less easy to provide clear barriers to indicate the proper application of natural selection. I will argue here, in the context of science, that if the concept of natural selection cannot be clearly defined with appropriate parameters then it is advisable to talk directly and more specifically of natural processes. The purpose of this thesis is to demonstrate that these issues can be resolved by some fairly simple changes to both the terminology currently employed and the expectations of the theorist. These changes will enable evolutionary theory to be perceived with more clarity, avoiding many of the philosophical pitfalls. To achieve this, the issues will be identified and examined critically but with a view to resolution that does not compromise evolutionary theory.

Arguably, natural selection has been perceived as the classical explanation of evolutionary change, with other explanations playing lesser roles. However, this is not without problem. My original ambition was to provide natural selection with a definition that was clear and precise, thus avoiding many of the controversies, paradoxes and problems that have afflicted evolutionary theory. This has proved elusive. The main problem is that if one tightens the definition of natural selection then one loses a great deal of explanatory power. On the other hand, if one generalises the definition then one has the spectre of tautology, untestability and vacuity, with natural selection looking synonymous with evolution. And yet, all is not lost. There is a solution to the dilemma: there are many underlying naturalistic processes that can explain why evolution occurs. These will be explored and argued for. Furthermore, it will be demonstrated that this approach is easy to articulate and follow in principle, avoiding many of the controversies and problems that emanate from the application of natural selection.

In short the thesis will proceed in the following manner:

First, I will demonstrate that there is a range of serious problems relating to Natural Selection. Then I will disambiguate the concept of Natural Selection, historically and ontologically. I will then consider

‘Structuralism’ as an alternative source of explanatory mechanisms. In the light of the foregoing I will then make two recommendations.

Namely, one ought either to

a) Recognise that there are no less than six distinct senses of Natural Selection to be found in the literature, and that each sense has it explanatory strengths and weaknesses.

or if failing then

b)
Replace the terminology of Natural Selection altogether with the terminology of ‘Natural processes’, and ‘conditions of existence’.

I call the first recommendation ‘reform’ and the second, stronger, recommendation ‘radical revision’.

## The Main Problems with Natural Selection

Since Darwin coined the term ‘natural selection’ in 1858, there has been continued controversy up to the present day. The originators, Darwin and Wallace, could not agree over the concept’s explanatory scope and the teleology implicit in the term ‘selection’ (See Ch.1). The problem of the relationship between ‘drift’ and ‘natural selection’ is still present and as controversial as it was when Nageli first identified it almost 150 years ago (See Ch.1 & Ch.2). The problems of vacuity, circularity and testability surface frequently in the literature and still require resolution. An unseemly and bitter dispute reared its ugly head during the 1970s concerning the application of natural selection, referred to as the ‘levels or units of selection debate’ (Rose & Rose 2000, Segerstrale 2000, Sterelny 2007). The ferocity of this debate has dampened somewhat but the issues remain unresolved. The aforesaid are the internal debates of the paradigm concerning natural selection but these are not the only problems. External to the paradigm, other evolutionists are concerned with issues of constraints, convergence and tensegrity and postulate a more deterministic structuralist approach that is seemingly not easy to reconcile with natural selection (Bejan and Lorente 2010, Goodwin and Webster 2011, Ingber 2011, Scarr 2012). This is not a new consideration but it has a growing number of adherents, also reflected in the recent literature. Finally, one must not forget the inappropriate use of natural selection to justify some rather suspicious eugenic, economic and socio-political agendas (Gasman 1971, Gillette, 2007). Dennett’s (1995) approving description of natural selection as a universal acid is, arguably, also of deep concern to many who perceive such an export as undesirable.

### Ambiguity

It will be argued here that much of the confusion emanates from the fact there is no clear and precise scientific definition of natural selection. For example, physicists achieve such a definition for the electromagnetic strong and weak forces (or more precisely interactions), which can be understood using clear parameters (Close et al 1986). If there is a comparison with natural selection then the second law of thermodynamics is more akin, with over 20 different definitions in current usage (Lockwood 2005). What began as a metaphor, as Darwin admitted, later translated into a scientific principle, or one should say a variety of principles, not all of them pertaining to science. It is often difficult to ascertain which species of ‘natural selection’ is being alluded to by proponents. Part of the key to this problem is an appreciation not only of how the concept has evolved into new variations but also that the old concepts of natural selection are retained and routinely employed. It is not simply that natural selection has changed meaning; it is that new meanings have been added. The term ‘selection’ now has so many contrary connotations that without reform or guiding criteria forthcoming it can be charged as meaningless. This is the most serious problem facing neo-Darwinism and the philosophers who endorse it. It will be argued here that unless terms such as ‘natural selection’ and ‘selection’ can be disambiguated then the terms should be replaced.

The historical explication discloses that the concept of natural selection had its origins prior to the coining of the term by Darwin and the formalisation of the evolutionary theory together with Wallace in 1858. What is of interest here is that the concept of advantaged traits spreading gradually through and increasing in number in a population was considered by several naturalists and was thought to be uncontroversial. It was widely accepted that members of species could manifest diverse morphologies, but it was not perceived that continuous diversification would eventually result in transmutation. It was Darwin and Wallace who extended this early concept of natural selection to account for speciation, breaking the chains of Linnaean fixity. Both men came to the same conclusion that Malthusian principles of competition for resources would identify the process of evolutionary change that resulted not only in such morphological diversity but also in the arrival of new species and the extinction of old. It was the latter two conjectures that proved controversial.

After the ‘eclipse of Darwinism’, (Huxley 1942) another variant to natural selection was added by the architects of the modern synthesis. The term ‘survival of the fittest’ was dropped for its perceived crudity, in favour of a more generalised concept of fitness. This, too, added not only plurality but also another layer of ambiguity, for now the fitness concept seemed to lack a scientific definition with any consensus. Further, it is unclear whether natural selection in the Malthusian sense was replaced by the new concept of fitness or whether both enjoy separate identities. Another ambiguity, which largely arises from the aforesaid, is whether natural selection is a positive causal process or whether it is a filter that is causally negative, merely conserving and eliminating. Then again, could natural selection be biologically omnipotent – causal, conservative and eliminative? Each of these alternatives carries a cost, all of which will be explored more fully.

The problem of finding an appropriate and acceptable singular definition of natural selection has produced a further problem, one of address. Which aspects of evolution is natural selection addressing? This problem can be most easily perceived through the historical exposition. Darwin had very clear views upon this: natural selection was one process amongst many, albeit the main process of evolutionary change. All processes, whether sexual selection, Lamarckian use, disuse and habit, correlation of growth, or the direct impact of the environment, were independent of natural selection (Appendix 1). Wallace, on the other hand, considered natural selection sufficient (Ch.1). Both men thought natural selection addressed the gradual accumulating diversity of life but also, most importantly and most controversially at the time, the advent of new species. Many twentieth-century biologists and philosophers, however, arguably shifted emphasis and focused attention upon the explanation of biological adaptation, with speciation a subject of secondary consideration. The most curious spectacle now emerging is that evolutionary change is said by some to be most likely to occur when natural selection is ‘relaxed’ or ‘lifted’ (Bell 2008, Deacon 2008), a perspective in direct opposition and contrast to the perspective of Darwin and Wallace. The underlying threat is apparent: such an assortment of contrary and contradictory explanations devalues what was originally a genuine attempt to afford a naturalistic account of evolution.

### Overextension

The generalisation of the principle of natural selection to one of reproductive success by whatever means has facilitated the logical extension of the principle to other disciplines. The universal acid, welcomed by Dennett (1995), is not entirely well received. Applying principles of generalised natural selection to such fields as cosmology, mineralogy and evolutionary psychology, it will be argued, does nothing to aid explanation in these fields and ignites the familiar charges of vacuity, circularity and untestability (Ch.5).

### Natural Selection and Evolution: The Differences

It will be argued that natural selection was originally conceived to explain how evolutionary changes or transmutations came about. The problem today is that natural selection has slowly transformed into ‘anomalous selection’. By this it is meant that the term ‘natural selection’ has over the years deviated from its original conceptions, increasing in ambiguity. Anomalous selection in turn has facilitated, in some quarters, the idea that natural selection is synonymous with evolution (See Ch.3). This again raises the charge of vacuity and hollowness to the theory. It will be argued that this can be resolved if one accepts that natural selection is only one aspect of evolutionary change amongst many. Clear parameters will therefore be sought and the distinction between the explanandum (evolution) and the proposed explanans (natural selection) fully identified (Ch.11).

### The Problem of Causality and Emergence

There is no agreement over the aetiology of natural selection. This will be fleshed out in chapter 4. The pertinent problem is that if natural selection is said by the theory to act only on variation then how does one account for the initial variation? Further, if one has an account of initial variation then cannot one explain the great diversity of life with those same principles and without recourse to natural selection? The challenge therefore is that natural selection by its own definitions cannot explain the sources of variation; recourse to random mutation and modification through descent is insufficient. The implication is that there must already be in existence some body or form that can randomly mutate or descend with modifications, and therefore a theory of emergence is required to explain this. As Reid (2007) said, his students would claim that ‘if it existed then it was selected’, which he countered by saying, ‘to be selected it must first exist’. Reid has further argued that the causal chain of neo-Darwinism is in fact an inversion of what actually happens: differential reproduction is not the cause of evolution but the effect.

## The Levels of Selection

One issue that has perplexed the concept of natural selection since the term was originally coined has been the 'levels' or 'units' of selection debate. This has been a source of continuing contention for very many biologists and philosophers (see Lloyd 2010 for an excellent philosophical overview, also Okasha 2006, 2008). The issue is that if natural selection is a 'force' or 'pressure' that is responsible for evolutionary change, then at what biological level does it 'act'? For instance, does natural selection 'operate' on the individual organism, the gene, the group or all of these? Moreover, is natural selection 'dynamic', fluctuating between the different phenomena, sometimes 'acting' on the gene and sometimes 'acting' on the group, for example? One hundred and fifty years on and still there is little consensus. Much of the problem here, it will be argued, stems from anomalous selection and the excessive use of metaphoric language. Perceiving natural selection as a force or pressure that can act upon objects is not justified, at least if one intends to be scientific. Further, if there is a presumption that natural selection is either the only explanation of evolutionary change or at least the main explanation, then it will be argued any such presumption has still to be established.

## The Problem of Language and Teleology

Evolutionary biology, it must be conceded, is rife with anthropomorphic language, metaphor and obtuse teleology; much more so than any other science. The use of metaphor, for instance, adds a further layer of ambiguity to an already overambiguous field. This is particularly so when commentators are describing natural selection, which can be commonly a 'force', a 'pressure', a 'filter', but also as a 'driving engine' (Ridley 2003), both 'negative' and 'positive' (Neander 1995), as 'sorting' and as a 'mistress' (Gould 2002), as both strong and weak (Reiss 2009) a 'whip hand' (Sober 1993), as 'creative' (Gould 1977, Neander 1988, Godfrey – Smith 2009) as a 'tracker' (Lewontin 1978), a 'stabiliser'(Hull 2001) or an 'arbitrator'(Lovtrup 1974), a crane or as acid (Dennet 1995) and last but far from least, as a 'Blind Watchmaker'(Dawkins 1986). Metaphor can be employed as a legitimate tool of explanation, but only where more precise scientific vocabulary is unavailable, and it should certainly not be used in a willy-nilly manner. Examination will establish whether such terms as 'force' and 'pressure' in this context have scientific credentials or are merely metaphors masking vacuity. Charges of teleology have recently re-emerged; Reiss has argued that natural selection was devised to answer questions that accept the premise of design, 'that adaptedness is a problem crying out for explanation' (2009 p353). Cummins (2009) has further argued that functional explanations can also be guilty of what he calls 'neo-teleology'. However, it should be noted that Cummins is not critical of use of the term natural selection. Both Cummins and Reiss advance some vocabulary that will help reduce the charge of teleology; this deserves consideration and some additional suggestions will be delineated (Ch.12).

## The Problem of Adaptation

Issues concerning the nature of 'adaptation' have a vast and controversial literature in both theoretical biology and the philosophy of biology. Although this topic is not the main focus of this thesis, recent events have brought it alive, especially in regard to the role of natural selection. Reflection upon the famous 'Spandrels' paper (Gould and Lewontin 1979) has given rise to a new interpretation by Fodor and Piattelli-

Palmarini (2010). These two have argued that one can only distinguish counterfactually between adaptive traits and traits that ‘piggyback’. If this is the case, they argue, then natural selection becomes superfluous as it cannot ‘act’ upon counterfactuals. This interpretation has been challenged by Block and Kitcher (2010), who represent a wide body of opinion within the circles of neo-Darwinism. The debate raises issues of explanation alongside the problem of teleology already mentioned.

## Research Programmes and Censorship

The danger of confining one’s understanding of evolutionary change merely to factors of natural selection and adaptive reasoning is that other avenues of insightful research may be precluded. Arguably, evolution by means of natural selection is regarded by some of its supporters to be beyond that which should be questioned, and regretfully sometimes defended with a passion that spills over to almost religious fundamentalism (Stove 1995, Midgley 2003). It will be further argued that dissent is received with hostility or completely ignored, papers are rejected, grants are withheld, positions denied and, in one case, a sacking implemented for advancing the ideas of Lamarck. It is hardly surprising researchers impose self-censorship and that an unpleasant atmosphere ensues. It could be argued that much of this is fuelled by a great fear of creationist ‘science’ or the movement that advocates ‘intelligent design’. Moreover, the fear has resulted in a move to conformity that stultifies research rather than emancipating it. Examples of this narrowing perspective will be considered in the light of important omissions that arguably can strengthen evolutionary theory (Ch.13).

## Limitations to the Explanans and the Issue of Constraints

Contrary to Dennett, one persistent line of criticism that has been levelled against natural selection since the theory was formalised by Darwin and Wallace is that its explanatory power is overburdened. By taking on more than it can possibly hope to explain, the theory reduces with generalisations that are little more than platitudes and simplistic truisms. This charge, it will be argued, holds true if one adopts a fully selectionist explanans but not if one accepts evolutionary pluralism. Popper (1977) was one of the first to appreciate that many of the vexing problems of circularity and untestability could be avoided if one accepted there were other evolutionary processes at work beside natural selection. This observation was consistent with the pluralism of Darwin but inconsistent with the views of Wallace and the definition of natural selection formulated by the architects of the modern synthesis. The following questions now arise and require address. What are these alternative evolutionary processes? Are there just a few supplementary processes or does each explanation have its own identity, as Fodor and Piattelli-Palmarini argue, forming a collection of natural histories? It will be argued here that although Fodor and Piattelli-Palmarini are correct to identify the constraints imposed upon evolutionary mechanisms and morphological form, they cannot conclude that there are no recognisable evolutionary processes. Illustrations will be provided to demonstrate what types of biological phenomena lie beyond the explanation of natural selection, but following this critical appraisal is the requirement to examine the alternative processes that are proposed to fill the explanatory gap. One such alternative process is termed, for the sake of this work, ‘structuralism’, but this should not be confused with the ‘structuralism’ of continental philosophy.

One of the difficulties here is that the structuralist alternative is composed of a disparate group of individuals spread over many years.[1] However, to evaluate their arguments it is necessary to identify the core themes and principles that unite them. It is one thing to criticise freely the prevailing views on evolutionary theory; it is another to provide a coherent alternative. Some time will therefore be devoted to understanding the fundamental arguments of the structuralists, pulling the strands together, before the emerging model of explanation can be evaluated alongside the model(s) of explanation provided by natural selection.

An examination of the constraints that effectively outline the parameters to morphological form, the necessary relationships between parts and the allometric nature of growth will be included. Furthermore, consideration will be given to the structuralist claim that much of evolutionary understanding resides outside the province of genetics; persistent regularities pervade both the inanimate and animate and can be witnessed in symmetries and order. The structuralist argues that, to appreciate these fully, one must engage in a wide range of disciplines, such as physics, mathematics, geometry, topology and chemistry. It will be suggested that structuralism does have more to contribute than has previously been appreciated and will strengthen our evolutionary theory, offering explanation that has historically proved problematic for natural selection.

## Natural Selection versus Structuralism

There is then a tension between advocates of natural selection on the one hand and advocates of structuralism on the other. To gauge and clarify this dichotomy, it is suggested that one needs to be clear as to 1) what the explanandum actually is and 2) what form of explanation should be taken. For instance, within evolutionary theory there are several issues demanding an appropriate explanation: how life emerged from a single ancestor to such diverse forms; how and why major transitions occurred; how individuals and populations adapt to environments; why some forms are more common than others; and so forth. It will be demonstrated why clarity here is of fundamental importance. The second issue touches on finding an appropriate method of explanation that might allow one to examine the explanandum at hand and then adjudicate between the conflicting explanantia of the selectionist and the structuralist. However, caution is required here, for the biological world is not recognised as conforming to any easy philosophical account of explanation. Also one is wary not to be presumptuous about the vexing issue of the ‘explanation of explanation’, for this issue itself is unresolved, controversial and demanding of consideration that would occupy another thesis. However, having said this, a method may be available that has some heuristic value whilst recognising that any universal application is unlikely.

It seems without controversy that biological explanation is mostly of a causal nature. The tool that one might employ to settle some issues can be derived from Schaffer’s proposal of ‘contrastive causation’, which takes the form: $c$ rather than $c^*$ causes $e$ rather than $e^*$. Before one can consider applying ‘contrastive causation’, however, one must determine what natural selection actually is. To answer the ontological question, one must unpack $c$ rather than $c^*$. This looks on the surface to be fairly straightforward, but it will be demonstrated that it is anything but. The task will begin with the historical explication of natural selection, followed by a

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[1] The principal figures include St George J. Mivart, D’Arcy Thompson, Antonio Lima-de-Faria and Robert Reid. (There is also another grouping that does not fit easily into any camp, which might include Ron Amundson, Noam Chomsky, Michael Denton, Jerry Fodor, Brian Goodwin, Massimo Piattelli-Palmarini, Ian Stewart, Stuart Kauffman, Mary Midgley, Simon Conway Morris, John O. Reiss and Alan Turing.) It should be noted that not all these would subscribe to the label ‘structuralist’; Lima-de-Faria, for instance, sees himself as an ‘autoevolutionist’.

conceptual analysis. Having determined what kind of animal natural selection is, one is in a position to see what work it can do.

# Natural Selection

## Chapter 1: The Historical Exposition

To fully understand the concept of 'natural selection', it is necessary to examine the origins, not only of the term itself but also of the ideas it represents. Such an examination is prerequisite to any solution or clarification to the manifold questions demanded. What is natural selection: is it a force, is it a process, is it a variety of different processes, is it a mechanism, is it a cause or is it merely of descriptive value, mapping changes as they occur? Seemingly simple questions such as these are in fact extremely complex and difficult to answer. However, one should address these before going on to face further questions concerning any possible explanatory power of the concept. Another set of questions will arise. For example, can natural selection account for all evolutionary change; does it explain speciation, variation and extinction, and adaptation? Moreover, does it 'operate' at the level of the gene, the genome, the individual, the group, the species or at all levels? Is it compatible with sexual selection and how far is it constrained within general evolution and natural law? Should the principle of natural selection apply to sciences other than biology? Awareness of the historical origins of the concept is necessary for such an understanding; for what one finds is that the term 'natural selection' undergoes changes and additions in meaning, leading to difficulties of ambiguity.

A fresh interpretation of the historical literature will establish that-

1. A primitive concept of natural selection existed prior to Darwin and Wallace.
2. Darwin and Wallace differed over the explanatory power of natural selection.
3. The 'Eclipse of Darwinism' is an incorrect interpretation of the history.

### *A primitive concept of natural selection existed prior to Darwin and Wallace*

There are several important thinkers who preceded Darwin and Wallace in appreciation that favourable traits were most likely to be preserved and passed on to future generations. This was the first inkling of a naturalistic explanation for how organisms might become adapted, multiply their numbers or conversely suffer extinction. There will follow a brief outline of the historical figures and the views they represent, Quotations from these thinkers can be accessed in Appendix 1. Within Appendix 1 there is included a quote from Darwin (1.5) that demonstrates the similarities of all included.

Hutton (1726–97) was a Scottish farmer with an interest in chemistry and natural history who might be called the father of modern geology. There is the early recognition here that members of a particular race may become better adapted, as favourable traits will be preserved through heredity (Appendix 1.1). Wells (1757–1817) expressed similar sentiments about the 'race problem' in a paper to the Royal Society in 1813, Wells recognises that nature, albeit with a longer time span, may be able to achieve the same results of phenotypic change as breeders might achieve through artificial selection (Appendix 1.2). Lawrence (1783–1867), a surgeon, began a series of lectures entitled 'Lectures on Comparative Anatomy, Physiology, Zoology and the Natural History of Man' (1819), which he hoped would be the basis of a book. The content of the lectures was well-advanced and included discussion of such concepts as mutation, selective breeding, sexual selection, adaptation and the dangers of inbreeding.

Matthew (1790–1874) discussed the ideas of natural selection in an obscure book, *On Naval Timber and Arboriculture* (1831). Without calling them such, he boldly introduces the processes of natural selection, with a possible explanation of the arrival of new species. He recognises the importance of heredity and reproduction, suggesting that evolution follows a progressive path toward 'perfection' (Appendix 1.3). What is unknown today is how widely his ideas and those of others of similar persuasion were read and discussed. Blyth (1810–73) has been the source of much controversy long after his death, championed by some creationists as the originator of natural selection but seen as relatively unimportant by most of the scientific community. Eiseley (1979) created a storm when he suggested that Blyth was a major contributor to Darwin's thought but not properly recognised as such. To Blyth, 'natural selection' was seen to restore the 'balance of nature', ensuring that species always returned to 'type'. Artificial breeding by man had an adverse effect on the creatures in question; when they were returned to reproduce in the wild, future generations would lose the attributes selected by man. This Platonic inheritance of 'type' or 'form' or the 'essentialism' of Aristotle was regarded as given in pre-Victorian times (Richards 2005). It is not clear that Blyth stopped short of admitting speciation. He does talk of deviations, such as the '*ancons* or otter sheep' that will never revert to 'form', unless forcibly bred so by man (Appendix 1.4). And what did Blyth have in mind when he talked of 'breeds'? Does the gradual accumulation of characters, generation by generation, that he mentions result in a new species? Unfortunately, all of Blyth's letters, including the correspondence with Darwin before and after the publication of the *Origin*, have been lost. Without them, we are reduced to speculation, and it is probably wisest not to go there.

*Darwin and Wallace differed over the explanatory power of natural selection.*

We could today be discussing 'Wallacism' rather than 'Darwinism' if Wallace had arrived at his views on natural selection just a few years earlier. As it was, Wallace sent his famous letter to Darwin from the Malay Archipelago, where he was working as a naturalist. It was quite a shock to Darwin to receive this letter, because Wallace had concisely outlined almost the same views on natural selection that Darwin had been working on for the past ten years but had been reluctant to publish. The following is a concise summary of the shared views, taken from Darwin (1859 & 1900) and Wallace (1870, 1886 & 1889). Both men effectively saw the end of the old paradigm and ushered in what one might reasonably call the '*laissez-faire*' or 'Malthusian' perspective of evolution. Both men arrived at the concept of 'struggle for existence' after reading the works of Thomas Malthus. That is that population increases would outstrip any increases in food production or resources, resulting in fierce competition. Both accepted that favourable characters would be preserved and passed on through the generations. Accumulation of such favourable traits would lead to further variation, even to new species. Equally, unfavourable characteristics would gradually be eliminated in the struggle for existence. Furthermore, both agreed that climatic changes could intensify the struggle for existence, leading in some instances to extinction. Gradualism, following from Lyell's 'uniformitarianism',[2] was the shared assessment, but Darwin emphasised more strongly that very many generations were required to effect change. The term 'evolution' was not used by either man. There are, however, differences and it is instructive to examine the opinions that each extended to explain the forces that shaped evolution.

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[2] See, Desmond and Moore (1992) for an excellent description of the development of Darwin's views on transformations. Also Wallace (1870) outlines his own perception on those formative years. Berry (2002) gives a very readable overview of Wallace, his life, his ideas and the relationship with Darwin.

The following summarises Kutschera (2003) –

- Wallace never used the term natural selection in his submission.
- Wallace never accepted any role for Lamarckian acquired characteristics.
- Darwin extended the 'struggle for existence' to the *Plantae*, whereas Wallace refers only to *Animalia.* Wallace argues that the struggle for existence would be influenced by competition between members of different species, the 'predator–prey' concept.
- Darwin saw the struggle as being between members within the same species.
- Wallace introduced the terms 'adaptation' and 'population' in the same sense as biologists might use them today.
- Darwin also included his grandfather's idea of 'sexual selection'. (Darwin, E 1792).

The last point of divergence was over artificial selection: Darwin used this as an analogous argument for natural selection but Wallace did not see domesticated animals as representative of what happened in nature. (Berry 2002)

## Forces Other than Natural Selection

As indicated above, Wallace and Darwin disagreed over the scope and limits of natural selection. Darwin was pluralistic concerning the number of factors that would influence evolution. Appendix 2 is provided with quotations illustrating evolutionary processes that Darwin considered distinct from natural selection.

The influence of Lamarck was incorporated in Darwin's early writings and remained so throughout his life. If one is to argue that Darwin only sought recourse to Lamarckian ideas in later life, after the *Origin* had been criticised for failing to provide a mechanism for adaptations, then one would be incorrect. If one checks the first edition of the *Origin*, one can see that Lamarckian principles are invoked. Darwin recognises the 'effects of use and disuse' and makes some observations on the effect of habit (Appendix 2.2). On one occasion, Darwin sees a compatible action to explain the loss of wings on beetles from Madeira: 'these several considerations have made me believe that the wingless condition of so many Madeira beetles is mainly due to the action of natural selection, but combined probably with disuse.' (Darwin,1859 p154.) Returning to the sixth edition of the *Origin*, Darwin devotes a chapter to answer the criticisms (mostly those from Mivart, 1871) of natural selection. To explain how the giraffe came to have such a long and unusual neck, Darwin combines the factors of natural selection and use: 'it is almost equally certain that this one kind alone could have its neck elongated for this purpose, through natural selection and the effects of increased use.'(Darwin 1900 p279). (See also Appendix 2.1).

In *The Variation of Animals and Plants under Domestication* (1868), Darwin extends his views on evolutionary processes supplementing natural selection. For example, he considers the 'correlation of growth' (Appendix 2.3), the direct impact of diet (Appendix 2.4) and that of the climate (Appendix 2.5). When one reads the *Variation*, one almost gains the impression that natural selection is playing second fiddle to a host of evolutionary explanations even though Darwin does maintain within the text on occasion that natural selection is the primary evolutionary process. Oddly, only two chapters extol natural selection, whereas the rest of the text is given over to many other considerations. There is also recognition by Darwin, of developmental biology, atavism and the fact that 'changes in the conditions of life cause variability' (Appendix 2.6). However, this pluralism and the Lamarckian influence on Darwin were never accepted by Wallace, and the invocation of 'use and disuse' was subsequently dropped by Weismann and, later, the neo-Darwinists of the twentieth century. Darwin also devotes a chapter in the *Origin* to hybridism. Although he recognises the formation of new species, he does not discuss, as far as one can see, any relationship there may be with natural selection.

The new '*laissez-faire*' paradigm was fractured over the scope and efficacy of natural selection. Darwin presented a more pluralistic account of evolutionary change, which included factors divorced from natural selection, such as sexual selection and Lamarckian mechanics. Darwin did not, it seems, become that much more pluralistic in the light of criticism after the publication of the *Origin*, he already was a pluralist. Wallace, on the other hand, presented a more singular explanation, advocating natural selection and rejecting nearly all additional explanations (Ch.1). This divergence, which has remained a controversial topic, leaves one in an uncomfortable philosophical position, as clearly the standpoints cannot both be true. Unfortunately, this ambiguity is never resolved, and as shall be demonstrated, this undesirable confusion is later compounded.

*The 'Eclipse of Darwinism' is an incorrect interpretation of the history.*

It is somewhat ironic that, following the famous publication of 1859, evolution (transmutation) would become almost universally accepted amongst naturalists but natural selection almost universally rejected as its cause. It is instructive to understand the demise of natural selection prior to its rehabilitation with the 'new synthesis'. Criticisms came in many forms, but what is of particular interest is that many of the issues that were hotly debated can be seen to re-surface in the 21st century (See Ch.2). Mivart (1871 & 1876) harboured serious doubts over natural selection as the primary explanation of evolutionary change.[3] Although he recognised natural selection as a factor, his field experience presented many counter examples; he thought natural selection could only be a secondary factor, with the causes of evolution unknown. (Appendix 3 is provided to illustrate quotations from Mivart). Mivart (1871) saw convergent properties as good examples of evolution in action but he thought that it was implausible that natural selection could explain such analogous forms (Appendix 3.1). The regularities that he recognised in nature could be distinct geographically and chronologically, and yet the same forms at different times and locations were recurrent and widespread.

Darwin and Wallace explained the beneficial features of organisms through a gradual progressive honing by natural selection, replacing the less beneficial forms in the Malthusian struggle for existence. Mivart (1871) argued that if the proposed process was a gradual one, then how could one account for the early incipient stages of an organ? (Appendix 3.2). For an organ to be beneficial, it had to be fully developed and functional; a partly formed organ was of no survival value and therefore outside the scope of natural selection. [4] Mivart

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[3] For a more detailed account of the relationship between Darwin and Mivart see Desmond and Moore (1992), also Peter Bowler (2003).
[4] This problem is discussed by Gould and Vrba (1982) and led to their conjecture of 'exaptation'.

(1871) contended that the fossil record did not support evolution by gradual transformations (Appendix 3.3). The argument follows from his previous problem of incipient organs.

Kropotkin (1842–1921) was one of the first supporters of Darwin and Wallace to recognise the problems with the Malthusian premises. This led him to the view that natural selection could have a broader application, extended to the group, and one could argue anticipating not just Wynne-Edwards (1962, 1986) and group selection, but also the twentieth-century interpretation of natural selection as one of ‘fitness’. Kropotkin travelled to Siberia and Manchuria at this time and to the glacial regions of Finland and Sweden later. During these trips, he observed the immense struggle for life in face of the most severe climatic conditions. The struggle for existence between individuals was not to be found; rather, there was mutual aid between individuals struggling against the climatic conditions (Appendix 3.4 & 3.8). Kropotkin identifies the ‘struggle for existence’ as an ambiguous term. It has a narrow sense and a wider sense (Appendix 3.5 & 3.6). Darwin, he argues, began with the narrow sense but later moved to incorporate a wider sense. The former is ‘that of a struggle between separate individuals for the sheer means of existence’ and the wider sense Kropotkin (1902 p11) quotes Darwin explaining the term in its ‘“large and metaphorical sense including (which is more important) not only the life of the individual, but success in leaving progeny”.’ Kropotkin observes that Darwin has illustrated this move by the time of the *Descent of Man* (1871). The fittest are then not merely the strongest or the most cunning; they are the ones that are best organised at bringing their young into the world. This will include those that are sympathetic, supportive and cooperative. Kropotkin says that under this new sense of ‘struggle for existence’, the old and narrow Malthusian sense is now discarded.

Kropotkin never denies that struggle exists in nature but argues that mutual aid is a more important factor in evolution and lists many examples of mutual aid among the invertebrates as well as the vertebrates. In one example, he cites natural selection as working against ‘individuals endowed with predatory inclinations’ (p13). Solidarity is favoured over the ‘cunningest and the shrewdest’ (p21). ‘Selection’ to Kropotkin works on the species on many occasions, the interests of the individual being secondary, for without mutual support there will be no chance of successful reproduction (Appendix 3.7). Observations of aquatic life on the lakes in the Russian and Siberian Steppes gave Kropotkin glimpses of cross-species mutual aid. Different species of birds resting on the shores would cooperate to fight off predators that continually lurked in the vicinity or in the air. Warning calls were mutually beneficial and, in one example, gulls and terns joined forces to chase away potential robbers.

Kropotkin questions the Malthusian idea of overpopulation leading to competition as a general rule. In nature, it is more uncommon than common, he continues and furthermore it is more the case that species struggle directly against changing climate than against each other. Moreover, competition plays only a minor role in providing checks against overpopulation. It is the natural checks – the sudden storms, the dramatic change in temperature, the drought – that suppress population growth. Other factors might involve the spread of disease or parasitic fungi (in one instance). Kropotkin considers the Darwinian counterargument that it is during periods of hardship, battling against the rigours of climate or disease, that the fittest survive and pass on their qualities. He then goes on to dismiss this on empirical grounds. Any areas ravaged by such calamities leave the surviving populations weakened, not strengthened: ‘If natural selection were limited in its actions to periods of exceptional drought, or sudden changes of temperature, or inundations, retrogression would be the rule in the animal world'. (ibid. p58) Further, and perhaps not without irony, Kropotkin says that natural selection favours those ant colonies that avoid competition with its deleterious consequences. To Kropotkin, then, the best chances of survival are enhanced by avoiding competition and instead practising cooperation and mutual aid.[5]

Butler (1882) was originally a supporter of Darwin but became disillusioned with the concept of natural selection and arrived independently at a critique not that dissimilar to that of his contemporary Mivart. Butler claims that Darwin has a problem. If natural selection only accounts for preservation then it loses its status as a cause and hence its *raison d'être* (Appendix 3.9). To Butler, the *Origin* explains little and should be compared to Paley's *Natural Theology* (1802). Furthermore, Darwin has committed a sleight of hand when he says of the eye 'variation will cause the slight alterations', when of course the slight alterations are the variations. Later, according to Butler, Darwin contradicts himself by maintaining that natural selection only preserves and accumulates small inherited modifications; it has no role in inducing or causing these modifications. Butler therefore draws a distinction concerning natural selection; its role seems to be one of preservation and not of cause. Darwin argues that the advantageous modification would be preserved by natural selection in the struggle for existence. Butler, however, considers the term 'struggle for existence' and asks whether it is necessary for evolutionary change. As long as a plant or organism fulfils the conditions required for existence, then it can continue to reproduce. He concludes that 'the conditions for existence' is a less misleading term than 'natural selection': 'I have said that there is a practical identity of meaning between 'natural selection' and the 'conditions of existence' when both expressions are fully extended'. (1882 p9)

Butler maintains that the latter term is more accurate and calculated to keep the thread of the argument. He also argues that descent with modification by means of natural selection is not synonymous with the theory of evolution or with the theory of descent with modification. The 'conditions of existence' and 'natural selection' are in effect the same thing, but natural selection is a misleading term because it implies some force or agency whereas 'conditions of existence' does not (Appendix 3.10). Butler concludes that the principle of natural selection is not really a theory at all but an observation of facts. Darwin gives us the *Origin of Species* but with the origin cut out (chapter XX1, p17). Butler thinks that if 'struggle for existence' had been employed to the exclusion of natural selection, then one would realise that the theory does not identify the cause of modification (Appendix 3.11). Butler says that "means" is a dangerous word; it slips too easily into "cause", implying perhaps that Darwin gets his causal chain in the wrong order. The issue of natural selection as causal or not remains live and will be considered in more detail later.

### Scepticism at the Turn of the Century

It can be argued that by the 1900s, biologists and naturalists had embraced the concept of transmutation, which was now universally discussed as evolution. One must recognise that evolution is a wider term than

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[5] Kropotkin submitted several articles and commentaries on the evolutionary debates to *Science*. These were collected together and reprinted in 1995, edited by Woodcock. What is of interest here is that Kropotkin discusses the issue of the direct impact of the environment upon individuals and populations. Nowadays, this phenomenon has resurfaced in the literature of the evolutionary developmental biologists and ecologists and is referred to as 'polyphenism'. The issue is important, because polyphenism when discussed in Kropotkin's time was seen to run contrary to natural selection but today some biologists see polyphenism as being embraced or subsumed within a framework of natural selection.

transmutation. Transmutation was almost exclusively seen in Victorian times as what one would call today 'speciation'. Of course, evolutionary considerations could embrace adaptationism and speciation. There was, however, a widespread scepticism over the ability of natural selection to explain either of these phenomena. The recurring theme in the criticism was that if natural selection only preserved or eliminated any changes that might occur, then it could not account for the causes of the changes. The study of variation and how variations arose was seen as the key to understanding the 'driving force' of evolution. Bateson (1861–1926) suggested:

> Perhaps the causes of evolutionary change are in variation itself and not in a superimposed external sorting as the more complex Darwinian mechanism proposed: variation, in fact, is evolution. The readiest way then of solving the problem of evolution is to study the facts of variation. (Bateson 1894 p6)

De Vries (1848–1935), most famous for his rediscovery of Mendelian genetics, was also sceptical about the aetiology of natural selection. Rather prophetically, he considers thus:

> Natural selection is a sieve. It creates nothing as is so often assumed; it only sifts. It retains only what variability puts into the sieve. Whence the material comes that is put into it, should be kept separate from the theory of its selection. (De Vries 1909 p609)

De Vries, as far as one can see, gives the first rendering of natural selection as a sieve or filter, and also recognises an important distinction here between two separate processes, the source of the variations and any subsequent action ascribed to natural selection. This is something to be considered in more detail later.
According to Kropotkin, at the beginning of the twentieth century the key debate focused on two perspectives of evolutionary change; one was the direct impact of the environment (direct adaptations) and the other, natural selection:

> The great question which now above all others interests the biologists and divides them into two camps is the question of the relative importance of natural selection on the one side, and the Direct Action of the environment on the other side, in the process of new species. (Kropotkin 1995 p139)

This debate was effectively buried for fifty years with the advent of the new synthetic theory, the explanatory focus being adaptation by natural selection. However, in recent years the debate has reopened and the direct impact of the environment is given consideration with our improved understanding of developmental biology and epigenomics.

## Conclusions

By the end of the 19th century the idea of Evolution was established, with a naturalist account based on the principles of heredity and change. The radical shift from the earlier advocates of a proto-natural selection was that speciation would result and this could be understood if the ideas of Malthus were applied. Both Darwin and Wallace sought to explain the 'modification' part in 'modification by descent' as a process of Malthusian struggle, but disagreed over the explanatory power of natural selection. This issue is however only the beginning of a problem that is to persist and complicate until the present. Wallace saw natural selection as a singular sufficient explanation, but Darwin disagreed: Malthusian struggle was primary but sexual selection and other factors independent of natural selection also contributed. Nevertheless, this Malthusian explanation was severely questioned by naturalists and biologists. Mivart (1871 & 1876) saw the pace of evolutionary change as being irregular and challenged the gradualist account. Butler and others thought that natural selection failed to provide any explanation in any detail or to provide an aetiology. Lyell, one of Darwin’s inner circle of friends, finally accepted evolution in later life but rejected that natural selection could provide the causes. Even De Vries, the staunchest of Darwinians, saw that natural selection as formulated could only preserve or eliminate but never create. Bateson argued that a science of variation would explain evolution, without recourse to natural selection. Kropotkin observed that the struggle between individuals was not a universal phenomenon and that successful descent could be achieved best by mutualism. Fitness under these circumstances demanded a new perspective. All of these considerations were to be taken on board and were instructive to a more refined view.  In would be wrong however to describe this period of scepticism as the ‘eclipse of Darwinism’ (Bowler 2003, Huxley 1942). Darwin’s pluralistic face was alive and thriving; it was the causal power of natural selection that received such scepticism and therefore one should really refer to the period as the ‘eclipse of natural selection’. In the following chapters it will be observed that natural selection was reprieved, revised and seen central to evolutionary explanation. Unfortunately, none of the historical problems are resolved and the problems caused by ambiguity are compounded.

## Chapter 2: Problems with the Concept of Fitness

### Fitness Replaces Survival of the Fittest

In the preceding chapter, it has been seen that there were disagreements between Darwin and Wallace concerning the term 'natural selection'. These included issues over the scope of the explanatory power of the concept. Moreover, criticisms from other evolutionists, such as Mivart and Butler, ushered in what has become known as the 'Eclipse of Darwinism' (Huxley 1942) and the revival of interest in the ideas of Lamarck. This period lasted until the 1930s, when the architects of the 'modern synthesis' reintroduced natural selection. Superficially, the modern synthesis looks to be a fairly precise body of scientific opinion, but the characters involved all gave their own interpretations of what constituted neo-Darwinism. Arguably, there was strong consensus on what should be purged, largely the Lamarckian elements contained within Darwin's pluralism. In addition, any references to the direct impact of the environment were thought inapplicable and therefore embryonic studies were largely perceived as non-evolutionary. However, there was controversy over which elements should provide the core principles of this intrinsic genetic perspective.

The classic debate to illustrate this point was between population geneticists Fisher and Wright.[6] Both men wanted to give evolutionary biology a mathematical basis, but whereas Fisher (1930) looked exclusively to natural selection, Wright (1932) saw drift playing a major role. But when the term 'natural selection' was reintroduced to biology, what did it signify? To Fisher, natural selection was an agent; to Wright, it was a mathematical factor; to Haldane (1932), a causal factor; to Dobzhansky (1937) and Huxley (1932 & 1942), a mechanism. Huxley, however, would also see natural selection as an agent. Smocovitis (1992) provides an interesting discussion of this period, perceiving an important reversal in the aetiology of natural selection. Whereas De Vries and Bateson (Ch.1) had confined natural selection as eliminative or preserving, Dobzhansky and others increasingly perceived natural selection as causo-mechanical. In the late nineteenth and early twentieth centuries, Mendelian genetics and mutation were seen as evolutionary factors in their own right, independent of natural selection. However, these factors were now incorporated within theories of natural selection. The emphasis was firmly directed toward genes or alleles and not species. Subsuming these previously independent factors of evolution was a radical departure from the Malthusian selection theories of Darwin and Wallace. One person who appreciated the departure from Darwin's concept of natural selection was Simpson:

> [Darwin] recognised the fact that natural selection operated by differential reproduction, but he did not equate the two. In the modern theory natural selection is differential reproduction plus the complex interplay in such reproduction of heredity, genetic variation, and all the other factors that affect selection and determine its results. (Simpson 1949 p268)

This was not an orchestrated plan, where the great men of the time sat down and ironed out a new and precise understanding of natural selection. It was more a gradual evolution of the concept, which carried with it all the ambiguities one still sees today and which never formally divorced from Malthusian natural selection. This issue of neo-Darwinism incorporating factors that were at one stage seen as antagonistic to natural selection was repeated throughout the twentieth century. One example is the inclusion in neo-Darwinism by Mayr (1942) of the concept of allopatric speciation. Mayr had demonstrated how a single species could split

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[6] For an excellent discussion on the issues here see Reiss (2009)

and populations become geographically isolated from each other. Over long periods of time, the eventual genetic changes to both populations would result in two new species. Mayr's work became famously embedded as the main factor of speciation within neo-Darwinian theory. The curious thing was that allopatric speciation was not a new concept; in fact, in the previous century, it was perceived as an argument against natural selection. Wagner (1868) published his work on the effects of isolation on generating new species and this was seen at the time as an evolutionary mechanism independent of natural selection. Wagner and Darwin had corresponded over the issue and Kropotkin some years afterwards appraised the correspondence and said 'Darwin frankly recognised that this was a factor which removed many difficulties unexplained by natural selection' (Kropotkin 1995 p134). In the same vein, Dixon published *Evolution without Natural Selection: Or the Segregation of Species without the Darwinian Hypothesis* in 1885. The title of this work embraces the sentiment expressed within and endorses much of Wagner's perspective. Both men realised the potential of isolated populations or the allopatric situation to explain speciation without recourse to natural selection. Mayr, however, subsumed 'isolation', 'segregation' and 'allopatry' under natural selection. This inversion of fortunes for natural selection is not without cost, for natural selection must take on a new meaning.[7] This proliferation and generalisation of the term 'natural selection' will be discussed in chapter 4.

Meanwhile, Spencer's synonym for natural selection, 'survival of the fittest', was deemed to be a crude caricature of the concept and gradually preference was given to the term 'fitness', which denoted any characters and behaviours that were likely to secure successful reproduction. This follows from Kropotkin's observations concerning the 'wider' meaning of the 'struggle for existence' (Ch.1). The language also altered, and the terminology included terms such as 'differential reproduction' and 'differential survival'. However, this reformulation did not escape the notice of philosophers, and the charge of tautology was again alleged by eminent figures, such as Peters (1976), Popper (1977) and Smart (1963). Concentration here will be directed to the views of Popper, as these are fairly representative of the criticisms but also because he later gives an interesting insight into how the problem of circularity can be avoided. There will also be some contemporary discussion of the problems, which includes the reservations of evolutionary biologist Dawkins concerning the term 'fitness'. What is also of interest is that the 'fitness' concept evolved from the concept of 'survival of the fittest', which itself was recommended to replace 'natural selection'. However, it will be seen that all three terms have retained separate identities but are often conflated.

Before examining Popper's views on evolutionary theory and its place in science, one or two misrepresentations should be clarified. Popper was not anti-Darwinist, nor did he doubt the existence or the importance of biological evolution. He was, however, very concerned about the 'demarcation problem', sifting pseudo-science from genuine science and attempting to maintain science as a rational pursuit. Evolutionary biology was never considered to be pseudo-scientific by Popper, but he did perceive that it was different in nature from physics or chemistry. Controversially, Popper introduced the term 'Metaphysical Research Programme'. However, he did not use the term 'metaphysical' in a derogatory manner that suggests something akin to the supernatural or the pseudo scientific. Rather, he saw metaphysical, in this instance, as something non-scientific but still worthy of intellectual pursuit. Darwinism is a Metaphysical Research Programme because it is not testable. Further, it 'does not really predict the evolution of variety'; it therefore cannot explain it (Popper 2002 p199). The best one can hope to achieve is the prediction of variety under

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[7] Mayr and later Coyne also remove the problem of convergence by addressing it in selectionist terms; see Coyne (2010).

‘favourable conditions’. However, favourable conditions are problematic because they are difficult to describe without falling back on a tautology, i.e. ‘in their presence, a variety of forms will emerge’. Popper is also dubious about adaptations:

> Take ‘adaptations’. At first sight natural selection appears to explain it, and in a way it does, but hardly in a scientific way. To say that a species now living is adapted to its environment is, in fact, almost tautological. Indeed, we use the terms ‘adaptation’ and ‘selection’ in such a way that we can say that, if the species were not adapted, it would have been eliminated by natural selection. Similarly, if a species has been eliminated it must have been ill adapted to the conditions. Adaptation or fitness is defined by modern evolutionists as survival value, and can be measured by actual success in survival: there is hardly any possibility of testing a theory as feeble as this. (Popper 2002 p199)

(It is important to remember here that the Darwin/Wallace account of adaptation by means of natural selection based on Malthusian principles is testable.) However, despite this apparent feebleness, the theory is still indispensable; it illuminates ‘very concrete and very practical researches’ (ibid. p200). Popper gives the example of the research into bacteria that become adapted to newly infested penicillin environments. Only this theory can explain the mechanisms at play but, he claims, it is little better than the theistic view of adaptation. Darwinism is important for science but it must be seen as a metaphysical theory and not a scientific one. As a Metaphysical Research Programme, Darwinism can make certain predictions: evolution will be a gradual process and small changes will be due to mutation. However, these predictions are limited in their explanatory power according to Popper. Moreover, Darwinism cannot predict a *particular* evolutionary change; at best, it can perhaps predict gene changes within a population, without being specific.

Popper notices a possible inconsistency. If mutations are ‘random’ and change could go in many directions, why does natural selection seem to ‘prefer’ sequences of evolutionary change that are similar? Why do ‘orthogenetic trends’ keep repeating themselves? Popper believes Darwinism could be enriched if it could answer these questions. He proceeds with his own possible solution, which includes two forms of selection. One is environmental selection, where the pressure is external; the other is internal and comes from the organism itself (ibid. p201). However, Popper goes into a lot of assumptions about the nature of genes that look unlikely to be supported by modern evidence. These assumptions include ‘a’ genes which control anatomy, ‘b’ genes which control behaviour and ‘Intermediate’ genes which have mixed functions. Further, ‘a’ and ‘b’ genes can be divided into other genes that might control preferences or skills respectively.

## Popper Recants on Natural Selection?

In 1977, Popper gave a paper which some said demonstrated a reversal. This is only partially correct.

> I still believe that Natural Selection works in this way as a research programme. Nevertheless, I have changed my mind about the testability and the logical status of the theory of natural selection; and I am glad to have an opportunity to make a recantation. (Popper 1977 p243)

Popper goes on to consider what can be explained without recourse to natural selection. One phenomenon is genetic drift, which can occur without any selection pressures; all that is required is reproductive isolation through geographical separation. It has been argued that reproductive isolation could be sufficient for genetic drift. Natural selection in its most sweeping form can be seen to explain all organisms and all complete structures, such as the eye. However, Popper maintains, this sweeping form is problematic, especially if one includes all forms of animal behaviour:

> In its most daring and sweeping form, the theory of natural selection would assert that *all* organisms, and especially *all* those highly complex organs whose existence might be interpreted as evidence of design and, in addition, *all* forms of animal behaviour, have evolved as the result of natural selection; that is, as the result of chance like inheritable variations, of which the useless ones are weeded out, so that only the useful ones remain. If formulated in this sweeping way, the theory is not only refutable but actually refuted. (ibid. p243)

The example of the peacock's tail is cited as a refutation, which was accepted by Darwin himself. This refutation was explained away by Darwin by recourse to the idea of sexual selection, according to Popper. The danger, as Popper sees it, is that any attempt to get round the refutation by verbal manoeuvre is likely to lead to a tautology. Further, it would be better to admit that everything that evolves may not be useful, and that evolution by natural selection is not strictly universal, though it seems to hold for a vast number of important cases. Biologists face the challenge to discover which characters are the results of natural selection and which are not: 'Yet in every particular case it is a challenging research programme to show how natural selection can possibly be held responsible for the evolution of a particular organ or behavioural programme.' (Popper 1977 p244.)

Selectionist theories are still seen by Popper as immensely important when considered historically. An important conceptual leap was made from the views of Paley, which implied some form of instruction, and subsequently replaced by non-theistic selectionism.

## Fitness and the Problem of Tautology

The replacement of Malthusian natural selection with the concept of 'fitness' has introduced the problem of tautology. This has vexed philosophers and biologists alike and has led to several responses. One solution has been to accept the theory as tautological but still consider the theory important. Another solution is to argue that the theory, when complete and within the Darwinian framework, is not tautological. The philosopher Sober outlines some of the possible solutions to the matter. First, however, it is best to try to state exactly what 'fitness' entails. According to Sober (1993 p70) –

'Trait X is fitter than trait Y if and only if X has a higher probability of survival and/or a greater expectation of reproductive success than Y.'

Sober argues that one could quibble over the finer points, yet overall the definition is reasonable, but he concedes that this formulation is indeed tautological. However, one should not be too concerned by this because, according to Sober, the tautology is only one part of a broader Darwinian Theory. One has to take a more holistic or integrative approach and recognise the other main feature of the theory: that all life is related. When one considers the whole idea, the theory is no longer tautological. 'The fact that the theory of evolution contains this tautology does not show that the whole theory is a tautology. Don't confuse the part with the whole.' (Sober 1993 p70.)

If one wants to defend the theory against those who are hostile to the whole concept of evolution, then this might be a satisfactory response. However, it does little to satisfy those who are committed to the evolutionary thesis but are sceptical of natural selection as an important mechanism. If one can develop a theory of evolution that does not contain a tautological component, then surely this is preferable? Defenders of natural selection would argue that this is unlikely to be achieved, the 'if' being too immense. This statement may be premature, however, as new evolutionary explanations are emerging and recent alternatives may not have been fully examined and appreciated. To continue, Sober points out that many of the theories in evolutionary biology are different in nature from the general laws of physics:

> In physics, general laws such as Newton's Law of Gravitation and the special theory of relativity are empirical. In contrast, many of the general laws in evolutionary biology (the if/then statements provided by mathematical models) seem to be non-empirical. That is, once an evolutionary model is stated carefully, it often turns to be a (non-empirical) mathematical truth. (Sober 1993 p71)

Examples of these mathematical truths are Fisher's sex-ratio argument (1930) and the Hardy–Weinberg Law. These too are tautologies, Sober argues, but they are not trivial. Tautologies are often seen as truisms, without value and therefore vulnerable. This is not the case with these two examples; Fisher's argument is something of a conceptual breakthrough, maintains Sober (1993 p73): 'Even so, it is very far from being trivial. And it was not obvious until Fisher stated the argument. Thanks to his insights, we now may be able to find obvious what earlier had been quite unclear.'

Sober gives the example of the Hardy–Weinberg equilibrium (HWE) to demonstrate that some tautologies can be insightful and increase our general understanding of the world. Although it can be accepted that the HWE is insightful, it is less clear that it is a pure tautology as described by Sober. Unlike the concept of 'fitness', the HWE takes the form of an equation, which under certain conditions allows one to make certain predictions. For example, if we took a given population and identified that one person in ten thousand had a particular genetic disease, we would be able to calculate the number of people who are carrying the recessive unexpressed gene (198 people in 10,000 in fact). Similar to other equations, once we know X, we can proceed to calculate Y. The HWE refers to the relationship between dominant and recessive alleles and tells us how the variation is distributed. It is important to remember, however, that the HWE can only be successful if the empirical genetic laws as we understand them are maintained. If Mendelian genetics were to collapse in the light of new discovery, then the HWE might have to be abandoned in its present form.

One must now consider whether the 'fitness' concept has the same vulnerability and reliance on empirical stability as the HWE. As it stands, 'fitness' could not be refuted, at least whilst reproducing organisms are still in existence. The charge is that there would be little point in going out and checking to see whether favourable attributes had survived and unfavourable ones been eliminated, for it could not be otherwise.[8] Nevertheless, let us grant that Sober has a point, for the sake of argument. The sex-ratio argument may be non-trivial and an important insight, containing mathematical foundations. However, can one also claim the same non-trivial status for the concept of 'fitness'? One might question whether any great conceptual advantage was made in the move from Malthusian explanations. This was Popper's point: the Darwin/Wallace Malthusian explanation was a great conceptual step forward, demarcating the theory from a theistic account. Can we argue similarly for the change to 'fitness'? It can be argued that the Malthusian explanation can be empirically tested. One can examine the situation to see, for example, whether there is

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[8] Stove (1995 p134), in his discussion of neo-Darwinian fallacies, gives a reminder that starting from a tautological premise, one cannot validly infer from it any conclusion that is not itself tautological.

food scarcity producing competition for resources. The observation could hold true or could be refuted. The situation is testable. But can the formulation of ‘fitness’ be empirically examined and tested?

The original motive for producing a more elastic definition of natural selection seemingly was to solve the problems that included, for example, co-operative behaviour between animals. The new elastic definition could also be extended further to embrace other types of behaviour not originally considered to be within the original Darwin/Wallace account. These might include ‘sneaky’ and ‘cheating’ behaviour, or any behaviour that led to successful future reproduction. However, is the formulation of ‘fitness’ sufficiently elastic to account for any form of behaviour? Hull has noticed just how elastic and accommodating this aspect of Darwinism can be:

> To some extent, the ease with which Darwinians co-opt positions that were presented to refute them looks suspicious. For example, early on Darwinians opposed Kimura’s neutralist views, but as the data piled up indicating that most mutations are neutral and not negative, Darwinians simply modified their theory and termed the result ‘Darwinism’. (Hull 1999 p501)

The desire is to avoid such refutations, but with such accommodations to the theory the spectre of tautology is invited. Neo-Darwinians are in something of a dilemma. Either one accepts the refutation and admits that natural selection is not a universal explanation or one commits to natural selection as a universal explanation but of a tautological nature.

There is a further problem with ‘fitness’ as a viable theory. What constitutes ‘fitness’ is not that easy to distinguish and the problem can lead to conflicting interpretations: “I do not think that a single measure of fitness, no matter how defined or operationalised, can be very significant because too many factors, many of them conflicting, contribute to an organism’s fitness” (ibid. p501). There is also the problem of non-realised or latent fitness. It has been said that with two identical brothers, one could be struck prematurely by some accident, perhaps a bolt of lightning, whilst the other survives, mates and has viable offspring. Does one then say the latter was fitter even though their genomes were the same? ‘Potentiality’ and the ‘probabilistic propensity’ (Beatty & Mills 1979 & Brandon 1990) need to be included in any calculation, it seems, but this requires considerable knowledge of environmental influences and future events (Abrams 2007). As an example of the difficulty, if one organism died as a result of an unexpected drought, one might still maintain that the individual possessed some measure of fitness. However, if all the members of the population were to die from the drought would one still bestow fitness? Considerations of probability or propensity were first added to the fitness concept in order to prevent the circularity charge. Beatty, however, has concluded that this attempt failed:

> To be sure, the claim that ‘the fittest are most likely to leave the most offspring’ is a tautology when ‘fittest’ is defined in terms of actual offspring contribution. But the claim is no more empirical when ‘fittest’ is defined as ‘best able to leave most offspring’. (Beatty 1994 p118)

Beatty goes so far as to suggest that the Principle of Natural Selection should not be considered equivalent to the centrality given to Newton’s Laws of Motion. Instead, one should focus on the deductive consequences of the Hardy–Weinberg Law, which Beatty considers suitably empirical.

## Modern philosophical considerations on the Fitness problem

Contemporary philosophers are continuing to work on the problems that Fitness presents. The ambition is still to provide some genuine explanatory value and curtail the threats of tautology, triviality and unfalsifiability. It is worthwhile to outline the responses to date before any conclusion is drawn. Philosopher Ariew and biologist Lewontin have produced a joint paper. The introduction of this nicely summarises the root of the problem –

> No concept in evolutionary biology has been more confusing and has produced such a rich philosophical literature as that of fitness. The confusions have arisen because a concept, originally introduced as an inexact metaphor by Darwin, has come to play an analytic role in the formal quantitative dynamics of evolutionary biology. (Ariew & Lewontin 2004 p347)

In other words the notion of 'fitness' has evolved, producing multiple definitions. One definition takes on a new identity as an analytic tool in population genetics. The authors argue that the original Darwinian definition of fitness is incommensurable with the numeric values associated with reproductive rates used in population genetics and recommend a more pluralistic approach. Nevertheless, there still remains a problem of biological identity; what are the referents to fitness? Should one consider species, populations, individuals, male and/or female offspring, cells, genes or amino acids? For instance, nature does not always fall into neat categories and complex organisms can be composed of more than a single individual. (Bouchard 2008, O'Malley and Dupré 2007) Earlier, Matthen and Ariew (2002) following on Dennett's ideas of design (1995) developed a new approach which they called 'vernacular fitness'. This is formulated as-

x *is fitter than* y *if and only if* x*'s traits enable it to solve the 'design-problems' set by the environment more fully than* y*'s traits do.*

Once again however there are problems, namely over the identification and measurement of the so-called 'design problems'. It could be argued that introducing such criteria obscures rather than clarifies the principle. Yet another possible solution is proposed, called 'Block fitness', where "(1) an individual's fitness is fixed over its lifetime, that is, its fitness cannot increase or decrease with time, and (2) fitness comparisons can only occur between conspecifics that occupy the same fitness environment", Ramsey (2006). Ramsey may have a point here concerning (1), for it could be argued that the size of an organism constrains its reproductive ability, for instance mice can multiply more quickly than elephants, and so forth. However, if one confines consideration only to conspecifics (2) then this general comparison across different species is prohibited. To complicate matters further Lewens (2010) is critical of Sober (1984)[9] - 'sometimes he appears to equate the force of selection with variation in fitness, sometimes with 'selection for properties'. The question of natural selection as a force is considered in the next chapter.

The difficulty here is to adjudicate as the subject matter is in a seemingly endless bifurcation. Any attempt to do so would transcend the parameters of this thesis and one wonders if there is a coherent solution after so many years. Moreover, is the concept(s) of fitness actually worthwhile retaining?

The ambiguity of the situation was anticipated well by Dawkins to the conviction that the term should not be employed or should at least be avoided wherever possible:

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[9] Sober's *The Nature of Selection* 1984 has become something of a classic within the philosophy of biology and noted for the important distinction between 'selection for' and 'selection of'. This early work of Sober sees 'selection for' as the 'causal concept par excellence'.

> ‘Fitness’, as it is normally used by ecologists and ethologists, is a verbal trick, a device contrived to make it possible to talk in terms of individuals, as opposed to true replicators, as beneficiaries of adaptation. The word is therefore a kind of verbal symbol of the position that I am trying to argue against. More than that, the word is actively confusing because it has been used in so many different ways. (Dawkins 1982 p179)

Dawkins – identifies five different interpretations of fitness, which he refers to as the ‘agony in five fits’:[10] It is worth noting that Dawkins see the earliest formulation of fitness as Spencer’s ‘survival of the fittest’, which is a metaphor for Darwin’s metaphor of ‘natural selection.’ Dawkins argues against this usage and also the other ‘fits of agony’ but recommends that if one is to use any formulation then it should be only ‘inclusive fitness’ and from the perspective of the gene. The suggestion of measuring fitness through the medium of the gene however presents more problems than answers. It can be argued that modern biologists give consideration to many factors other than genes.[11]

> Once one looks at actual mechanisms, it becomes clear that no phenotype is due to genes alone. The external environment comes in many ways: nutrition, micronutrients, temperature, photoperiod, pheromones, social environment, and many more. And the internal environment also plays an critical role: cell-cell signaling, endocrine signaling, ion gradients, membrane potentials, etc. (Nijhout 2013)

There seems no reason, in principle, why a researcher should not investigate the fitness at any level of taxonomy. Attempting to measure every biological change through the medium of the gene is problematic for several other reasons. Not many genes are discrete entities that simply code for a particular trait; they can be very difficult to individuate and identify (Barnes and Dupre 2008). The idea that a gene can be seen as an object that codes for a particular protein is nowadays considered an oversimplification: an individual gene can code for up to 38,000 different proteins (Alberts 2002). Definitions of a gene are proving highly elusive. Barnes and Dupre argue that early definitional attempts have failed to recognise the complexities involved and question whether a gene is even an entity:

> If genes are objects, then they are objects that vary enormously in their constitution, and they are composite rather than unitary objects – objects only in the way that the solar system is an object, or a forest is, or a cell culture is. (Barnes and Dupre 2008 p53)

Moreover, genes take on multi-functional processes:

> One striking illustration of the change of perspective involved here is the increased interest now being taken in how many ‘copies’ of a given gene or DNA sequence are to be found in the genomic DNA of an organism (Radon et al., 2006). It is hard to find a place for such a question within a framework in which a gene is simply a unit of inheritance: what would be the role of several copies of a gene for brown eyes? But if genes are recognised as having other functions things can look quite different. (ibid. p50)

Barnes and Dupre are not representing a maverick perspective[12]. There could be, for example, a change in the genotype of an organism but no change in its phenotype. Conversely, there could be a change in an organism’s phenotype but no change in its genotype. Jablonka and Lamb (2005) argue that a single genome,

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[10] Inspired by Lewis Carroll from ‘The Hunting of the Snark: An Agony in Eight Fits’.

[11] The problems and consequences of genetic reductionism have been well discussed by both biologists and philosophers, see Fox Keller (2002), Moss (2003), Morange (2000, 2001), Dupre (2004) and Waters (2007).

[12] For an excellent modern introduction to all the complexities and implications of epigenetics, see Carey (2012). Carey also argues that we are witnessing a paradigm shift.

either unicellular or multicellular, could potentially yield an enormous variety of phenotypes and furthermore populations that become geographically or ecologically separate can display distinct phenotypes even though their genomes remain unchanged. One could consider the genome as a vast switchboard of genes which can be turned on individually or in groups or sequences with the combinations yielding countless results. The factors that determine the switching on or switching off are also of interest. Jablonka and Lamb suggest an epigenetic explanation. Another concern arises when wishing to contrast fitness at higher taxonomic levels. This is a difficult procedure even when counting identifiable phenotypes; both survival and reproduction have to be quantified with objective criteria. However, does multiplying the number of offspring by the number of generations give us the fitness of individuals, or the fitness of species, or even the fitness of lineages? It is not entirely clear. As Fox Keller says, along similar lines and noticing an ambiguity:

> A chronic confusion persists in the literature of evolutionary biology between two definitions of individual fitness: one, the (average) net contribution of an individual of a particular genotype to the next generation, and the other the geometric rate of increase of that particular genotype. (Fox Keller 1994 p120)

## Conclusion

The perspective of natural selection as universally Malthusian was challenged in the 1930s; other factors such as cooperation, sheer luck and cheating might also play important roles in evolutionary changes. To embrace these factors, the architects of the ‘modern synthesis’ focused upon any behaviour that facilitated replication, reproduction and fecundity over the generations; the concept of ‘fitness’ was established. However, this adjustment from the original perception of Malthusian natural selection invited criticism of tautology, with Popper illustrating the dichotomy that faced the new formulation: either one accepted that other factors such as ‘drift’ were important in evolutionary changes or one accepted the Principle of Natural Selection and fitness as circular, without any predictive power and of little explanatory value. However, many years after Popper’s remarks, the issue is as controversial as ever and attempts to resolve matters have become increasingly complex, with no consensus amongst philosophers. Dawkins anticipated the ambiguity in these endeavours and advised against the use of the term ‘fitness’, suggesting that the inclusive fitness concept developed by Hamilton (1964) could be advantageous if one adopted a genic perspective. It was argued here, however, that this suggestion was itself problematic, especially in the light of recent biological discoveries. Further, developments since the adoption of Mendelian genetics and the ‘central dogma of molecular biology’ suggest that matters are far more complex, with the role of the gene now seen as essential but without a privileged or celebrity status. Despite all of these problems, one can still ask, is the neo-Darwinian explanation the only viable one we have and it should therefore be maintained for heuristic reasons. However, this could be an *argumentum ad ignorantiam*, as the structuralists will argue that any resolution will only take place by considering factors outside the normal Darwinian domain.

The principal conclusions reached from this discussion is that the concept of ‘fitness’ has evolved from the term ‘survival of the fittest’, has added a further layer of ambiguity and confusion. The philosophical endeavour to clarify definitions has failed and in fact clouded the issue rather than resolve it. Moreover, whatever definition one subscribes to, none is sufficient to explain how major or small evolutionary transformations occurred. At most, it can only be seen as mapping population changes. However, such stability is more akin to the ideas of fixity that Darwin and Wallace sought to replace. Even the creationists would accept that population numbers might increase, decrease or become extinct over time. Evolution, embracing novel traits and speciation, however, is another matter and one must look beyond the conservative concepts of fitness to explain these. In chapter 13 a fresh approach to the age-old problem will be presented which will hopefully simplify matters. Nevertheless, before this, one must decide what natural selection actually is.

## Chapter 3: The Ontological Question

In the search to understand what natural selection actually is, it is useful to eliminate that which natural selection is not. Consideration will be given to natural selection as a force, as a pressure and as having the ability to act.

### Is Natural Selection a Force?

This question has been addressed by several individuals (Endler 1986, Denton 1998, Ghislen 2007). Their consensus is that natural selection cannot be considered strictly as a force in the scientific sense. This view is endorsed here but it is further argued that if natural selection cannot be considered as a force then it must follow that it cannot also be considered as a pressure, at least in the scientific sense.

To paraphrase one general science textbook, force is that physical quantity that changes or has the potential to change a body's uniform motion in a straight line or change its state of rest. Forces as employed in physics require some object for the force to act upon. However, if natural selection is a force, then what object or objects is it acting upon? For instance, Endler discusses Newton's classic law $F = ma$ and concludes that natural selection cannot be formulated in a similar manner:

> A force is meaningless without an object. If natural selection were a force, it should be possible to decompose it into a mass and acceleration. In this case 'acceleration' is phenotypic selection, but what is the mass? (Endler 1986 p32).

Endler believes there is a further deeper problem, for he argues that physicists only employ force when they do not know what causes an object to be accelerated and he gives the examples of gravity and magnetism. This may be true of gravity, but it is no longer thought to be true of magnetism. In the non-Newtonian world of the 'Standard Model', what are known as the three (of four) fundamental 'forces' of nature are more accurately 'the weak interaction', 'the strong interaction' and 'the electromagnetic interaction'. Each interaction involves different types of particle: for instance, the weak interaction is mediated by the W (negative and positive) and Z particles, which interact with quarks and leptons, giving rise to radiation. One can appreciate that natural selection has no corresponding particles or body essential for an interaction; therefore the description of natural selection as a force is inappropriate. Nor can one assimilate natural selection with the remaining 'force' not accommodated by the Standard Model – gravity. For gravity, too, requires at least two physical objects for a simultaneous attraction. How this attraction occurs and whether the carrier is the graviton particle is still to be determined, but this can be left to the physicists.

### Is Natural Selection a Pressure?

If natural selection is not a force, can it be considered as a pressure? One often hears the term 'selective pressure', but what might this mean? The problem here is that, in scientific vocabulary, a pressure requires a force, measured often in Newtons, and an area. Pressure is equal to force divided by area, with the resulting pressure measured in Pascals. As it has already been established that natural selection cannot be a force, it follows that it also cannot be considered a pressure as in the sense used in physics. The usage is more akin, one could argue, to Economists talk of 'market forces'. Users of the term 'selective pressure' are employing it in some loose manner that cannot strictly be considered synonymous with the use of the term pressure in the physical sciences. One of the triumphs of scientific practice is its adherence to logical thinking and that terms are defined as clearly as possible without ambiguity and equivocation. Moreover, it is most important that definitions of terms are accepted by consensus within the scientific community. This is not the case at the moment with the term 'selective pressure'. One cannot be sure whether the adherent is considering factors that give an organism an advantage over other organisms or is considering factors that simply help an organism to survive and replicate. If these two perspectives are blurred, then clarity and validity are the first casualties within scientific enterprise.

## Can Natural Selection Act?

Natural selection, as evaluated to date, is neither a pressure nor a force in the sense demanded by science. With this in mind, does it follow that natural selection cannot 'act' upon something as it is not a scientific object? Ghiselin and Endler both argue that it is imprecise to talk of natural selection acting upon substances as if it was an agent or some form of agency:

> In various places the exposition might have been improved by not saying that selection 'acts' on something. Selection is not an agent, and talking about it that way can be most misleading. (Ghiselin 2007)
>
> Natural selection no more 'acts' on organisms than erosion 'acts' on a hillside. (Ghiselin 1969) It is a *result* of heritable biological differences among individuals, just as erosion is a result of variation in resistance to weathering and running water. (Endler 1986 p29)

Endler believes this is a source of confusion concerning cause and effect: if natural selection is the result of heritable biological differences among individuals, then it cannot also be its own cause. Endler says natural selection can be seen as a process; but more on this below. One can see here the distinction between natural selection and artificial selection. The latter entails the agency of humans to direct the selection of desired traits. This is not the case with natural selection as there is no selecting agency residing in nature. Nature is blind to future events, and to argue otherwise would be to court the teleological.

So far, it has been established that, as natural selection is not a material body, it therefore cannot be rightly described as a force or a pressure. Neither can natural selection act upon events; this is a metaphorical statement. Moreover, that the term 'selective pressure' requires some consensual clarification. Later, natural selection will be considered as a series of events, or a process, or even as representing several different processes. The examination will be necessary to see if Natural Selection can be characterised more clearly.

## Evolution and Natural Selection: The Distinguishing Features

It is very important to bear in mind that evolution is the explanandum and natural selection is the proposed explanans. However, one reads not only in the popular media but also in the peer reviewed literature terms such as 'evolution selects', 'evolutionary pressures' or 'evolution favours'. For example, 'The evolutionary pressure that produced the emergence....' (Csibra & Gergely 2011), 'Evolution shapes and selects for symbiosis' (Gilbert et al 2010) and 'Evolution favours a medium level of assertiveness in all individuals……'(Conradt and Roper 2009). It should be noted that these are not selective instances but are representative of frequent use by evolutionary biologists. Unfortunately, there is a lax tendency to equate the terms evolution and natural selection to such a degree that they become synonymous. The authors are not alone in such descriptions, for one can find similar in the biological literature, both peer reviewed and the popular. It is imperative, however, to distinguish the two terms 'biological evolution' and 'natural selection' from each other. A good starting point is to remind ourselves what evolution and natural selection are each addressing. Principally, evolution is concerned with change; it is not concerned with historical epochs that remained in a similar form. History, on the other hand, describes both periods of change and periods of no change. Evolution is devoted to the former. One sometimes hears, however, the term 'evolutionary history'. This may sound a little misleading but it could be that the speaker is acknowledging that life on the planet is punctuated by periods of nil or very little change and periods of gradual or rapid change. Of course, it does not follow that evolutionists are uninterested in periods of stasis; quite the contrary, understanding the reasons for stasis informs why it is that evolution occurs.

If it is to have any distinguishing feature, therefore, evolution is about change. But what sort of change does it address? The big picture here encapsulates the emergence of the first cellular organism or organisms and the proliferation that has occurred since, from one or a few to many millions of much diversity. Many have alluded to this as the tree of life, some more recently as the web or mosaics of life and others see the changes that have occurred as discontinuous or episodic.[13] All agree that evolutionary changes have taken place; all agree that there is much diversity where there was once singularity; all agree that nearly all of what was extant is now extinct; and all agree that there is greater complexity rather than less. The big picture of change is uncontroversial, creationists notwithstanding. This cannot be said, however, when it comes to explaining how these changes came about, for here there is great controversy and much confusion. The study of micro evolution has advanced enormously since the 1950s and has accelerated of late. The mass of detail is difficult for any one researcher to comprehend in evolutionary terms and this has led to much interpretation, debate and controversy, which is still ongoing. However, despite this discussion, it is important, for the purposes at hand, to recognise the distinction between evolution and the different processes that explain how changes came about. Natural selection is said to explain biological evolution, not to reiterate it.

## Natural Selection and the Causes of Evolutionary Novelty

> Virtually everybody agrees that the theory of natural selection is a causal theory – it aims to provide a causal-historical explanation for changes in gene/trait frequency over time. (Okasha 2008 p148)
>
> Natural selection as the chief causal process behind all organisms. (Ruse 2006 p103)
>
> Friction heats, and oxygen corrodes, but fever and inflammation are effects of disease, not its causes. If the same logic is applied to Selection Theory, differential reproduction is real but it is an effect of evolution, not its cause. (Reid 2007 p29)
>
> It is important to note that the term 'natural selection' is often used in the inaccurate yet fairly harmless metaphorical sense as having causal status. To be precise, natural selection is not truly a 'mechanism' in itself, as opposed to something like gravity. Instead, natural selection is the result of genetic and environmental forces acting upon an organism. (http://www.biologydaily.com/biology/Natural_selection)

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[13] See Ragan et al (2009) for a modern assessment of the 'tree of life' metaphor.

> Nonetheless, mutation is the ultimate source of genetic variation and thus makes evolution possible. It is important to remember, however, that the likelihood of a particular mutation occurring is not affected by natural selection: that is mutations do not occur more frequently in situations in which they would be favoured by natural selection. (Raven et al. 2005 p438)

> Some have even imagined that natural selection induces variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life. (Darwin 1900 p99)

One of the greatest difficulties in discussing natural selection is that there is no consensus over the definition of the term, as the quotations above illustrate. These are just a few examples but unfortunately they do not fully represent the full scale of the problem. Margulis (2001) argues that natural selection has no causal powers other than to eliminate or preserve novel entities, such as those produced by symbiogenesis. In other words symbiogenesis is a 'driving force' or a causal processes of evolution. Identifying the cause, 'symbiogenesis' is to give explanatory satisfaction. Natural selection, on the other hand and according to Margulis, preserves or eliminates the changes resulting from symbiogenesis.

There is some equivocation also over natural selection, on the one hand, it can be seen as either preserving favourable traits or eliminating unfavourable traits once they have arisen and, on the other hand, as the creative cause of evolutionary novelty. (See below a discussion on what philosophers have considered the positive or negative faces of natural selection). Darwin himself was ambiguous about the term (Butler 1882, Denton 1998): sometimes he spoke of the theory of natural selection as a naturalistic causal theory to counter the prevailing theories of fixity; other times he maintained a more modest role for natural selection, as expressed in the quotation above. This measured account of natural selection, one of preservation and elimination, is foundational to the concept of natural selection as a filter, which, by definition, renders natural selection conservative or eliminative. This is consistent with the view that natural selection can only 'act' if variation is present, but it therefore follows that natural selection under such an understanding is not the creative or causal factor of the variation. If John Stuart Mill (1843) were still alive, he could say that the situation can be considered within his 'method of difference', where changes in gene sequence are the relevant differences that give rise to variation and are therefore said to be the cause. This is analogous to the boy who dropped the lit match into the straw and therefore caused the field to burn, with the counterfactual being that had he not dropped the match the field would have remained in its pristine state. Similarly, had a change in genetic sequence not occurred, *ceteris paribus* the organisms in question would not be subject to evolution. One might argue that 'differential reproduction' is the cause of evolutionary change. It is, however, important to get the chain of causality in the correct chronological order. For differential reproduction to be evolutionarily significant, some event, such as a genetic rearrangement, must precede as the causal factor. As Reid puts it (above) in Selection Theory, differential reproduction is real but it is an effect of evolution, not its cause.

It could be argued that any proponents of natural selection as a causal theory might feel some disquiet with the ideas expressed by Reid above and with the idea that natural selection only plays a conservative role of arbiter or filter. In the eyes of those that see natural selection as positive, natural selection is both the driving and creative force that produces the evolutionary changes that eventually lead to speciation and adaptation.

How might this be established? For the sake of argument and illustration, one could consider natural selection to be an entirely causal process or mechanism rather than a filter. This process conceivably begins with a breeding population that experiences differential reproduction, perhaps following some form of genetic rearrangement in the chromosome. This on occasions produces a new trait that allows an individual organism to breed more effectively than those without the newly acquired trait. Thus, over a long period of time and generations, this trait is more likely to spread through a population. In this light, natural selection is a series of steps or a particular process rather than a force or single causal factor. The proponent of natural selection as a filter might argue that natural selection requires additional qualities to distinguish it, as it is presumed by some neo-Darwinists that natural selection is the cause of adaptation. However, this in turn raises the awkward question of what is the distinguishing feature that characterises natural selection from drift. If genetic changes are small and cumulative, then one cannot know at the time whether the initial changes will prove to be of adaptive value; this can only be recognised retrospectively. The matter then becomes a difference of designation but not of different processes. All one can do is wait to see whether the trait becomes an adaptation and, if so, call this natural selection; but if the trait remains neutral, then call this drift. The difficulty here is that there is no causal factor, as in Mill's methods, once the small mutation has taken place to determine whether the process is to be one of drift or one of natural selection. How does one therefore distinguish Drift from NS? Do initial changes begin as neutral then as they accumulate produce a trait that in turn increases fitness? Or is it that each small mutation must demonstrate fitness?

## The Reification Fallacy

Is part of the confusion here explained by the reification fallacy? This is said to occur when an abstract idea is transformed into something more concrete, or when a process transforms into a physical entity. It could be said that natural selection actually denotes a variety of processes but eventually concretises into a thing, such as a filter. In other words, what begins life as a verb (perhaps an adverb) becomes, later in life, a noun. In this case, natural selection is now both a verb and a noun. This may explain why it is that one talks of natural selection 'acting' upon organisms as some kind of force rather than a particular process. A process is a clearly defined series of events which describes the features involved and arrives at a result. The result is natural selection producing biological adaptation and, in some people's view, speciation. In this light, it is hard to conceive of a process 'acting' upon something, but rather a process should be seen to 'concern' something. Therefore perhaps one should speak of natural selection as a filtering process rather than as a filter; this avoids the charge of the reification fallacy.

## Conclusion

It has been argued that the term 'natural selection' cannot be considered as a force or a pressure in a strictly scientific sense. If this is so, then it follows also that natural selection cannot act upon biological objects. The perception of natural selection as a process looks more promising and avoids the reification fallacy. However, it is important that natural selection as a process does not become conflated with evolution. Evolution is the explanandum and natural selection is proposed as the explanans. The difficulty here is that the process of natural selection and the process of drift both share the same causal component of small mutational changes; therefore it is necessary to identify why it is that either neutral or adaptive traits follow in a non-arbitrary manner.[14] The next chapter will consider, in more detail, natural selection as a process and as a filter, as has been proposed in the literature.

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[14] See Futuyma (2006) for an outline of this problem. Futuyma argues that drift is often a source of speciation.

## Chapter 4: A Critical Analysis

Before examining the problems of causality further, it is pertinent to outline the Principle of Natural Selection (PNS) as perceived and discussed in the contemporary biological textbooks and in the accompanying philosophical literature. However, there are several problems with this approach as not all agree on the content.[15] Nevertheless, a fair attempt will be made to come as close as possible to the foundations of a consensus, without hopefully constructing a straw man. It has been observed (Ch.1) that a clear expression of natural selection was found wanting and this problem has never been resolved. The problems of ambiguity are discussed more fully later. Rosenberg and Arp (2010 p1) provide the following definition of the PNS in terms of a process:

1. There is variation in organisms such that they differ from each other in ways that are inherited.
2. There is struggle or competition for existence, since more organisms are born than can survive.
3. There is natural selection of the traits that are most fit in an organism, given a particular environment which the organism inhabits.
4. Organisms fortunate to have the variation in traits that fit a particular environment will have an increased chance of surviving to pass those traits on to their progeny (survival of the fittest).
5. Natural selection leads to the accumulation of favoured variants, which may produce new species (evolution), given the right environmental conditions and a certain amount of time.

The great advantage here is that the argument is open to empirical examination, escaping the charge of circularity that was levelled at the concept of ‘fitness’. However, under closer examination there are many problems.

Point one, *there is variation in organisms such that they differ from each other in ways that are inherited*, looks at first glance to be fairly uncontroversial, but the premise overlooks the reproductive nature of the prokaryotes. This domain constitutes the small organisms that reproduce by binary fission, producing identical daughter cells. (Audesirk and Audesirk 1999). The premise should be rewritten- *there is often or sometimes variation* ............ There is a world of difference between universal and general statements, it is fundamental in logical reasoning to ensure the premise is an accurate one, otherwise soundness is threatened. The second evolutionary factor that is unclear here is whether the authors conceive of inheritance as purely a vertical transmission. It must be noted that differences can also arise from lateral transmissions of genetic exchange, such as lateral gene transfer, endosymbiosis and hybridisation, but more of this in Chapter 7.

Point two, *there is struggle or competition for existence, since more organisms are born than can survive*, is indubitably contentious. One cannot conclude that because there are more organisms born than can survive that there is necessarily a struggle or competition for existence. The major clause *there is struggle or competition for existence* requires clarification. Does it state that the struggle is a permanent feature facing organisms *all* of the time, or are there periods of struggle and it is only during these that evolutionary changes may occur? Further, is the argument that all organisms are forced to struggle against one another? If this is the claim, then it is clearly refuted by the vast reservoir of biological literature devoted to symbiosis (see also Chapters 1 and 13).

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[15] See Hull (2001), who demonstrates just how difficult it is to characterise natural selection.

It could be argued that the term *struggle* is rather emotive and evocative of Victorian *laissez-faire* values, and not an accurate description of nature. In order to survive, an organism does have to fulfil certain requirements, but that does not necessarily mean that the task is always an onerous one. Point two could be rewritten to reflect the original Malthusian spirit that so inspired both Darwin and Wallace in their searches for the elusive evolutionary mechanism. This includes the perception that food resources tend to be scarce and increase only arithmetically in availability, whereas population numbers rise exponentially and outstrip the available food resources, hence the struggle.[16] Unfortunately, this argument is far from universal, failing empirically. One only has to consider human society: historically, food production mostly stays ahead of human reproduction, with any scarcity often the result of maldistribution.[17] One might argue that humans are atypical but then consider also those organisms that colonise virgin territory: they often have bountiful resources, which can support fairly rapid evolutionary radiations (Russell et al. 2008). Microbes colonise the most varied of territories, lichen colonise many a mountain, rhododendrons colonised large areas of Great Britain and have succeeded, it is said, because they are free of predators in their new environment (Seckbach 2004). Hawaiian islands only 8 million years old have witnessed a radiation of the fruit fly from a single ancestor to an estimated 500 unique species (Whittaker & Fernandez—Palacios 2006). Fish speciation can be rapid in lakes that were previously without fish, thus facilitating evolutionary changes free from scarcity of resources and competition (Russell et al. 2008). The modern biologist is in an advantageous position, appreciating that mutational changes, as an example, do not require the Malthusian element to secure evolutionary changes (Roughgarden 2004 p181).

In defence, one might argue that there is no necessity to demonstrate a universal application but just that it is frequently true. The question arises however, can one demonstrate that it is frequently true? If anything is demonstrated, then it could be argued that the converse to individuals struggling is more likely achieve survival. Is it not the case that the eusocial insects have achieved ‘evolutionary successes’ by means of strong cooperation between individuals and not by struggling against each other? Proponents of kin selection might counter the claims of group selectionists by arguing that eusocial insects manifest an example of genetic selection, but then who has the last word? Wilson, D & Wilson, E. O. (2007), Nowak et al (2012) have argued that kin selection does not have the explanatory power that its proponents believe.

In point three, *there is natural selection of the traits that are most fit in an organism, given a particular environment in which the organism inhabits*,. It is difficult to see why this point is necessary to their argument as the main thrust of the argument is repeated in point 4, below. Furthermore, it is not generally helpful when explaining a term or principle (natural selection) to use the same term as part of the explanation.

In point four, *organisms fortunate to have the variation in traits that fit a particular environment will have an increased chance of surviving to pass those traits on to their progeny (survival of the fittest)*, ‘survival of the fittest’ is far too strong a term. As Gould (1992) remarked, ‘survival of the fit enough’ is closer to the truth. Gould’s ascription captures the spirit of the modern synthesis, thinking the term ‘survival of the fittest’ rather

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[16] Stove (1995 pp54–58) argues that there are many factors other than resource shortage that can check population growth; these include epidemics, contraception, wars and predation. (The criteria of natural selection are, one assumes, expanded to include epidemics and predation).

[17] See Cribb 2011 for a modern assessment of the ‘food crisis’.

crude (and one could add inaccurate). Without Gould's reform there is an unwritten premise or assumption at work to the effect that only organisms with superior qualities will survive and go on to reproduce. It could be that offspring of mixed quality all manage to survive and procreate. In this instance, the population could grow in numbers, accumulating variation and complexity – but only, of course, if resources are available. In Cuvier's terminology, this would read that progeny that 'meet the conditions for existence' are more likely to develop and reproduce, whereas those that fail to meet the conditions for existence will wither from the scene. Empirically, this phenomenon is observed when a species or several species colonise virgin territory such as a newly formed volcanic island. The points discussed so far are insufficient for speciation; point five is requisite.

Point five, *natural selection leads to the accumulation of favoured variants, which may produce new species (evolution), given the right environmental conditions and a certain amount of time*, again confuses whether natural selection is the explanandum or the explanans. It may be clearer to simply say that the 'accumulation of favoured variants may produce new species (evolution), given…………' Or it would perhaps be better to substitute the term 'natural selection' with 'inheritance'. Again, natural selection is to be explained and therefore cannot be explained by including the term itself. That said, some serious questions remain. For instance, *a certain amount of time* is very vague for any scientific measurement and *the right environmental conditions* is so wide and open that almost anything could apply. Furthermore, an organism may possess traits that do not confer reproductive advantage or disadvantage but a change in the environmental conditions may mean that those traits previously considered neutral are now highly beneficial (or even detrimental).

Population genetics can only apply quantitative tools when measuring changes to gene frequencies after the event, never before (Fisher 1930). This leaves the claim to scientific credence resting almost wholly on the theory's explanatory power, but the problem here is that the explanatory component of neo-Darwinian theory is still to be determined. One of its critics is Margulis (following Goldschmidt (1940)), who raises the pertinent empirical question that goes to the core of the justification of the PNS. She asks whether there is a single documented case in the biological literature that demonstrates in nature a succession of mutational changes that has gradually accumulated through heredity, leading to the establishment of a new species:

> I once asked the eloquent and personable palaeontologist Niles Eldredge whether he knew of any case in which the formation of a new species has been documented. I told him I'd be satisfied if his example were drawn from the laboratory, from the field or from observations from the fossil record. He could muster only one good example: Theodosius Dobzhansky's experiments with *Drosophila,* the fruit fly. (Margulis 2001 p9)

Unfortunately, even this example proved not to be an example of speciation through genetic mutation and accumulation. Instead this is, Margulis continues, an instance where flies bred at hot temperatures had lost an intracellular symbiotic bacterium. This loss explained the speciation. Uncontroversially, one can find many examples of mutational change leading to variation, *Biston betularia* being one classic example, but finding evidence of actual speciation by this means has proved elusive. However, a note of caution is called for here: the advent of melanism in the peppered moth may not necessarily be a straightforward mutation; there could be extrinsic factors that induce the biochemical processes that result in the darker colouring. This classic example of evolution in action gave rise to a heated debate as to the causes and mechanisms involved (Coyne 1998, Hooper 2003, Majerus 1998 and 2005, Sargent et al. 1998). Nevertheless, it is one thing to give an example of variation through single mutation but it is much more problematic to provide an illustration of mutation through generations followed by established speciation.

The *accumulation of favoured variants* is itself a term that requires further elucidation, for how does one identify a favourable variant? Are there criteria that can provide objectivity and escape the charge of researcher subjectivity? To judge a variant as favoured, one must recognise the contingency of the immediate environment. The variant will remain favourable unless the environment changes and becomes more hostile. The new favoured variant must therefore still be favoured in subsequent generations and this also holds for each additional accumulative variation. For a new species to arrive, the favourable trait must spread through a population successfully. It would take many generations for a variant to become established and more time still for a further favourable mutation to occur and follow the same procedure. Under these conditions, the emergence of new life forms looks remarkably fortuitous and could be problematic unless there is a good deal of phenotype plasticity. One could plausibly consider that a species that is particularly specialised and dependent upon a small range of attributes within the environment is more likely to become extinct than to evolve. Hence it can be said that generalists are more apt to survive in the longer term than specialists. However, there is still a significant barrier in the explanation of speciation that relies upon accumulative mutations.

## Some Empirical Problems for the Theory

Consider chromosome accretion. One could argue that a good defining characteristic of a species is the quality and number of chromosomes it possesses. As simple examples, donkeys have 62 chromosomes, horses have 64 and hermit crabs a massive 254. One must tread cautiously here, for zebras of different subgenera can have between 32 and 46 chromosomes. Recent research discovered the Indian muntjac (*Muntiacus muntjak*) has the lowest number of chromosomes for a mammal, a diploid number of seven for the male and only six for the female. This compares with a diploid number of 46 for Reeve's muntjac (*Muntiacus reevesi*).[18] When a new species of animal emerges there often is qualitative and quantitative differences chromosomally, but it is very difficult to see how the process of continuous single mutations can account for such differences. The accretion of chromosomes from the early prokaryote to the eukaryote may be better understood endosymbiotically. Further, accretion can be achieved in plants by the process of polyploidy. But how does one explain the accretion of chromosomes within the kingdom of *Animalia*? Our distant ancestors in the form of a single eukaryote cell probably had no more than two million nucleotide base pairs on its single chromosome but over the course of time one can witness the increase to a massive 3.2 billion base pairs on 46 chromosomes in humans (Van Straalen & Roelofs 2006). How can this highly significant evolutionary accumulation of genetic material be explained by the mutation theory described in the new synthesis? Large mutational changes were traditionally perceived in the biological textbooks to be very rare events and almost always resulting in abnormal phenotypes with zero fitness (Stearns and Hoekstra 2005 p101). The modern view is however somewhat different: genetic rearrangements and accretion of DNA are far more complex than conceived by the founders of the new synthesis. It is now appreciated that whole genomes can be acquired or duplicated, sometimes quadrupled (Shapiro 2011)

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[18] For research upon the various species of muntjac deer see Wang and Lan (2000). For a good general overview of chromosomal distribution in animals see Makino (1967).

Natural selection looks to have explanatory value concerning the elimination of undesirable traits and the preservation of the biological status quo, but does it provide a convincing explanation of the emergence of the diverse and numerous species that have blossomed over the past two billion years? Providing a naturalistic causal account of evolutionary diversity and replacing the prevailing Linnaean ideas of species fixity could be a serious problem for the theory as it was originally conceived. For natural selection to explain how species come into existence and then flourish or not, there is a need for more elaboration than the model here presents.

## The Filter Analogy

These shortcomings do not always seem to be appreciated within the philosophical literature for one often comes across arguments that purport to be in defence of natural selection but seemingly only confirm its essential conservatism. Take the 'filter analogy'. For the purposes of this argument, and as discussed in Chapter 3, we will refer to natural selection as a filtering *process* rather than as a filter (which is a reified noun). Nevertheless, arguably natural selection can be seen as a filter that sorts the biological chaff from the biological wheat, whether it is at the level of the gene or the individual or even perhaps the group. Rosenberg and McShea (2008 p18) have argued that the filter analogy is suggestive of teleology, for there is no force or body in nature that is purposely selecting traits that one might see as beneficial. Rather, it is better to see the environment as the filter, or a continuous series of changing filters, blindly interacting with organic bodies. This is indeed a step in the right direction, as it reduces the teleological implications inherent in the term 'selection'. Nevertheless, there are still problems, regardless of whether one calls it an environmental filter or a natural selection filter. Both types of filter would act to reduce variation, as all filters would invariably do. Further, if natural selection were simply a filter, then it would not be able to account for the emergence of new varieties. What would be the source of the diversity all around us? As Camilla Berry is quoted by Reid (2007 p27), 'If natural selection is the filter, what's making the coffee?' A filter is not a creative process; it can only interact with material that is already present. By definition, selection or filtering can only take place if variation already exists; selection must logically follow form, whether one is applying selectionist thinking to reproducing mammals or to the emergence of life from the primordial soup or even, as some do, to the distribution of chemicals and minerals after the Big Bang. An account for the emergence of the 'stuff' is needed if one perceives natural selection simply as a filter.

One can construct a logical argument to illustrate the problem. At some point, a founder species (A) must have evolved to become two species (A and B). For the sake of argument, assume that this was the result of mutational changes and that the new B species is sufficiently phenotypically different to create a mating barrier within the same location. What would be the role of natural selection in the creation of species B? Natural selection cannot 'act' upon A, as A is singular, other than to eliminate A. In other words, if Natural Selection is contrastive, i.e. A rather than B, then this must entail at least two entities. One could not place a single apple on the table and then say please select an apple from the table. Selection is only meaningful if there are two or more apples available. As the presence of both A and B are necessary conditions for selection they cannot be the cause or result of selection. All filters, material or metaphorical, require a plurality of material to sift and separate. The question is then how does this plurality arise? Moreover, if A and B are now both present, then natural selection can only 'act' to eliminate one (or both). But if it were to do so, then any diversity would be lost. How does one explain the emergence of B, if natural selection only has eliminative or filtering powers?

How does one explain by natural selection the fantastic diversity of life as we witness it today if natural selection is simply a filter? Darwin's solution to such problems was to recognise natural selection as preserving or eliminating changes. The first problem here is that preservation is not causal in an originating sense, as it occurs after the event. The second problem is that to say that the evolutionary emergence of 2,000 species of cichlid fish is preserved by natural selection is, by all accounts, rather hollow. The third problem is that if mutation is the factor that caused the creation of new species, then why does one need to invoke natural selection when step-by-step causality is more parsimonious? In short, if natural selection acts on variation, then how does one explain the origin of the variation? If variation can emerge prior to natural selection, why not investigate the sources and incorporate these within the evolutionary framework? This point was raised by Bateson (1894) and referred to in Chapter 1.

One hundred years later philosophers are once again debating the same issues that were extensively discussed during the period known as the 'eclipse of Darwinism'. Today the issue of natural selection is discussed in terms of 'negative' or 'positive' causality, but the arguments are essentially a repeat of what was argued before[19]. Several philosophers have advanced the view that natural selection has negative causality. Sober (1995) discusses the concept of 'distributive explanation' and derives the view that natural selection cannot explain why organisms have the traits they do have. At best natural selection explains the frequencies of traits in populations. Pust (2001) reflects what has been written above in the preceding paragraph, when he considers the 'doctrine of origin essentialism'. Brunnander (2007) argues also that natural selection cannot be considered a force that creates adaptations. Fodor (2008) argues that natural selection has no causal powers and that evolutionary explanations are consigned to a collection of natural histories. Matthen and Ariew (2009) also defend the negative view, citing the reification problem to justify their position. It should be noted perhaps that, apart from Fodor, the above are not critical of neo-Darwinism in general but see room for philosophical clarification of natural selection. In Chapters 9 &10 it will be demonstrated, however, that evolutionary explanation can draw on resources other than just selection and natural history.

Supporting the positive causality view Millstein (2006) argues that natural selection takes place at the level of populations, and it is a causal process. Birch (2012) questions the 'doctrine of origin essentialism' in his attack on negativism. Pigliucci (2009) defends natural selection against the criticisms of Reid (2007), maintaining that only natural selection can explain adaptations. Reid's criticism will be discussed in Ch.11. Huneman (2012) suggests selection is "both causally and explanatory relevant (rather than being shorthand for infinitely numerous individual causal processes)". Martinez & Moya (2011) defend the positive role of natural selection in the generation of organismal form and incorporate a role for 'downward causation' ;

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[19] Both sides of the argument are represented in a collection of essays in *Evolution in Modern Thought* (1909). The claim for the causality of natural selection is attacked by Bateson (1894), Dennert (1904) and DeVries (1909).

> In other words, the adaptive success or failure of certain higher-level entities has a decisive effect on the future presence and distribution of the lower-level entities that (re)produce them.

Rather than extrapolate from lower-level activity such as the gene to explain higher-level activity, one can extrapolate from macro–entities to explain the more micro entities. This is an interesting and novel contribution but even if one accepts this there are still severe limits to its causal power. For instance, one could argue that speciation, the origin of new traits and major evolutionary transitions, are beyond its scope. The other danger here is to divert from natural selection as it was conceived to a more anomalous form. Macro incidents such as a meteor strike inflicting damage on higher-level entities would indeed also have severe consequences for lower-level entities, that much is uncontroversial. Nevertheless, one can question whether mass extinctions and their consequences are embraced under the principle of natural selection.

## The Problem of Ambiguity: What does the word 'selection' mean?

Natural selection was originally employed in reference to the competitive struggle for resources under increasing population numbers but in the twentieth century, the PNS was broadened and applied to any phenomena that might give advantage or disadvantage to an organism's ability to reproduce. Darwin also conceived of sexual selection as an additional process *independent* of natural selection in order to explain traits that on the surface may inhibit successful competition. (Ch.1) The peacock's train was the classic example. Sceptics of this latter form of selection saw it as an *ad hoc* measure to plug anomalies in the original PNS (Popper Ch.2); whereas neo-Darwinism, to summarise, saw it as a legitimate extension of the paradigm. The situation has grown most bizarre, natural selection was originally conceived to explain evolutionary changes but now evolutionary changes are said to occur when natural selection is relaxed or lifted. (See below) This is why one must conclude that the term 'natural selection' has become anomalous.[20] There is now such a proliferation of forms of selection, many are detractive. These terms will be considered in an attempt to establish why the introduction of these forms was thought necessary and whether these new forms of selection are processes independent of natural selection or whether they are subsumed under an overarching umbrella of natural selection. Finally, consideration will be given to the sceptic's charge of *ad hoc* manoeuvring.

Although Wallace never accepted sexual selection as an evolutionary factor, the term was introduced by Darwin in the 1858 submission and maintained by him throughout his life. (Ch.1) Under pressure from Wallace and Mivart, Darwin was forced to add a further term of 'reversed sexual selection'. This was intended to cover what Wallace (Quoted in Berry 2002 p89) and Mivart (1876) saw as an anomaly in the theory, for example, it was the males rather than the females that appeared to be selecting partners. Explanations of a selective nature fell from fashion after Darwin's demise, but were revived again some 50 years later. Schmalhausen (1949) introduced the term 'stabilising selection' to denote an organism's robustness in early development against the background of an unpredictable environment. Quite why the term 'selection' was affixed here is not entirely clear, as the term 'stabilising' imputes order and regularity. 'Canalising selection' was coined by Waddington (1942) and today denotes either environmental or genetic

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[20] Anomalous, in the sense defined by the Merriam – Webster dictionary: *inconsistent with or deviating from what is usual, normal, or expected and of uncertain nature or classification*

canalisation. Again, one must wonder why the term selection was applied when canalisation implies order with only a little variation. Nowadays one mostly hears or reads ‘canalisation’ without the suffix being unnecessarily applied. More recently, ‘balancing selection’ or sometimes ‘overdominant selection’ is said to ‘act’ within a population and is able to maintain stable frequencies of two or more forms of phenotype.[21] A mutant homozygote or the normal homozygote is said to have less fitness than the products of the heterozygote. Contrast this with ‘purifying selection’, which is ‘acknowledged by most evolutionists as the predominant form of selection’ (Bustamante et al. 2000 p103), where mutations are eliminated and the existing genetic stock is highly conserved. Purifying selection can also be strong or weak. Continuing in this vein, ‘orthoselection’ was introduced by White (1973) to denote how chromosomal arrangements might become fixed, which included both the symmetry and asymmetry of forms. Orthoselection proved controversial, though, not because the term has undertones of an oxymoron but because White’s empirical data was questioned (King 1995). It was suggested by King, however, that the selective terminology was unnecessary.

All of the selective terms above, apart from those concerning sexual selection, have in common a conservative foundation where order and consistency are maintained at the different biological levels. With selection here displaying such a conservative nature, one might wonder how evolution occurred. However, the list is far from complete, and opposing forms of selection are now examined. The most commonly used of these is ‘directional selection’, which can also be referred to as ‘dynamic’, ‘linear’ or ‘progressive’. There is some ambiguity concerning the events that directional selection is said to represent. One account Ridley (2003) gives the example of greyhound dogs being selected for speed, which is actually a form of artificial selection, and later gives the example of the selection in nature of body size. However, directional selection could result in fitness for larger bodies and also in fitness for smaller bodies. For instance, predation could eliminate a particular size, thus favouring the remaining size. Similar to directional selection, ‘frequency-dependent selection’ considers how different organisms may have their fitness improved when their frequency is considered in relation to the frequency of other organisms. There may also be a more conservative maintaining role, including a 50:50 sex ratio, polymorphism in prey species, males with rare attributes, and even left-handedness in humans (Dorak 2007). However, one must be careful, for there are said to be various forms of ‘frequency-dependent selection’, including ‘stabilising frequency-dependent selection’, ‘disruptive frequency-dependent selection’, positive frequency-dependent selection’ and ‘negative frequency-dependent selection’. Further, ‘frequency-dependent selection’ is also said to be strong or weak. It is not surprising that this proliferation of terms has caused some confusion and led researchers Heino et al. to lament:

> Frequency-dependent selection is so fundamental to modern evolutionary thinking that everyone ‘knows’ the concept. Yet the term is used to refer to different types of selection. The concept is well defined in the original context of population genetics theory, which focuses on short-term evolutionary change. The original concept becomes ambiguous, however, when used in the context of long-term evolution, where density dependence becomes essential. Weak and strong frequency dependence, as distinguished in this article, refer to two very different forms of selection. (Heino et al. 1998 abstract)

This ‘enigma’, as the researchers say, is the result of a term being employed to denote one set of events at perhaps the micro level but the same term being employed at the macro level to denote a similar but

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[21] All definitions of the various forms of selection, other than those referenced in the text are extracted from Bell (2008).

nevertheless different series of events. There is a profound problem here and it is not simply one of semantics. Appendix 4 provides a compilation of selective terminology but is far from exhaustive. The selective terms cover an enormous range of phenomena from many forms of sexual selection, environmental and ecological selection, artificial selection and much biochemical selection. With such diversity of events denoted, one is left to wonder what the term 'selection' actually means. The term has become so elastic that it has lost any meaningfulness and has led to the charge of being a biological 'phlogiston' (Lima-de-Faria 1988 see below).

In efforts to reform the anomalous use of the term 'selection' as perceived in neo – Darwinism, Reiss (2009 Table 12.2) has demonstrated how selective terminology can be explicated and passages re-written in a clearer and more parsimonious manner. Two examples, from the many that Reiss provides, follow. From his survey of the literature Reiss identifies a common usage first, followed by his explication.

Example 1 -

> "Because it is difficult for small forest fliers to soar, the selective pressure to increase horizontal range by switching to flapping should be considerable".

Reiss's explication-

> Because small forest fliers can't soar, an increase in horizontal range *can only occur* by switching to flapping.

Example 2

> Whatever the reason, *selective evolution* has resulted in an arrangement in which dinosaurs best adapted for operating in well-lit conditions mainly fly during the day, and mammals well suited for flying in the dark take over after sunset.

Reiss's explication-

> Whatever the reason, *evolution* has resulted in an arrangement in which dinosaurs best adapted for operating in well-lit conditions mainly fly during the day, and mammals well suited for flying in the dark take over after sunset.

Reiss should be congratulated upon some excellent reforming work and hopefully his book will reach a wide audience.[22] (In chapter 12 Reiss's views on neo-teleology will be considered). Let us now return to an earlier critic of selective terminology.

## The Phlogiston Problem

The phlogiston theory of combustion makes a frequent appearance in the philosophy of science literature when issues of realism and anti-realism are discussed (Cohen et al. 1996). It is an example of a postulated entity that has subsequently been shown not to exist, and yet it enjoyed a fair amount of empirical success. The following historical summary is extracted from Larson (2008).Phlogiston was considered to be a substance that every object possessed: for example, the earth or soil was low in phlogiston whereas metal and fire were high. When metal is heated at high temperatures, it reduces in size; this was said to be because of the loss of phlogiston. The theory 'explained' that fire burns out in an enclosed space because the air becomes saturated with phlogiston. Moreover, any creatures confined in airtight spaces would die from such

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[22] Dupre 2011 gives a very favourable review of Reiss's 'Retiring Darwin's Watchmaker', see http://www.americanscientist.org/bookshelf/pub/the-conditions-for-existence. For a more critical review see Deprew 2010.

saturation. In describing what the phlogiston theory explained, Larson says further, 'some metal calxes turn to metals when heated with charcoal because the phlogiston from the charcoal restores the phlogiston in the metal.' Lavoisier was one who was sceptical of the theory, in particular when supporters of it ascribed additional properties to phlogiston in order to overcome anomalies. In the following example, phlogiston was 'discovered' to have negative, neutral and positive qualities:

> The problem was that when some metals were calcined, the resulting calx was heavier than the initial metal. Some proponents of the phlogiston theory tried to explain this phenomena by saying that in some metals, phlogiston has negative weight. Furthermore, it was discovered that mercury could be turned back into a metal simply by heating it, that is without a phlogiston rich source such as charcoal. Rather than except [*sic*] this theory that phlogiston could have positive weight, negative weight, and sometimes no weight at all, Lavoisier suspected and later proved that the weight increase was a result of the metal combining with air. (Larson 2008)

The theory of phlogiston enjoyed longevity of over 100 years and acceptance by the vast majority of scientists and thinkers. There were persistent critics, but these were often outsiders and marginalised. There was also enormous peer pressure to accept what everyone knew to be true; if one harboured any doubts, it was better to keep such reservations to oneself, especially if one was career minded. Those who did question the majority view, though, discovered they were attacking shifting sands. This was principally due to the ability of the proponents to invent new terminology each time an anomaly was encountered or to suggest external inconsistencies, such as the quality of the air, to explain away any potential loopholes. The theory also lacked any predictive power; one was only wiser after the event:

> Of course, one didn't use phlogiston theory to *predict* the outcome of a chemical transformation. You looked at the result first, then you used phlogiston theory to *explain* it. It's not that phlogiston theorists predicted a flame would extinguish in a closed container; rather they lit a flame in a container, watched it go out, and then said, 'The air must have become saturated with phlogiston.' You couldn't even use phlogiston theory to say what you ought *not* to see; it could explain everything. (Yudkowsky 2007)

There are, it seems, some striking and alarming parallels between the extended PNS and the phlogiston theory. Is this the case and does the charge of a biological phlogiston put forward by Lima-de-Faria hold? The criticisms are now outlined and their strength, if any, evaluated. Lima-de-Faria recognises that selection does exist but, similar to phlogiston, it has no material body: 'selection cannot be weighed, stored or poured into a vial.' (Lima-de-Faria 1988 p7) A better comparison, it is argued, is that of 'heat'. Heat was once considered to be a material component but, following the insight and work of Joule, heat was later deemed not to be matter but to be only a state of matter. Selection is similar to heat or work, in that it represents a state in progress. The conclusion is that 'selection cannot be the mechanism of evolution for the simple reason that it is not a material component of organisms.' (Lima-de-Faria 1988 p7)

There are a couple of concerns with this analysis. First, it is not clear that any evolutionary biologists or philosophers would consider natural selection to be a material entity. Second, it does not seem unreasonable to consider natural selection as series of causal interactions that constitute a process. The real difficulty is to clearly identify without ambiguity what constitutes this process. However, there is a common lax tendency to talk of the PNS as if it were a force or pressure and this usage is more difficult to substantiate.[23]. The second

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[23] Incidentally, Lima-de-Faria's own hypothesis of 'autoevolution' fails to meet the criteria he sets out for a mechanism, for autoevolution too has no particular material components.

charge within the analogy is more serious and concerns the proliferation of selective terminology discussed above. The similarity here, according to Lima-de-Faria, is that phlogiston enjoyed properties that could explain all manner of chemical reactions. The example that phlogiston could have weight, be weightless and exhibit negative weight is disturbingly of the same order of the properties that selection is said to have: 'Selection has been ascribed the most conflicting properties. Selection can be both "directional", and "accidental", it can "canalize" and it can "diversify".' (Lima-de-Faria 1988 p9) What is perhaps more disquieting is that since these words were written in 1988, there has been a mushrooming of selective terminology, which embraces a much wider range of biological phenomena (see Appendix 4). Several of these contrary terms have already been mentioned and further evidence suggests there is a genuine quandary here. What has happened with 'selective terminology' is that because a formal definition of natural selection or the term selection has never been agreed, selective terminology has been unwittingly added ad-lib, with no foreseeable parameters. It has been applied so widely, from molecules to genes and to universes (See next chapter). It is not the case that individual instances of selective terminology do not represent biological phenomena, or at least attempt to represent biological phenomena, but it is the case that the term 'selection' has become superfluous. It would be a clearer practice to individually name, or refer to each of the natural processes the selective terminology is thought to represent. Every eventuality, it seems, could be given the term 'selection' as a referent; but with so many referents, what does the term 'selection' actually mean? When a commentator says 'there is selection of' or 'there is selection for' or 'there are selection pressures', it is difficult to know what they have in mind as there are so many ascriptions to 'selection'. What began as recognition of one important naturalistic process of evolutionary change has multiplied over the years into recognition of very many different naturalistic evolutionary and non-evolutionary processes. Darwin was correct to appreciate that his Principle of Natural Selection was one process amongst others, and that the other processes were entirely independent of selection.

## Natural Selection and Variation

Natural selection is said to act on variation, that much is uncontroversial. Selection is therefore chronologically post-variation and independent from the sources of variation. However, it seems these parameters are not that secure. To compound the serious problem of anomalous selection yet another form of selection is employed: 'antagonistic selection'[24]. This form of selection actually has a causal effect upon variation, 'we currently know little about the evolutionary interactions between antagonistic selection, recurrent mutation, and genetic drift, which should collectively shape empirical patterns of genetic variation' and 'First, antagonistic selection inflates heterozygosity and fitness variance across a broad parameter range…….'(Connallon & Clark 2012). This extension of selective terminology undermines what originally was a fairly clear and straightforward formulation of the selection process. Moreover, with these additions the term 'selection' becomes increasingly difficult to pinpoint.

## Conclusion

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[24] Antagonistic selection can take different forms, sexually antagonistic selection, antagonistic balancing selection, antagonistic directional selection

This chapter has demonstrated that if natural selection is seen as a filter, or more correctly as a filtering process, then its role is eliminative or conservative only; it cannot be the creative force that gives rise to biological diversity. This recognition at least reconciles fitness and natural selection as preserving but not causal of *de novo* features. The role of causal factor is given to mutation, but it was argued that single point mutation is insufficient to account for the accretion of genetic materials and complexity. Mutation in the modern sense is recognised as much more multifaceted, with genetic duplication occurring. This goes some way to addressing the accretion problem. However, it was recognised that other factors, such as lateral gene transfer and viral vectors, are now established as playing an important role in genetic accretion and phenotypic expression.

The problem of ambiguity is the most serious for natural selection. Much of this difficulty has stemmed from the gradual introduction of selective terminology to cover newly discovered biological phenomena, some of which were originally conceived as being opposed to natural selection. This has given natural selection a host of contrary attributes, prompting the charge of a biological phlogiston. Under examination, the analogy between selection and phlogiston was held to be largely and seriously true. The disturbing similarities require consideration and some clear criteria are demanded to determine what constitutes ‘selection’. Is the word selection shorthand for natural selection or does it have its own identity? Selection, without a formal definition, has evolved from its Malthusian origins to something meaningless one might call ‘anomalous selection’.

## Chapter 5: The Further Extended Principle of Natural Selection

As stated, the main objective of this thesis is the disambiguation of natural selection. If this can be achieved then one is in a better position to evaluate proper application. However before this can be achieved it is important to identify the current applications of natural selection and to examine exactly how far it's powers are thought to extend. It has been fashionable of late to apply neo-Darwinian principles to other fields of enquiry. In particular, the PNS has been used to try to provide a further layer of explanation to such fields as cosmology, mineralogy and chemistry. In the social sciences, neo-Darwinist ideas have permeated areas such as psychology, economics, ethics and anthropology.[25] There is a proselytizing website called 'universaldarwinism.com' and Dan Dennett (1995) has aptly talked of the 'universal acid of natural selection' to describe this spreading phenomenon. Historically, natural selection has been employed to justify some dubious economic excesses of laissez faire and in the 1920s until the 1940s the evils of Nazi eugenics. Unfortunately without parameters then anything goes. Focus here however will concern the extension of natural selection to cosmology and mineralogy, for these areas concentrate upon the import of natural selection rather than the entire neo-Darwinian thesis. This singularity will make it easier to identify what manner of natural selection is being employed and whether this move adds or subtracts explanatory power. First, consideration will be given to cosmology and the arguments of Lee Smolin. This will be followed by consideration of a similar line of argument that applies to molecular and mineral evolution.

### Cosmology and the PNS

'Cosmological natural selection' is a hypothesis projected by Smolin (1998) and intended as a scientific alternative to the anthropic principle. In the outline that follows, the accuracy of Smolin's descriptions of cosmology will not be questioned. The only question will be, '*If* Smolin's description is true, then can one apply principles of natural selection to it?' Smolin takes it as given that there is a multiverse, an almost infinite number of universes rather than just the singular. Within these universes, there can be black holes, absorbing matter that passes through to the 'other side'. In the event horizon of a black hole, a child universe is created and this child universe inherits almost the same value for parameters as its 'parent' universe. Reproduction of the new child universe is not perfect owing to 'mutation', and this can affect the quality of the parameters. It is these parameters of physics which determine the lifetime of the emerging child universe and also the number of black holes in each offspring universe. From this, it follows that universes with the highest number of black holes will predominate over universes with fewer or no black holes. In other words, the universes with the largest number of black holes are the fittest as they are the ones that will produce the greatest number of child universes. *Ceteris paribus*, these child universes are more likely to contain the greatest number of black holes within the population of universes.

One thing that is clear from this analogy is that it is not analogous with the Malthusian form of natural selection. There are no problems, it seems, with rising populations of universes in competition for resources. The analogy does, however, seem quite consistent with the concept of fitness at its bare bones: successful reproduction is more likely to beget further successful reproduction in later generations. This more general

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[25] See Barkow (2006) for an overview of the influence of neo-Darwinism on other sciences. Also Blackmore, S. as a supporter of 'universal darwinism'(1995).

principle is more accommodative and applies if one is considering vertebrates, invertebrates, prokaryotes or black holes. Nevertheless, one might argue that the analogy with respect to the biological world begins to break down when one considers that the fitness of an organism is dependent upon a changing and unpredictable environment (Vaas 1998). This is in contrast to the environment that the child universe encounters; here, there is predictability, because the void is, one assumes, of a constant nil quality. (Also, one assumes that the void presents no barriers, so there is no problem of competition for biological space.) One might also argue that Smolin has actually given a presentation of 'drift' rather than one of natural selection. The difference between drift and selection is said to be that natural selection leads to adaptation, whereas drift does not. In Smolin's account of evolving universes, there is no talk of adaptations. A further breakdown of analogy concerns the mutation of the parameters. According to neo-Darwinism, aforesaid, in the biological world, mutations are mostly considered to be harmful but, on very rare occasions, a beneficial mutation subsists and then, at a later date, another beneficial mutation subsists, and so forth with cumulative success. Mutations here are considered to be random (not uncaused) and cumulative, but is this the same for the mutations that are said to alter the parameters of the developing child universe? Moreover, are the mutations in the formation of parameters random? They are certainly not cumulative.

Despite all of these dis-analogies, one could still accept that there are these differences but that, in principle, the fundamental line of successful reproduction, however it is achieved or comes about, remains the same in the biological and the cosmological realms. There is within the principle of fitness a clause of *ceteris paribus*, which removes such extrinsic factors and considers only the fundamental principle. Let us remind ourselves what the fitness principle actually is, or at least consider what purports to be a fair representation of a difficult concept: 'Trait X is fitter than trait Y if and only if X has a higher probability of survival and/or a greater expectation of reproductive success than Y.' (Sober 1993 p. 70.) In cosmological terms, this simply translates to 'Universe X is fitter than universe Y if and only if universe X has a higher probability of survival and/or a greater expectation of reproductive success than universe Y.'

Under this light, Smolin could argue that his version of cosmological natural selection is quite consistent with the fundamental principles of biological fitness. Indeed, there is nothing in either of the above formulations that concerns the random nature of mutations or the effects of changing environments or the controversy over the relationship between drift and natural selection. Cosmological natural selection is consistent with biological natural selection translated into the principle of fitness, but it is not consistent with the original Malthusian concept of natural selection. One concern here, however, is the use of the terms 'natural selection', 'survival of the fittest', 'fitness' and 'fitness landscapes'. The last term is a visual representation of fitness concerning the relationship between a genotype or a phenotype and its reproductive success or lack of success (Wright 1932). Fitness itself was intended as a refinement to the 'survival of the fittest' and Malthusian natural selection. (Ch.2) However, Smolin (2008) says that 'natural selection works on properties like fitness', but is there confusion here? What sense of the term 'natural selection' is Smolin alluding to? As discussed, Smolin's analogy with Malthusian natural selection does not hold; therefore Smolin must employ the 'fitness' version of natural selection. However, Smolin's statement translates to 'fitness works on properties like fitness', an undesirable circularity. The issue raised here concerns the term 'fitness', which is said above to be a *property*; but 'fitness' can also be construed as a more refined *process* than its predecessor, 'survival of the fittest.' It is unfortunate to have the term 'fitness' as both a process and a quality. Perhaps it would be clearer to identify an organism enjoying the property fitness, which resulted from a particular process, and then to illustrate whatever the process was. A further problem for cosmological natural selection is that the analogy rests exclusively upon mutation providing the process of evolutionary change. This may have been the 'received view' for many biologists up until the 1990s, but arguably this is no longer the case. Issues of genetic exchange are now incorporated into evolutionary theory (See Ch.7). The analogy is out of date with the extended modern synthesis (Pigliucci and Muller 2010). This is a major oversight within Smolin's analogy; it is very difficult to see how two universes could ever combine to produce a child universe.

The analogy also has its limitations. For instance, there must be a maximum number of black holes a universe can sustain. This consideration can only be understood mathematically, and recourse to 'natural selection' is not necessary or helpful. Further, the account of successive universe reproduction seems little more than a mathematical progression. Consider different banks offering different rates of interest to investors; one does not have to be a genius to realise that the accounts providing the higher interest will grow at a faster rate than those providing a lower interest rate. This simple type of reasoning is sufficient to explain why universes with greater numbers of black holes are more likely to predominate, *ceteris paribus*, after successive generations.

Further limitations to the employment of cosmological natural selection concern the origin of a first universe in comparison to the origin of our distant ancestor in the biological literature. An original universe cannot have been the result of a black hole, because a black hole's existence can only follow from the existence of an earlier universe. If there were an 'original' universe, it could only have emerged without the facility of a black hole. How do we know that this phenomenon might not repeat itself? This ontological problem is not exclusive to cosmological natural selection, but it does illustrate the same problem that biological natural selection faces with first emergences of life. Selection, by definition, can only operate once a variety is already in existence. However, if there is already in existence a biological variety, then how did this come about? Natural selection seems only to preserve and eliminate; a conservative role has already been suggested but will be discussed more fully later.

### Molecular and Mineral Selection and Evolution

In a similar vein, Darwinian principles have also been used to try to explain the distribution of molecules, minerals and chemical compositions. Cairns-Smith (1985) was probably the pioneer of this extension when he first introduced the idea that clays played an important role in pre-biotic evolution. Some crystals within the clays were more likely to flourish and replicate than other crystals in particular environments, hence the analogy of a selection process. Recently, Cairns-Smith (2005) has argued that the driving force for the transition from geochemistry to biochemistry was natural selection.[26] Hazen goes further still, applying selection to both molecules and minerals:

> Molecular selection, by which a few molecules earned starring roles in life's origin, proceeded on many fronts. Some molecules were inherently unstable or unusually reactive and so they quickly disappeared

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[26] Not all bio-geologists subscribe to interpretations couched in selection, see also Sandstrom (2006), Yushkin (2008) and Bejan and Lorente (2010).

> from the scene. Other molecules proved to be soluble in the oceans and so were removed from contention. Still other molecular species sequestered themselves by binding strongly to surfaces of chemically unhelpful minerals or clumped together into gooey masses of little use for the emergence of life. (Hazen 2005 p234)

Hazen, however, sees no role for randomness, an element of importance for neo-Darwinists concerning the introduction of evolutionary novelties. Instead, all evolving systems are seen as stochastic processes, which may influence specific outcomes of some selective events, but selection is ultimately guided by physical and chemical principles. What is analogous here? Clearly, there is again little similarity with the Malthusian brand of selection, which incorporates competition resulting from diminishing resources in the face of increasing population numbers. Further, as already mentioned, there is little similarity with the neo-Darwinian mechanism of differential reproduction fuelled by random mutation. Also, what exactly is meant by ‘selective events’? For instance, could one not, for the sake of parsimony, rewrite ‘all evolving systems are seen as stochastic processes, which may influence specific outcomes of some selective events, but selection is ultimately guided by physical and chemical principles’ as ‘all evolving systems are seen as stochastic processes ultimately guided by physical and chemical principles’?

One could complain that ‘selective events’ and ‘selection’ above seem to be doing little work when it comes to explanatory power and that they confuse issues rather than illuminate them. On the other hand, Hazen would argue along the lines that evolution only occurs in systems with combinatorially vast numbers of possible configurations:

> What we observe in nature in every one of these systems (elements, isotopes, minerals, organic molecules, etc.) represent the tiny fraction of all possible configurations that are functional. Such observed configurations are selected (deterministically in most cases) from the vast number of possibilities because of their functionality. That’s why you will find quartz (function = minimum Gibbs free energy) on every terrestrial planet and moon. It’s selection, pure and simple. (Hazen, private correspondence)

Once again, it is difficult to perceive what work the term ‘selection’ is doing here. One could say it is *determinism*, pure and simple, rather than ‘It’s selection, pure and simple’. Elements, isotopes, crystals and so on may be distributed throughout the universe by virtue of their functions (or perhaps dynamics), but determinism is sufficient here and more parsimonious than adding another layer of selective terminology. Why should one introduce a new terminology that is tainted by teleology, contentious and divisive in biological theory to a science that has enjoyed freedom from such controversies?

## What is Life?

One of the problems with extending natural selection to other disciplines is that it could erode natural selection’s explanatory power in the biological domain. One perplexing question for biologists and philosophers is what is it that distinguishes animate matter from inanimate matter? What is it that special quality that characterises life? There have been many proposals to this and one currently suggested is that life is a “self-sustaining chemical system capable of Darwinian evolution.” (Benner 2010) By this, one assumes that ‘Darwinian evolution’ includes natural selection as the major mechanism. From a Darwinian perspective the inclusion in the definition of ‘capable of Darwinian evolution’ does not seem an unreasonable inclusion. Leaving aside the first part of the proposed definition, ‘sustaining chemical system’ one could argue that ‘Darwinian evolution’ is an important characterisation that distinguishes life from non-life. However, there is a problem. If one advocates natural selection as an explanatory substrate suitable for export to other sciences such as those discussed above then natural selection cannot be used by biologists to distinguish life from non-life. One must therefore on the one hand stop the characterisation of life by recourse to Darwinian evolution if one wishes to extend natural selection to other sciences, or, on the other hand, refrain from extending natural selection to other sciences if one wishes to maintain natural selection as a defining characteristic of 'life'.

## Conclusion

The concern here is that, when extended to other fields outside the biological realm, the PNS becomes overgeneralised, so much so that all that is achieved is an undesirable vacuity. 'Cosmological natural selection' is yet another term that can be added to a list of 'selective' terminology. When unpacked, the term is consistent with the principle of fitness, but in this instance applied to universes and black holes rather than to reproducing biological populations. However, the analogy fails to recognise the difference between evolutionary drift and natural selection that is said to lead to adaptation. 'Cosmological drift' may be a more accurate description of the manner in which universes reproduce, for the matter is really one of mathematical and logical progression. Similarly, one could suggest that the evolution and distribution of minerals, crystals and other chemical compositions is simply and more accurately described as determinism; talk of mineral A 'competing' with mineral B adds nothing but undesirable anthropomorphic language. Importing biological terminology adds nothing of explanatory value to non-biological evolution or cosmology and in fact only adds unnecessary confusion. To import selective terminology to these fields is to import an area of biology that is already ambiguous, confused and controversial.

Without parameters to determine the correct application of natural selection there is nothing to prevent a perverse use of the concept. For example, if natural selection takes the contrastive form *a* rather than *b*, then under the wider extension *a* and *b* could signify anything one chooses, from particles to universes, even to ethnic groups. One could argue for instance, that during the last 'ice age', ice (*a*) was selected as it extended from the poles, in favour over organic life (*b*). Or even that the present desertification of the planet is the selection of sand (*a*) in favour over arable land (*b*). Clearly then parameters are necessary to prevent such unhelpful nonsenses. Unfortunately, without a formal definition of natural selection or clear characterisation of the 'substrate', these parameters are very difficult to establish. This is the subject of the next chapter.

# Demarcation

## Chapter 6: Seeking Boundaries

There are a wide range of biological scientific objects, processes and behaviours that should be considered beyond the scope of explanation by natural selection. Some of these are uncontroversial and are accepted to stand outside of the parameters provided by any definition of natural selection, but some prove more controversial. Part of the problem here may arise because there are different definitions of natural selection in play and it may even be that an individual unwittingly subscribes to more than one definition. Darwin and Wallace disagreed over the scope of the explanatory power of natural selection primarily because they held similar but not identical theories (Ch.1). It could be argued that those who are the most selectionist consider themselves neo-Darwinians but in truth their selectionism is more reflective of Wallace, who had little time for all of Darwin's pluralism. Nevertheless, Wallace himself did not believe that all of nature could be explained by his principles and he listed a range of such phenomena under the heading 'What Natural Selection Cannot Do' (Wallace 1869/70). Both men recognised things in nature that they thought had no bearing on the struggle for existence, which they perceived all organisms must face. These were quite wide ranging and included Darwin's view that the colour of the blood was simply the direct result of physical determinism.[27] Wallace included human characteristics such as moral awareness and the ability to perform complex mathematics. Since then, our knowledge has increased immensely; however, the controversy over the issue has not receded but seemingly multiplied. As one recognised philosophy website puts it:

> Natural selection is a causal process. Distinguishing it from other processes in evolution is one of major conceptual and empirical problems of evolutionary biology. (http://plato.stanford.edu/entries/natural-selection)

How does one then distinguish items that are covered by natural selection from items that are not? What criteria should one employ? To answer these questions, one must first be clear what is meant by natural selection and, as witnessed, this is no mean feat. For instance, there is a stricter sense of natural selection that denotes 'differential reproduction' and 'differential survival'. There is also a looser sense of natural selection, a non-originating sense that simply involves the filtering of whatever emerges of biological novelty. This latter perspective could have serious consequences for demarcation of the different evolutionary processes.

One can logically infer that anything that does not conform to the processes above is, by definition, outside the realm of explanation by natural selection. For example, if there is no differential reproduction, with all the offspring cloned, then natural selection need not be invoked. Neutral evolution is considered to be independent of the PNS. This is not because of a lack of any differences in phenotypes that occur via reproduction or replication but because these differences do not confer either fitness or lack of fitness. One of the difficulties here is that the fitness concept is philosophically controversial and difficult to quantify in a meaningful manner (Ch.2). This is particularly so if fitness is contingent to the environment, for the environment can be highly variable and unpredictable. If one could stabilise and control the environment, as experimenters in the lab can do, then calculations would be easier. Unfortunately, this is not afforded in nature, which is our principal concern. One is faced with the problem of trying to clarify an ambiguous and

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[27] See Darwin 1868 for different accounts of the direct impact of the environment upon form.

messy affair concerning natural selection by appealing to the concept of fitness, which is itself an ambiguous and messy affair.

One criterion that seems less controversial when demarcating against natural selection is the direct impact of the environment upon a whole population. The important consideration here is that it refers to the *whole* population and not to some members or an individual being advantaged or disadvantaged. Differentials are not relevant at this juncture when the environment impacts on the whole. An example might be an expanding ice age that destroys everything in its wake. Suppose, however, that a few individuals manage to escape such rigours by migrating to warmer climes. Does one say, in this instance, that the surviving handful was selected for and the majority that perished were selected against? The danger is that if one generalises selection to this extent, then one can also claim that whatever happens to exist is the result of natural selection and whatever does not exist is also the result of natural selection. The overgeneralisation of a theory could be considered a form of 'underdetermination'. Some of the biological phenomena that may not pertain to natural selection will now be identified.

## The Forgotten Cause in Evolutionary Theory

One area of concern and debate is the revival of interest in the origin of the form and structure of organisms. Muller and Newman (2003) argue this is in contrast to the major focus of many evolutionary biologists, who address mainly what is preserved and quantitatively varied. The authors raise pertinent questions concerning what they call the 'Origination of Organismal Form: The Forgotten Cause in Evolutionary Theory'[28]:

1. Why did metazoan body plans arise in a burst? [*This is in reference to the advent of new morphologies in the Cambrian explosion 530 million years ago*.]
2. Why do similar morphologies arise independently and repeatedly?
3. Why do distantly related lineages produce similar designs? [*The question of convergence that perplexed Mivart.]*
4. Why do building elements organize as fixed body plans and organ forms?
5. How are new elements introduced into existing body plans?
6. Why are design units reused repeatedly? [*In reference to modularity*.]
7. Why are not all design options of a phenotype space realized? [*The issue of constraint*.]
8. Why do characters long absent in a lineage reappear? [*Atavisms.*]
9. Why are the rates of morphological change unequal?

Reflection upon these nine difficult questions should indicate that the concept of natural selection as a filter is not a helpful explanation. It would be facile, for example, to answer question five by stating that new elements are introduced into the body plan because they are successful and if they were not successful they would not be incorporated. The question already acknowledges that the new elements are incorporated into the existing body plan, so success or fitness is conferred. The pertinent question is *how* these elements were incorporated: what are the underlying physical processes that caused these new (and to be maintained) features? How things come about is a different matter from how things become established. Perhaps the question could be reformulated to make the point here clearer: 'How did these novel elements, which have now become established into the body plan, originate?' One can now focus on the causes of the novelty and ask whether the 'natural selection as a process' version of natural selection provides the explanation. In other words, do a series of accumulated random mutations explain how such novel features are formed and

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[28] The text in italics is added to the original.

incorporated into the body plan or does one need to look outside this framework for other conjectures? This is an open question, of course, but the authors, by raising these fundamental questions, have in mind the exploration of alternative explanations. It should be noted that there is no implication of intelligent design or supernatural properties at work; the researchers are seeking naturalistic explanations.

## The Major Evolutionary Transitions

In an earlier work than that above, Smith and Szathmary (1995) discuss what they call the ‘major transitions of evolution’. The salient ones here include the origin of chromosomes, the origin of eukaryotes, the origin of sex, the origin of multicellular organisms, and the origins of animals, plants and fungi from non-cell-differentiating protista. Within a selectionist framework, the authors discuss the more unfamiliar territory (to neo-Darwinists) of symbiosis, autocatalysis and self-assembly. These latter inclusions are welcome but Reid doubts whether the explanations are satisfactory:

> But they do not explain how the steps were generated. Moreover they admit that paradoxical situations must have existed for which it is difficult to imagine what that the selective advantage might have been, and they invoke undefined ‘special circumstances’ to explain those situations away. (Reid 2007 p22)

Reid has a point; Smith and Szathmary fail to convince one that they provide a satisfactory aetiology concerning these major transitions. ‘Special circumstances’ go undefined and it is not clear that there is ‘selective advantage’ present, it is assumed by the authors but never demonstrated. It also illustrates the need for a more pluralistic approach that embraces causal chains other than accumulation of successive mutations. Trying to apply the same explanatory formula to all biological transformations will not always succeed and, when it does not, one will be faced with ‘paradoxical situations’. The paradox is only there, of course, if one’s starting premise is that each change must necessarily include some superior advantage over the status quo. If one accepts that changes can take place and persist alongside the existing biological scenery, the paradox disappears and one can appreciate how the diversities of life have become established. When the eukaryotic cell originated, it did not mean death for the prokaryote; both were able to flourish and have done so to the present day. This also applies to all the major transitions discussed: multicellularity did not displace cellular singularity, meiosis did not displace mitosis, fungi did not displace protista, and so forth. New forms emerge and exist alongside the forms from which they emerged. Natural selection as a filter is redundant to such emergences, as it is uncontroversial that these events occurred and it is parsimonious not to invoke that the results were also selected. That much is obvious. What are under investigation and subject to possible controversy are the causal factors that brought these transitions about. It is also worth noting that Malthusian natural selection, with its emphasis on competition for diminishing resources, looks equally inappropriate as a model of explanation.

## Vestigial Organs and Pseudogenes

Following on from the problem of the major evolutionary transitions, there is the issue of vestigial organs. It was suggested earlier that natural selection might be best considered as conservative or eliminative, i.e. conserving or preserving the emergence of traits that confer fitness or eliminating those traits that are detrimental to the organism. However, vestigial organs are a class of traits that were probably once of functional significance but have become redundant over time, although they have not been divested from the organism. There are many examples of these. (The following empirical facts are extracted from Spinney 2008 unless referenced otherwise). In humans, for instance, the appendix is thought to have been of value in digesting cellulose, in a diet mainly of plants, but redundancy ensued as diets changed to include much more cooked meat and fish, although the appendix remained. Male nipples and breast tissue raise an interesting question: does one assume that the ancestral male once breastfed? If one embraces functional explanations for the existence of traits, then it follows that male nipples were selected for.[29] Another vestigial feature in humans is the paranasal sinuses. In other animals, the sinus cavities are lined with olfactory tissues, but this is not the case in humans and consequently the sense of smell is much diminished. The coccyx is thought to be a remnant of a tail which was lost as our ancestors converted to bipedalism. There are muscles in the ear that persist in humans but are very rarely used. Many animals can pick up and direct their ears but, apart from a few people who can wiggle their ears, this function has been lost in humans. (The ability to wiggle one's ears is not thought to be of any advantage to survival or reproduction in humans.) It is also arguable that our four smaller toes are remnants of our arboreal past and that only the big toe is necessary to ensure good balance. Further examples of vestigial items include a third eyelid, which persists in miniature in the corner of the eye, a set of cervical ribs within the neck (only found in less than 1 per cent of all humans) and the palmaris muscle, which runs between elbow and wrist and is found in 10 per cent or so of humans. Most of us have a subclavius muscle that stretches from under the shoulder to the first rib; some individuals even have two. Wisdom teeth are thought to be a relic of a herbivorous past. The erector pili are muscles common in animals that cause fur to stand up and give the impression of a larger body, which is deemed useful in deterring predators. In humans, this manifests itself as Goosebumps. Vestigial organs or parts are by no means exclusive to humans; other animals carry non-functional components. Many species of whales, for instance, still retain hind legs, pelvis and, in some cases, feet with digits, all inherited from ancestors that were originally terrestrial. One curiosity from the plant world is the production of pollen by dandelions and yet the pollen is sterile. Dandelions basically clone themselves through a process called apomixis, which is reproduction without the need for fertilisation. (Asker 1992 p186-189)

There are also many vestigial or pseudogenes at the molecular level. Humans have lost many of the abilities enjoyed by our ancestors but the genes remain, sometimes intact but unexpressed and sometimes as mutated remnants. For instance, the L-gulonolactone oxidase gene, the gene required for Vitamin C synthesis, and multiple odorant receptor genes were found as pseudogenes in humans-

> Our predicted ancestors, like other mammals, had a more acute sense of smell than we do now; humans have >99 odorant receptor genes, of which ~70% are pseudogenes. Many other mammals, such as mice and marmosets, have many of the same OR genes as us, but all of theirs actually work. An extreme case is the dolphin, which is the descendant of land mammals. It no longer has any need to smell volatile odorants, yet it contains many OR genes, of which none are functional — they are all pseudogenes (Freitag et al. 1998 p635).

Such non-functional vestigial organs and genes present a problem of explanation for natural selection. Bodies encumbered with these relics of the past are unable to divest themselves of them but, despite these redundancies, the organisms still manage to survive and reproduce. As a general rule only, the more complex

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[29] There are examples of male lactation in the anthropological and medical literature; some claim that males can breastfeed if the nipple is suitably stimulated (http://www.scientificamerican.com/article.cfm?id=strange-but-true-males-can-lactate).

the organism the more difficult it is to divest non-useful parts. It is known, for example, that prokaryotes can divest themselves of parts of their own genomes. However, one must tread carefully, for what may appear as a vestigial organ in one environment may spring into life in another environment. Take *Astyanax mexicanus*, the cave fish that live in waters without light and whose eyesight degenerated over evolutionary time (Yamamoto et al. 2004). The evolutionary and developmental mechanisms underlying this are unknown, but individual mutations are now thought unlikely to be responsible, as a result of an experiment devised to see whether the eye had become totally redundant. The researchers were surprised by the result. Within eight days of transplant of a lens from a surface dwelling fish the once blind fish developed a functioning eye with a pupil, cornea and iris.

## Order: Regularities and Regularities Disturbed

There are many phenomena at the molecular and biochemical level that proceed in a regular and seemingly ordered manner, independent of differential reproduction, which could have profound evolutionary consequences. A few examples will demonstrate this.

The diminishing Y chromosome is a recently observed occurrence affecting male mammals in particular. It is not entirely clear why there has been a significant decrease in the size and number of genes in the Y chromosome (Russell et al 2008). To date, this has not affected fitness in any manner in humans, but the implications could be significant for the future. Research with amphibians indicates a more disturbing story:

> We investigate the effects of exposure to water-borne atrazine contamination on wild leopard frogs (*Rana pipiens*) in different regions of the United States and find that 10–92% of males show gonadal abnormalities such as retarded development and hermaphroditism. (Hayes et al. 2002 abstract)

Whatever the culprit, be it some form of pesticide or the introduction of plastics into our environment, the salient point is that the consequences derive directly from the environment. This causal factor may produce differentiation but it may also be the death knell for a species. Another consideration is that telomere erosion and a regular mitotic clock could be implicated in cancer, vascular disease and diabetes in the short term; in the longer evolutionary term, they could be implicated in the sudden demise of a species.[30]

Mutation rates are also considered to be of regular order, independent of any form of natural selection. Zuckerkandl and Pauling (1962) noticed that amino acid changes were consistent over time. The observations led to the hypothesis of a ‘molecular clock’, which provided the rates of change for a particular protein molecule over evolutionary time. Kimura (1983) expanded the hypothesis to other regularities, including spontaneous errors in DNA replication. The *Neutral Theory of Molecular Evolution* was accepted by most molecular biologists, but some evolutionary biologists found the implications too controversial and the ‘drift’ versus ‘selection’ debate reopened. (Hull 1999, Mayr 1991) The whole concept of molecular clocks has been challenged, as not all the results could be calibrated against the fossil records. Some evolutionary biologists

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[30] In 1973, Olovnikov proposed that cells lose a small amount of DNA following each round of replication due to the inability of DNA polymerase to fully replicate chromosome ends (telomeres) and that eventually a critical deletion causes cell death. Observations showing that telomeres of human somatic cells act as a mitotic clock, shortening with age both *in vitro* and *in vivo* in a replication-dependent manner, support this theory’s premise (Harley 1991).

(e.g. Ayala 1999) have argued that all the rates of change can be influenced by other factors, including natural selection.

## Conclusion

The demarcation between what natural selection can and cannot explain is a difficult problem. At issue is how to determine which causal factors to appeal to in any given case. Without a clear and single account of natural selection, the problem is compounded. It is unclear whether ‘selection’ or ‘selection pressures’ entails that an organism simply meets the prevailing conditions for existence or whether it also entails that an organism has superior fitness to comparable organisms. The illustration began with a list of biological phenomena that seem difficult to explain by recourse to traditional Darwinian methods. The major evolutionary transitions identified by Smith and Szathmary were deemed ‘paradoxical’ by the authors when they propounded selectionist explanations, leaving many challenges for evolutionary theory in general. An additional issue is the vestigial ‘organs’ that resist functional explanation and leave an explanation gap that needs to be addressed. The notion of natural selection as a filter proved redundant when faced with the emergence of novel forms and the notion of natural selection as a process of accumulative mutation seemed too narrow to explain much of the biological phenomena discussed.

## Chapter 7: Genetic Exchange

What is genetic exchange and why is it thought to be of evolutionary significance? Is genetic exchange part of the ‘modern’ synthesis? If not, then is genetic exchange not subject to natural selection? If genetic exchange is included within modern neo-Darwinism does one then extend the explanatory scope of natural selection to cover non-vertical inheritance?

Genetic exchange is sometimes referred to as ‘reticulate evolution’. It includes such biological phenomena as hybridisation, introgression (backcrossing), horizontal or lateral gene transfer and even meiosis. As the words lateral and horizontal imply, the transmission of genetic material is not by means of modification with descent. These sideway processes, however, can all radically alter the genetic composition and the DNA sequencing of the organism. The possible changes range from the harmful and non-viable to the evolutionary emergence of new traits and species. It is the latter that concerns this study. One could argue that only a few biologists have appreciated the full potential of genetic exchange in the evolutionary arena, with many evolutionary biologists dismissing its significance.[31] Moreover, when new researches establish empirical satisfaction, the results are nevertheless received with scepticism and marginalised as of peripheral interest only. It will be argued here that not only is such a dismissal a serious omission but also that genetic exchange has implications for how one thinks about natural selection. Genetic exchange adds to the sources of evolutionary pluralism, but is it compatible with or antagonistic to natural selection? Before this question is addressed, it is important to sketch out in a little more detail what genetic exchange entails.

### Symbiosis and Symbiogenesis

Symbiosis covers a wide range of relationships that can exist not only between members of different species but also between members of different phyla. Sometimes the relationship can be mutually beneficial for both participating members: plants and fungi, for instance, provide each other with resources they could not access if they remained independent. One example is known as mycorrhiza (Jackson and Mason). Mycorrhiza is not always mutually beneficial, as with other forms of symbiosis; sometimes the benefits can be one-sided, with only one partner seeming to benefit, and sometimes the relationship can be pathogenic to one partner but not to the other. One recent and surprising discovery was the ubiquity of endophytes, fungi living within the tissues of a plant and being an integral part of the anatomy (Faeth and Fagan 2002). Furthermore, fungi have been found to infiltrate the seeds of some plants, thereby establishing a presence in subsequent generations. The relationship can be a precarious one, for on the one hand the fungus can protect the plant against dangerous infection and act as a defence against the invasion of other plants, but on the other hand a single mutation within the fungus could convert it to a predator that feeds upon and eventually destroys its host (Gilbert and Epel 2009 p83). When the first researchers discovered the ubiquitous genetic existence of endophytes, they questioned whether they were looking at plants or whether they were looking at fungi that had taken on the shape of plants. In fact, when one thinks of an individual organism – perhaps a human or a fish or an aardvark – one is given to granting the quality of uniqueness, such that entities are autonomous and segregated from other individuals. However, this perception may not be entirely accurate. Take the human

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[31] The last five years has seen an increased awareness of the importance of hybridisation.

body as an example. Adults carry up to 100 trillion micro-organisms internally and externally, reflecting more than a thousand different species, including worms, bacteria, amoebae, fungi and mites. It is believed that up to 90%, in number, of the cells in our bodies are actually bacteria.[32] Bacteria start to colonise the intestines and colon shortly after birth, acquired in the birth canal by ingesting the mother's vaginal and faecal flora, including a wholesome mix of *Lactobacillus*, *Bifidobacterium*, *E. coli* and *Enterococcus*. (Child and Macfarlane 2008). Passage through a mother's abdomen provides a different assortment: hospital-acquired micro-organisms such as *Clostridium* and *Streptococcus*. Additional types of bacteria join the gut flora in the first few days after birth: *Staphylococcus aureus*, for example, is transferred from the mother's nipple during suckling, but also from the kisses and embraces of others. Child and Macfarlane suggest thinking of the human body as a mobile eco-system:

> Genetic analysis shows that our gastrointestinal tracts are home to more than 100 000 billion ($10^{14}$) individual micro-organisms of perhaps 36 000 different species. And more than 90% of the cells in our bodies are non-human.[1] These bacteria form a diverse and complex ecosystem with a total gene pool (microbiome) more than 100 times larger than the human genome – in effect we are hybrid 'superorganisms.' The types and numbers of bacteria differ from the stomach to the distal colon, reflecting the changes in pH, concentration of oxygen, and availability of nutrients. Small numbers persist in the stomach (notably *Helicobacter pylori*, which causes ulcers) and the small intestine, but most of these organisms are found in the anaerobic environment of the large intestine. (ibid 2008)

Bacteria play a necessary role in everyday functions.[33] Estimates show that 5–30% of the host's daily energy requirements might be procured through bacterial fermentation. Intestinal bacteria also play an important role in suppressing dangerous micro-organisms such as other bacteria and yeasts. There are suggestions that bacterial colonisation is responsible for full initiation of the immune system. Antibiotics tend to be indiscriminate about the micro-organisms that they destroy. The adverse symptoms after a course of antibiotics result from the removal of the beneficial bacteria that would normally reduce the body's ability to ferment carbohydrates and metabolise bile acids. In some rare instances, removal of these valuable bacteria by antibiotics has led to the death of the unfortunate individual. There are approximately 600 different species of bacteria within the mouth.[34] Some are harmful, playing a role in tooth and gum diseases, but many are active in preventing such maladies as well as in breaking down and digesting food, absorbing the converted nutrients and dietary fibre, synthesising vitamins and degrading toxins.

Ryan (2009) has argued that the role of the virus has been enormously important in animal evolution, conforming to what he calls 'aggressive symbiosis'. (See below for further discussion on viral genetic exchange.) There are many examples of symbiotic relationships in nature, which demonstrates that life is not just a matter of predator–prey relationships, or individuals in Malthusian struggle (Sapp 1994, Weiss and Buchanan 2009, Wakeford 2001, Watson 2006). What is of particular interest here is symbiogenesis, for this illustrates instances of evolutionary novelty, where two previously distinct species can confederate or merge to create a wholly new species. *Elysia chlorlotica*, for example, is an alga/slug that evolved from ancestral slugs that once consumed algae. The algae subsequently permeated the slug's organs and became an acquired characteristic, causing the slug to be green in colour. One interesting novel feature is that the new being does

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[32] See the Human Microbiome Project - http://www.hmpdacc.org/2012

[33] The empirical facts concerning the relationships between microbes and the health of humans are extracted from the website- www.hmpdacc.org/impacts_health/impact_health.php 2012.

[34] Antonie van Leeuwenhoek back in the 1600s was the first person to observe 'animalcules', as he called bacteria enjoying life in the human mouth.

not need to feed but can sunbathe along shorelines and derive its energy photosynthetically (Ryan 2009). Another well-documented example of symbiogenesis is the 25,000 known species of lichen. Lichen is the combination of fungi with either cyanobacteria or green algae and is not a plant as many botanists once believed (Russell et al., 2008 p632-633).

These are just a few simple examples of symbiotic relationships in a field of research that is largely under-studied but is proving to be of high evolutionary significance. As Margulis argues:

> Life evolved in the sea, but the argument is strong that interliving – symbiogenesis – made habitation of the hostile new dry land possible for life. Solar ultraviolet radiation, devastating desiccation and nutrient scarcity were much more serious problems on land 500 million years ago than they are now. Symbiogenesis developed the Earth's terra firma into occupiable real estate. (Margulis 2001 p134)

Another aspect of symbiogenesis operates at the microbial level. The Endosymbiotic Theory was first conceived by Russian botanist Mereschkowski in 1905,[35] then popularised and expanded more recently by Margulis (1981). Endosymbiosis can be seen as a form of genetic exchange, but the term 'confederation' may be more appropriate. The theory was received with considerable scepticism by some Darwinists (see Ch.13) but is now almost universally accepted and endosymbiosis can be considered to be an aspect of genetic fusion that does not conform to evolution by vertical descent. It is now thought that *Archaea*[36] engulfed bacteria, confederating its attributes and giving rise to the eukaryotic cell, with nucleus, mitochondria, chloroplast and all. This step is seen as of great evolutionary significance, as the eukaryotic cell is the foundation to multicellular organisms, such as plants, fungi and animals. Some eukaryotes, called protists, remained without tissue development, many unicellular but some also multicellular (Russell et al., 2008 p559-581) (*Protista* is no longer considered as a separate taxonomic kingdom). This great leap of evolutionary speciation and variation seems difficult to explain in terms of natural selection, be it the Malthusian variety or the neo-Darwinian variety based upon a series of mutations gradually accumulating favourable outcomes. It seems to be more a matter of biochemical convergence, leading to a new form that in turn facilitated more diverse functions such as meiosis.

### Horizontal or Lateral Gene Transfer

The earliest occurrence of lateral gene transfer is thought to be at the most primitive stages of life.[37] Clues are gleaned from the observation of contemporary prokaryotes, which has shown a common process of 'conjugation'. This involves a donor bacterium resting alongside the host bacterium, the membranes opening at the join and DNA material being transferred as what is known as a plasmid, from the donor cell to the host. Another mechanism of transfer is through the medium of a virus. This is often referred to as 'transduction'. The genetic material is thus passed horizontally or laterally and not vertically from parent to offspring. Fossilised evidence suggests that these earliest single-cell organisms are three-and-a-half billion years old, probably composed initially of RNA which provided the ability of replication ('RNA world hypothesis', Woese 1968, Woese and Fox 1977). This situation was then thought to be superseded by prokaryotes that

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[35] See Khakhina (1993) for an overview of early Russian advocates of evolutionary symbiosis.

[36] This grouping includes methanogens – organisms that require methane rather than oxygen – and numerous extremophiles that can survive in austere environments, sometimes at extremely high temperatures, in some cases above 100°C.

[37] Unless otherwise referenced all the empirical data presented here is extracted from Russell et al., 2008.

contained DNA. Studies by Woese led to the valuable identification that the prokaryotic world consisted of two discrete groups of organisms, the bacteria and the *Archaea* (Wharton 2002). Evidence for lateral gene transfer did not appear until the middle of the last century, when it was discovered in Japan that antibiotic resistance could be passed on from one bacterium to another bacterium of a quite different species. Lederberg and Tatum received the Nobel Prize in 1958 for discovering, 11years earlier, how the mechanics of plasmid gene transfer worked. At the time, there was scepticism because their observations did not conform to the prevailing view that genetic material was only passed vertically. Nonetheless, exchanges within both prokaryotes and unicellular protists are now recognised and subject to much active research. In fact, as much as 25% of a prokaryote genome is thought to emanate from such lateral transfers. This has wreaked havoc for the traditional phylogenetic tree, and taxonomy is now more problematic than ever (see Figure 2 later).

> Since the time of Darwin, the evolutionary relationships between organisms have been represented as a tree, with the common ancestors at the base of the trunk and the most recently evolved species at the tips of the branches. Microbiologists have argued for a long time that this representation doesn't really hold true for microbes, which often exchange genes among different species. Their claim has been that the evolution of these organisms is better represented by a net. Unfortunately, no-one knew exactly where to draw the horizontal lines in this net. (Kunin et al. 2005)

Lateral gene transfer is also an evolutionary factor in other taxonomic kingdoms and evidence is mounting that transfer also takes place across the different biological kingdoms. Sequencing the genome has revealed unexpected results, including HGT insertion about 400 million years ago for vertebrates which has consequences for the development of the immune system in humans. (Park & Deem 2007) Park and Deem recall the specialised protein that bacteria use to swap genes. They argue that this is of significant evolutionary importance, complementing researches that have traditionally focused on random mutation of single base nucleotides or recombination as in meiosis. Recently, scientists at Indiana University Bloomington and at the University of Michigan have independently discovered another vector for gene transfer between members of different species – parasites:

> [Palmer, Stefanovic and Young] report two new examples of horizontal transfer of the important mitochondrial gene atp1 from parasitic flowering plants to weeds in the genus Plantago. Three Plantago species possess both a normal, functioning copy of atp1 and a second defective atp1 that bears a striking resemblance to the atp1 gene found in parasitic 'dodders' in the plant genus Cuscuta. Evidence suggests Plantago weeds acquired the defective atp1 through horizontal transfer recently – not more than a few million years ago. (http://scienceblog.com/4628/gene-exchange-between-species-is-aided-by-parasitism/)

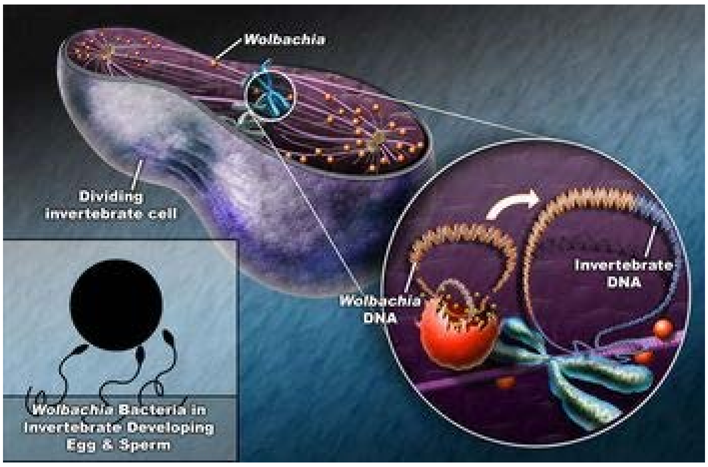

Figure 1

Source: http://phys.org/news107702428.html

It has been suggested that the attacking parasitic cells have mechanisms that enable them to penetrate the cell of the host, depositing some of its own DNA. Furthermore, this DNA may actively function in protein production. Not only plants are subject to parasitic invasion: after much initial disbelief, it has now been recognised that many invertebrates may host almost the entire genome of a completely unrelated species, the bacteria *Wolbachia*. This parasite has implanted itself inside the cells of 70% of the world's invertebrates, co-evolving with them. There is at least one species where the parasite's entire or nearly entire genome has been absorbed and integrated into the host's. The host's genes actually hold the coding information for a completely separate species. (Newman 2009.) The ironic thing here was that researchers were not looking for such bacterial inclusions, because they were not part of the preconceived expectations. When some strands were initially identified, they were dismissed as contamination without any checks to see whether this was in fact the case (ibid 2009). Perhaps this is an example of theory ladenness.

*Viral lateral transfer*

The discovery of retroviruses identified yet another lateral process that added to an organism's genome. Again to everyone's surprise, retroviruses are understood to make up around 8% of the human genome (Shapiro 2011). These viruses can invade a cell, reversing the usual course of genetic code from DNA to RNA. This is achieved by deployment of a special enzyme, called reverse transcriptase, that enables it to copy itself and then paste its own genes, which it carries in its RNA, into the host cell's DNA (Temin and Mizutani 1970). If the virus infects the germ cells and the newly acquired genetic material is passed on to offspring, then the process is known as *endogenous.* Endogenous retroviruses are generally considered harmful to the host. Much cancer research has discovered large quantities within tumour cells, and two forms of leukaemia in humans are the result of such invasions. However, such infections are not always harmful; sometimes the invasive retroviruses can block attack from even more harmful viruses (Ryan 2004). From an evolutionary perspective, it is now thought that endogenous retroviruses are responsible for important changes, such as the origin of the placenta (Harris 1998). To summarise, ancestors of mammals laid eggs, but at some stage the embryo no longer created a shell but implanted itself within the mother's womb in a rather parasitic manner. It was discovered in the 1970s, again to much surprise, that the layer of tissue that divides the womb from the embryo, the placental syncytium, was composed of a protein called syncytin which binds the placental cells together. Moreover, the mechanism employed was precisely the same as that which enables retroviruses to bolt on to infected cells. Endogenous retroviruses thus add another dimension to the plurality of possibilities for evolution. Ryan is an advocate of what he calls 'aggressive symbiosis', arguing that a virus can form a permanent relationship with a host organism to the mutual benefit of both. He cites the example of parasitic wasps and polydnaviruses:

> The partnership has become so intimate that many of the viruses have entered the germ line of the wasps, to emerge, as fully formed viruses, when the wasp is laying its eggs. Whether the viruses live around the wasp ovaries, or whether they emerge from the wasp genome at the time of egg-laying, they are inevitably into the caterpillar prey along with the wasp's eggs. In normal circumstances the wasp's eggs would not survive – they would be detected and destroyed by the immune system of the caterpillar. But here viral aggression comes into play, paralysing the immune system of the caterpillar, and then taking over key aspects of its internal chemistry to convert it into a brood chamber for the emerging wasp larvae. The full complexity of the symbiosis has proved to be a source of wonder to biologists, with viruses compelling the caterpillar to produce sugars to feed the larvae, and even going as far as to disrupt the caterpillar's hormonal system, thereby preventing its natural metamorphosis into a butterfly or moth. (Ryan 2009 p94)

Although this account is quite fascinating and illustrates how unexpected behaviours can occur, the example stops short of any speciation event. Rather, the inclusion of the virus confers fitness upon the wasp and the death sentence for the infected moth or butterfly. What does seem certain, however, is that we have underestimated until recently the many different processes that have contributed to DNA variation and richness.

## Hybridisation

Another example of under-appreciation, neglect and near dismissal is the process or processes of hybridisation. It can be argued that the architects of the modern synthesis saw little of evolutionary significance here and focused upon random mutation. This does seem very odd in retrospect, almost, as it were, choosing to be blind in one eye. For hybridisation offers excellent empirical examples of evolution in action, including speciation. It was the process that most disturbed the religious views of Linnaeus, who maintained that there were no new species other than those provided by providence. (Marks 1995 p9-13) Darwin wrote extensively on the subject, corresponded with many fellow experimenters and yet failed to give it an evolutionary accommodation. He was aware of the earliest experiments carried out by Koelreuter (1760), who crossed different strains of tobacco plants, producing viable offspring. The hybrid offspring were highly variable and quite unlike the parents, but if the subsequent hybrids were crossed, the features of the grandparents could sometimes reappear. Did Darwin exclude hybridisation because he saw evolution as only a gradual process slowly leading to new species? Or did he simply see a mass of empirical evidence before him that seemed to lack any universal trends or regularities and give the subject up in the genetic ignorance of his times? Whatever the reason, his decision had an impact upon the later neo-Darwinists. Mayr (1942) argued that the majority of hybrids produced were sterile and therefore of little evolutionary significance. Any backcrosses that maintained viability were of an inferior nature and the offspring would eventually be eliminated by natural selection. Mayr had reinvented the 'Biological Species Concept', first introduced by Wallace (1886) seeking to give some coherence to taxonomic endeavours. However, hybridisation presents some problems here, as Arnold illustrates:

> A strict application of the biological species concept negates the possibility of species exchanging genes; reproductive isolation defines species and it is thus incorrect to speak of species exchanging genetic material. (Arnold 2006 p25)

Today, the Biological Species Concept looks increasingly inadequate. Arguably, Botanists never really embraced the idea, because of what was known about greater complexities in the methods of plant reproduction and frequent polyploid hybridisation. Take the evolutionary history of wheat, for example. This has been the subject of hybridisation on two occasions, doubling its number of chromosomes spontaneously so it now stands at 42 (Haung et al., 2002). Another more recent example is that of *Tragopogon dubius*, commonly seen as a weed but nevertheless an instant new species. *T. dubius* is a 24-chromosome plant whose parents are distinct species, *T. pratensis* and *T. porrifolious*, which each have only 12 chromosomes (Bennett 2004). Plants and fungi, it seems, reproduce in a different manner from animals. Being sessile has its consequences, and being less restrictive over genetic exchanges between individuals of different species seems to be one such consequence.

What also makes the Biological Species Concept even less credible is that microbiology has no association with it, as the creatures of study simply do not reproduce sexually. So it does look a marginalised concept oriented in a zoological aspect at the outset. But even here there are now serious doubts:

> What is becoming increasingly evident, however, is that hybridisation is not all that uncommon in animals, either. In recent years, many cases of substantial hybridisation between animal species have been documented. One recent survey indicated that almost 10% of the world's 9500 bird species are known to have hybridised in nature. (Raven et al. 2005 p477)

The authors above note that the work of Peter and Rosemary Grant concerning the famous Galapagos finches has identified that up to 2% of the finches had mated with members of finch species other than their own, producing fertile offspring and, to date, maintaining viability through subsequent generations. In evolutionary terms, this is a very significant figure compared with mutation rates that provide characters that are evolutionarily advantageous. Hybridisation is less rare than was previously believed, but even rare events can have important evolutionary consequences, as Arnold says the neo-Darwinists have always maintained:

> However, it is equally crucial to emphasize that the rarity of a particular event is not predictive of its potential evolutionary importance. If it were the case that rarity of occurrence predicted unimportance, then mutations that result in an increase in fitness – which of course form the basis for Darwinian or adaptive evolution – would be disregarded. (Arnold 2006 p27)

Arguably, hybridisation events are much more prevalent than most biologists thought. The recognition here is that interspecific (between species) examples are much more common than intergeneric (between genera) examples. Intergeneric hybrids are less frequent, but still highly significant from an evolutionary perspective. One accidental discovery concerning salamanders illustrates that hybridisation can result in fertile offspring with such hybrid vigour that they became a threat to the existing species.

> In the middle of the 20th century, local fishermen who relied on baby salamanders as bait introduced a new species of salamander to California water bodies. These Barred Tiger salamanders came into contact with the native California Tiger salamanders, and over time the two species began to mate. 'To give you a sense of the difference between these two species, they are about as closely related as humans and chimpanzees,' said UT assistant professor Ben Fitzpatrick. (http://www.eurekalert.org/pub_releases/2007-09/uota-urs091307.php, reporting on Fitzpatrick and Shaffer 2007)

Recent research into the *Acropora* corals of the Indian and Pacific Oceans has suggested that rarer species can successfully breed interspecifically:

> When we looked at the genetic history of rare corals, we found that they exhibited unexpected patterns of genetic diversity. This suggests that, rather than being the dying remnants of once-common species, they may actually be coral pioneers pushing into new environments and developing new traits by virtue of the interbreeding that has enabled them to survive there. (Richards et al. 2008 pp207–237)

Fungi have also recently been observed to hybridise in their own fashion. Two species of yeast have yielded unexpected results in the laboratory. The spores from these two species joined to produce hybrid offspring which were then allowed to autofertilize. (Greig et al. 2002) Closer to home, there is evidence of hybrid zones among many primate species. The gibbon in particular has been noted and also the baboon. (Lass 2001)

> Olive baboons also hybridize with yellow baboons (*P. cynocephalus*) in Kenya and Tanzania, most notably in Amboseli National Park, Kenya. Historical and long-term crossbreeding of these two species may have contributed to the formation of the subspecies *P. cynocephalus ibeanus.* (http://pin.primate.wisc.edu/factsheets/entry/olive_baboon)

Arnold (2006 pp82–108) discusses and gives examples of hybrid fitness from micro-organisms to plants to animals, arguing that such products are of equivalent fitness *ceteris paribus* to other novel genotypes. Mallet (2008) argues that we could have easily underestimated the degree of hybridisation in the wild; most research is ‘based on morphological identification of hybrids in hunted or museum specimens’ and therefore it is possible that some hybrids are erroneously recorded. Further, he laments ‘as far as I know, there has been no concerted genetic study to verify interspecific hybrids across a large faunal group.’ From Mallet’s own research, he estimates recorded instances of hybrids as a percentage for species to be 25% for plants in the UK, 16% for butterflies in Europe, 9% for birds worldwide and 6% for mammals in Europe.

> On the other side of the species boundary, hybrids between many pairs of animal species (as well as plant species) are also known. These hybrids are often (though by no means always) fertile enough to backcross to the parents. Genetic studies have shown that hybridization can be evolutionarily important, leading to limited gene flow or introgression among species, and sometimes to hybrid speciation. (Mallet 2008)

## The Implications for Phylogeny

Arnold has argued that our method of taxonomy based upon the phylogenetic tree is a poor representation and should be replaced with a web-like or mosaic model. It should be stated that Arnold is not attempting to replace ‘evolution by mutation’ by ‘evolution by genetic exchange’; the latter is seen as a supplement, adding to evolutionary richness.

> In the past decade, numerous research groups – studying a wide array of species complexes – have reported findings that indicate an evolutionary pattern best described as a web rather than a bifurcating tree … Because these examples include viral, bacterial, plant and animal species or variants. (Arnold 2006 p21)

If genetic exchange is as pervasive as Arnold declares (and the evidence does seem fairly formidable even though the subject matter has not been the centre of active research), then the evolutionary implications are large and none more so than those concerning phylogeny.[38] Conventional ideas on taxonomy and the Biological Species Concept look increasingly under threat. Furthermore, it does not seem that genetic exchange can be easily accommodated by the inclusive fitness concept and early thoughts on the motivation implied by biological relatedness. All these aspects demand much consideration and evaluation to maintain coherence in our biological and philosophical studies.[39] If the virus, the bacterium and the parasite (and possibly the prion) can all act as vectors of genetic exchange across kingdoms, then how would a representation be plotted? Kunin et al. (2005) have produced one perception of a prokaryotic tree of life, shown in Figure 2.

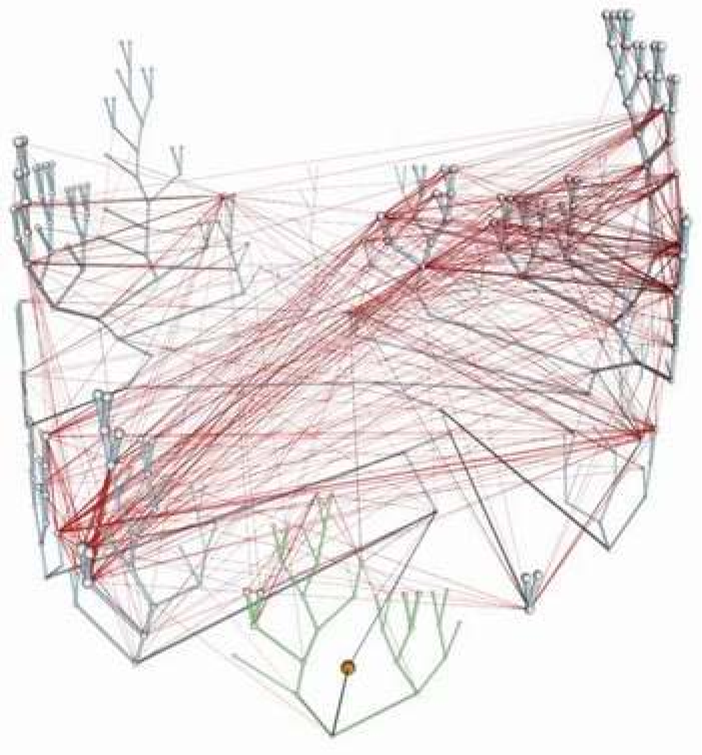

Figure 2

Source: Kunin et al. 2005

*Image: A bird's-eye view of the tree of life, showing the vines in red and the tree's branches in grey [Bacteria] and green [Archaea]. The last universal common ancestor is shown as a yellow sphere.*

Conclusion

The discoveries of the last fifty years have increased our understanding of the many pathways that shape evolutionary change and provide novelty in both genome and phenotype. Genetic exchange takes many forms, from conjugation at the level of the micro-organism to hybridisation at the level of the more complex eukaryote. The researchers who first reported these observations were treated with much scepticism and, in some cases, hostility. Although acceptance was gradually accorded, the full impact of this combined research has only been appreciated by a few. It can be argued that Hybridisation mistakenly remains unrecognised for

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[38] See Garvey (2007 pp152–156) for a philosophical scrutiny of the taxonomic problems connected with hybridisation.

[39] See also Schilthuizen's (2001) contribution to the empirical evidence for hybridisation. He also considers whether the many subspecies in nature are the result of introgression.

its evolutionary significance by many zoologists. Reflecting on all the recent researches and evidence discussed, one must ask whether a considerable revision of the Darwinian paradigm is required in order to accommodate these pluralistic modes of evolution. The idea of evolution moving gradually by tiny increments, with bifurcation into shapely branches, has never sat well with the episodic evolution suggested by the palaeontologists. Nor has it more recently been seen as compatible with our understanding of prokaryotic evolution. There are advantages in recognising evolution not as monolithic gradualism but as pluralistic combination of pathways capable of both slow and rapid evolutionary change. This recognition would do much to negate the pseudo-science of creationism, which appeals to the 'weakness' of the fossil record in an attempt to refute evolutionary theory. On the other hand, those who cherish ideas of inclusive fitness will be under pressure to resist the full implications of genetic exchange, for the two perspectives seem contrary rather than compatible. The model of genetic relatedness, it could be argued, relies heavily upon an oversimplified Mendelian method of inheritance and overlooks many of the complications illustrated here.

There are several questions to be addressed in the light of all these now-recognised evolutionary processes. For instance, what is the relationship to natural selection? Is this evolutionary pluralism subject to natural selection or is each evolutionary process, as Darwin believed, distinct from natural selection? Has the identification of these many aspects of evolutionary change made any explanatory power of natural selection redundant? In the final stages of this thesis, issues of explanation and causation will be discussed in order to clarify the matter.

## Chapter 8: The Constraints: Symmetry, Asymmetry and Patterns in Nature

The issues of constraints can be viewed from two different perspectives. One could ask, how is natural selection constrained? Alternatively, how are the features of life constrained? In the former, there is the presumption that natural selection is the dominant factor when explaining evolutionary change. The latter makes no such assumption; the question addressed is the physical limitations of biological form. Regardless of natural selection, in our present understanding there are considered to be limits to sizes, combinations, speeds and processes, which it would be impossible to exceed. Gould observes that constraints can be positive or negative. He gives the following as an example of a negative constraint: 'we toss a group of miscreants into a jail cell in order to keep them close and restrict their movements'; and the increased speed of fluids forced into narrow tubes as an example of a positive constraint (Gould 2002 p1026). There could be a problem with this distinction, however: one might ask why the increased speed of water is seen as positive and the reduced movement of cellmates as negative. It seems a little arbitrary; for reduced movement could be seen as positive and increased speed as negative under some circumstances. Despite this philosophical problem, seemingly all agree there are constraints of some form. The controversy begins when one assesses their prevalence and importance. It will be helpful to outline the basis for any claims before making any evaluation. To elucidate the situation, one might consider why it is that in nature there are no flying elephants, fire-breathing dragons or any animals that have evolved with wheels as appendages. The laws of aerodynamics and gravity and the physical relationships of the relevant anatomy will provide the obvious answer and ensure that dragons, elephants or pigs will never fly. The question concerning the evolution of a biological wheel is less straightforward. The difficulty arising, therefore, is just how far natural laws will restrict the amount of variation within nature.

Structuralism as an alternative explanation to neo-Darwinism is in its formative and tentative years and not as yet known to a wide audience. It is important then to elucidate the main themes that underlie this perspective. As the name suggests, Structuralism addresses principally questions of structure, why it is that this object takes the form it does. This enquiry applies to all objects from a snowflake to an elephant. The objective is to identify recursive patterns and shapes that run through nature. Rightly or wrongly, Structuralism sees an evolutionary link between the inanimate and the animate, one of a natural order that constrains all form. Any understanding of the importance of the constraints that exist in nature must begin at the fundamental level, that of space. 'Of all the constraints of nature, the most far reaching is imposed by space. For space itself has a structure that influences the shape of every existing thing.' (Stevens 1974 p4) Stevens illustrates how Einstein and other non-Euclidean geometers changed our perceptions of space and its effects on form and patterning. Space is no longer seen as a neutral, passive background to life but as an integral part of nature's mysteries:

> It turns out, however, that the backdrop, the all pervading nothingness, is not so passive. The nothingness has an architecture that makes real demands on things. Every form, every pattern, every existing thing pays a price for its existence by conforming to the structural dictates of space. (ibid. p5)

It was Mendeleev (1834–1907) who perhaps first broke the Kantian conceptual deadlock. His discovery of the periodicity of the elements led him to speculate that space was not nothingness, an empty background in which objects could be placed, as Kant had argued. Space was actually tiny particles that the senses could not directly apprehend. Arguably, this perception has been endorsed by modern physics. That space has shape has fundamental consequences in nature; it constrains and dictates form and pattern. 'Nature too is similarly constrained. She makes cups and saddles not as she pleases but as she must, as the distribution of material dictates.' (Stevens 1974 p9) Stevens outlines how the growth and development of an object (biological or non-biological) will conform to certain shapes dependent upon the point at which the growth begins. For example, if a centre grows faster than a perimeter, then the shape of a bowl or saddle will occur. A bowl or saddle shape will also occur if the perimeter grows more quickly than the centre. However, if the centre and the perimeter grow at the same speed, then a plane figure will be maintained. With this and other such principles in place, one can continue to an understanding of how the complex forms found in nature might develop. Stevens gives the examples of the mollusc shell and the human ear:

> Since the perimeter of the shell grows at a faster rate than the centre, the perimeter curls and wrinkles. No genes carry an image of how to place the wrinkles; no genes remember the shape of the shell: they only permit or encourage faster growth at the perimeter than at the centre.
>
> The convolutions of the outer ear arise like the convolutions in a piece of paper that has been sprinkled with water. The living tissue and the paper both bend and warp in accord with the differential expansion of their surfaces. (Stevens 1974 p9)

In the inanimate world, things are different from in the animate world. The inanimate follows clearly defined geometric principles. For example, are there inanimate forms that exhibit five faces of symmetry? Is any snowflake or crystal is ever pentagonal? It is only the animate that exhibits more complicated forms with five equal sides. However, in nature, these forms are rarely perfect and they often reduce to the best economy in the circumstances, but always within the limited ways in which matter can be distributed in space.

> The players perform a limited repertoire: pentagons make most of the flowers but not of the crystals: hexagons handle most of the repetitive two dimensional patterns but never by themselves enclose three dimensional space. On the other hand, the spiral is the height of versatility, playing roles in the replication of the smallest virus and in the arrangement of matter in the largest galaxy. A look behind the footlights reveals that nature has no choice in the assignment of roles to players. Her productions are shoestring operations, encumbered by the constraints of three dimensional space, the necessary relations among the size of things, and an eccentric sense of frugality. In the space at nature's command, five regular polyhedrons can be produced, but no more. Seven systems of crystal can be employed, but never an eighth. Absolute size decrees that the lion will never fly nor the robin roar. Every part of every action must abide by the rules. (ibid. p4)

In nature, there are limited possibilities, favourites often reoccurring in different guises, meeting economy and fitting the circumstances. How far does this determinism pervade? Is life as we know it consigned to no other choices? Do the fundamental regularities explain convergence in biological forms? At this point, it is appropriate to examine some identified regularities in nature and to determine whether they impose any constraints upon evolutionary changes. Graham Scarr (2012) considers the geometrically constrained Platonic solids to be some of the fundamental building blocks of nature and biological form-

> The ancient Greeks considered that just five shapes could describe everything in the universe because they were pure and perfect; they are the basis for understanding more complex forms in biology. The platonic solids naturally form in 3-D through the efficiencies of geodesic close-packing and principles of

> symmetry. Three spheres pack together to form a triangle and four spheres as a tetrahedron. Adding more spheres allows other shapes to emerge because of the similar packing arrangement. The outer faces of each one are all the same with just 3, 4 or 5 sides and each vertex is formed from 3, 4 or 5 faces. The models shown here are made from ping-pong balls or ball bearings joined with magnetic sticks; the magnets represent the energy bonds that join them into a lattice.

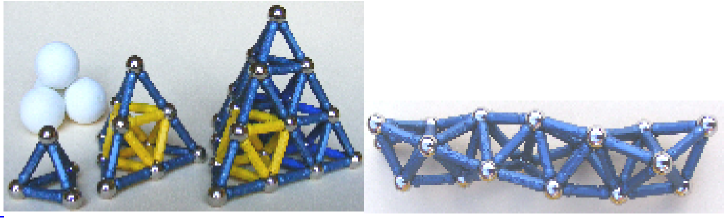

Figure 3. Source: Scarr, 2012. http://www.tensegrityinbiology.co.uk/geodesic.html.

Indeed, to summarise Scarr, the 3D or topological is constrained at this level but combinations of these forms can begin to explain the more complex forms one finds in nature and life. The icosahedron for instance can combine to form a helix, which is fundamental to DNA and protein structure. Spheres, when packed in fours, form the shape of a tetrahedron which when further combined can form lattice structures and helixes that could be left or right handed. Chirality is fundamental to stereochemistry and biology. (See below)

## What is Symmetry?

Lima-de-Faria's (1988) challenge is that the concepts of symmetry and asymmetry are fundamental to evolutionary change. This perspective has recently been embraced by molecular biologists Li and Bowerman (2010). Symmetry is precursory for form but asymmetry is necessary for change. Symmetry must be broken before evolution can begin[40]. These concepts may seem far removed from our biological concerns, so it will be instructive to see why they are thought by some to be related. Symmetry has long been recognised in the arts as something desirable and aesthetically pleasing. In geometry and topology, it has been observed as a fundamental quality.[41]

> Modern physics has confirmed that at its deepest levels, the universe runs on symmetric lines. Principles of symmetry govern the four forces of nature (gravity, electro-magnetism, and the strong and weak nuclear forces that act between fundamental particles); the quantum mechanics of elementary particles; the nature of space, time, matter, and radiation; and the form, origin, and the ultimate destiny of the universe. We don't know *why* but we are pretty sure that it is so. (Stewart 1998 p38)

Symmetry suggests equality, consistency, invariance and regularity in pattern. These descriptions apply not only to physical objects but also to the more abstract applications of mathematics and theoretical physics. In symmetry's purest form, one might think of a perfect sphere placed upon a table. If one were to observe the sphere from one end of the table then proceed to observe the sphere from the opposite end of the table, one would notice that, from whichever perspective one took, the sphere would always remain the same. This invariance is attractive to those who maintain that the laws of nature do not vary from context to context.

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[40] For a recent discussion of the relevance of symmetry breaking for biology see Werner (2012). For a more fundamental philosophical discussion see Chalmers (1970).

[41] Its practical implications, however, were not recognised until the nineteenth century, with Louis Pasteur discovering its significance for chemistry. This observation was followed, chronologically, by mathematicians in the 1920s, who were trying to come to terms with the new challenges of quantum theory. From exercises in Babylonian quadratic equations, they were able to formulate what is known as group theory. This work, grounded in principles of symmetry, facilitated the equations of the mathematician/physicist Paul Dirac. Without realising, at first, the potency of his equations, Dirac had predicted the existence of anti-matter, opening a new era in particle physics. Physics flourished with the patterns that symmetry yielded. See Farmelo (2009).

These laws are said to be ‘invariant’, meaning that, whether applied yesterday or today, they will still apply in the future; or further, that they will apply equally in different geographical locations, be it the village hall, the North Pole or the centre of a black hole. This contention may not be entirely without controversy, for some have raised the spectre of *ceteris paribus* (Cartwright 1980). However, this consideration need not concern us for the present purposes.

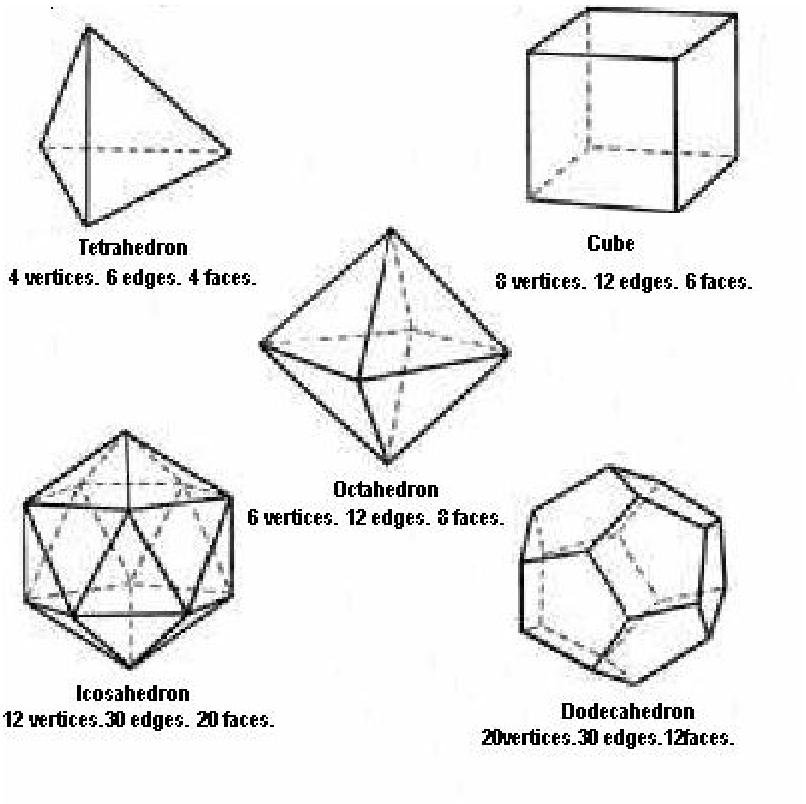

Figure 4

Source: http://www.goldenmeangauge.co.uk/platonic.htm

*The platonic solids are all said to be symmetric because each has faces that are equal in every measurement. Curiously, there are only the five despite attempts by the ancient Greeks and others to discover more. It is now realised that further such solids would be geometrically impossible to form: nature constrains at the deepest levels.*

A sphere, then, is an example of symmetry at its purest, but this is not so for a circle drawn on a piece of paper and placed horizontally on the table. If one observed the circle from directly above, it would maintain the form of a circle; but if one stepped to the side and viewed the paper from an angle, then one would observe an elliptical shape. This does not mean, however, that the circle is asymmetrical, because symmetry can take other guises. The circle is said to contain axes of symmetry. This means that if one were to cut the circle with any straight line going through the centre, then the resulting two halves would be identical in every respect.

An oval plane does not afford the infinite number of equal divisions of the circle: only two lines of axis are possible with this figure, one through the centre vertically and the other through the centre horizontally. An equilateral triangle has three axes but an isosceles triangle only one. Consider the capital letters. Many of them have at least one axis; for example, the letter A can have one axis from the apex dropping vertically, but the letter D must be cut horizontally to achieve two symmetrical parts. The letters F G J L P Q R are all asymmetrical. The importance of these fundamentals is not initially obvious when considering biological issues, but their value becomes more apparent when one considers bilateral and mirror symmetries.

### Mirror Symmetry

Looking in a mirror gives a reflection of oneself. However, the image is not the image that others see in everyday acquaintance. To see how one looks to others, an interesting simple experiment is to place two mirrors at right angles and then look at where the mirrors join. The image now seen is horizontally opposite to the one normally seen in the single mirror. This is how the world sees you. Mirror symmetry reverses any left-to-right bias. A mole or freckle on the left cheek will be on the right cheek in the reflection. Holding up the open left hand to the mirror gives a right hand in the reflection. Apart from the left-to-right ordering, everything else remains the same; the overall dimensions and the relationship between the parts are identical.

Not all things in nature have a right–left bias. The starfish is said to have fivefold symmetry, but in a mirror reflection it looks exactly the same. In both the organic and inorganic world, symmetries up to thirteenfold can be detected. It is worth noting, however, that unlike the perfect sphere, things in the natural world are never perfectly symmetrical. Nature comes with imperfections and each imperfection locks away a hidden history. It is tempting to say that symmetry is the default position and the rigours of life inflict the toll of imperfection.

In the nineteenth century, Pasteur (1822–95) discovered attributes regarding the symmetry of crystals within chemistry that would later have enormous implications for biology and, in particular, human welfare. Pasteur followed on from the work begun by Hauy (1743–1822), originally a botanist, who turned his attentions to physics and chemistry. Hauy wanted to know whether the regular patterns and geometric structures bursting forth in the plant kingdom every spring could indicate similar laws of nature for minerals also. (Later thinkers, such as Turing and Lima-de-Faria, asked the opposite question: can the study of minerals yield answers in biology?)

> How does the same stone, the same salt, assume the form of prisms or of the needles without changing its composition by one atom, while the rose always has the same petals, the acorns the same shape, the cedar the same height and the same development? (Reprinted in Debre 1998 p35)

The following historical sketch summarises Debre (1998}. Hauy found his answer quite by accident, when he dropped a piece of calcareous spar that had crystallised into prisms. He observed that the geometric structures of the fractured parts were exactly the same as those of other crystals he was already familiar with. By way of this insight, he smashed open his entire collection to discover that all contained the geometric shape of a rhomboid. Hauy had discovered a symmetrical law that explained certain form or structure. The principle of symmetry in science took a great step forward. However, it was not long before an anomaly perplexed those in the field and threatened to undermine all that had been achieved within chemistry. It was noticed that tartaric acid polarised light in a certain direction but paratartaric acid did not. The curious thing was that both acids had exactly the same chemical composition and crystalline form. So why did one polarise light and the other not? Pasteur was familiar with the work of Hauy but his brilliance went further, with an intuition relating geometric form to chemistry. In an experiment, Pasteur isolated right- and left-handed crystals in separate prepared solutions. Shining a light through both, Pasteur's intuitions proved correct: the right-handed crystals polarised light to the right and the left-handed crystals exactly the opposite. Pasteur had discovered the principle of molecular asymmetry that established the concept we now call stereochemistry. The foundation of stereochemistry by Pasteur has proved to have enormous implications not only for our health and diets but also for the evolution of biological forms. As Close (2000 p69) puts it, 'Handedness pervades the living world and has some bizarre manifestations. We can smell it and taste it, while forensic science and the whole pharmaceutical industries rely on it.'

What does this entail? Well, an example is the drug thalidomide that was given to pregnant mothers during the late 1950s and early 1960s to reduce morning sickness. The results were a disaster, with huge numbers of fetal deaths and the surviving babies born deformed, many with no limbs. It was not realised at the time that the molecular structure of the drug comes in both left- and right-handed forms. One form is pernicious to the human body but the other is not and is actually now prescribed to treat leprosy[42]. Organic bodies such as humans have evolved to interact with compounds of a particular hand.[43] Close gives the example of how our noses perceive things. The nose itself is constructed of proteins that are themselves mirror asymmetric, which enables us to distinguish between left- and right-handed molecules. Carvone comes in two handed forms: our olfactory organs identify one as caraway and the other as spearmint. Another example is the nature of sugar. Dextrose is a sugar from grapes that polarises light to the right, whereas levulose or fructose is found in fruit and polarises light to the left.[44] Although the molecules are identical, our bodies interact differently with each enantiomorphic form. (Gardener p119) Moreover, both forms taste the same but dextrose can be harmful in large quantities to diabetics. Dextrose is also more easily converted to energy, whereas levulose is more beneficial for those attempting to lose weight. Levulose is noted to do less damage to teeth, as it does not interact with the harmful bacteria that have co-evolved in our bodies. The question is, 'why can we accommodate molecules of one hand but not the opposite hand?' or even 'why can we not interact with both handed forms of molecules?' The answer is intriguing and revolves around the concept that Lord Kelvin named as chirality.[45]

> Since every asymmetric molecule has a mirror-image stereoisomer, there is no reason why all life on earth could not function just as well if all organisms were suddenly transformed into their mirror images. Of course, if only a single organism, say a man, were reflected, he would probably not be able to survive. (Gardner 1990 p133)

One suggestion is that, just as it is postulated that symmetry at the time of the Big Bang required an asymmetric breaking, life also required its own asymmetry. Once an asymmetry is established, it begets further asymmetries and this process is ongoing. However, it should be remembered that asymmetries can also be manufactured from symmetric origins. Gardner (p53 – 63) observes that plants are capable of converting compounds that can be symmetric, such as carbon and water, into compounds that are asymmetric, such as starches and sugars. Another clue to the relationship between the symmetric and the asymmetric might be gleaned from a transformation after death: living bodies are a community of left- or

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[42] The dark story of thalidomide and the medical aftermath are discussed by Stephens,T and Brynner (2001).

[43] See also Buckingham (2005 p215) for a modern chemist's discussion of handedness of DNA.

[44] *Dexter* and *laevus* are Latin for right and left respectively.

[45] From the Greek for hand – *kheir*.

right-handed compounds and helices that exert a bias; however, this all changes after death, when symmetry is eventually realised.

> When an organism dies, the molecules of certain of its amino acids start to 'flip' (change handedness) at a very slow but fairly uniform rate. After millions of years, these amino acids eventually become racemic, containing about an equal proportion of left and right molecules. (ibid. p119)

Chirality, then, is lost after death. Does this mean therefore that chirality is a necessary condition for life?[46] What is important here is that, once organisms are locked into a particular chirality, all subsequent reproductions will also follow that form until death. This fundamental constraint has profound implications as to how organisms and species will interact within the world and any future evolution. McManus is aware of these fundamental issues and ponders the example of the amino acids that persist in all organisms, touching on constraints within nature:

> The genetic code and the entire translation machinery are based on L-amino acids. As far as we can tell, that is true for every organism on this planet. Such a complete dependence on L-amino acids raises many fundamental questions for biology, the answers to which stretch beyond biology itself, both outside our solar system and deep into sub-atomic physics. (McManus 2002 p128)

One has also to be cautious and not overestimate the significance of chirality. For example, after the thalidomide disaster, further tests demonstrated that the drug is not a teratogen in the majority of species tested, which includes closely related primates. (Stephens and Brynner) This is odd and one now has to explain why human chirality is different from the chirality of our closely related species.

## Bilateral Symmetry

It has been seen how organisms show a bias internally, possessing chirality, but this is not the case for the external body form. Nearly all *Chordata* display a bilateral symmetry. The symmetries are never perfect: for example, in humans, one foot may be a tad larger than the other, one ear slightly higher, one arm fractionally longer. Some minor asymmetries can be difficult to explain: for instance, the testes of the human are at different heights and there seems to be no clear agreement over which spacing is most common; however, equal height is very rare, but once again there is no clear consensus why this is so. (McManus 2002 p94)

Bilateral symmetry, or near symmetry, is near ubiquitous among higher animals but there are some fascinating exceptions. Wherever there is a limb on one side of a body, there is nearly always a corresponding limb of equal proportions on the other side. Consider any creature that flies, be it an insect, bird, bat or pterosaur: all have symmetrical wings. It could be argued that symmetry here is essential for flight, which may be true, but one must remember that flightless birds also have symmetry of wing. (The following summarises Blackstone 2007, Close 2000, DeSalle and Schierwater 2007). Wherever there is a pair of horns in ruminants, say, they are equal in proportions. It should also be noted that these near symmetries are not just features of contemporary life but have persisted through millennia going back to the Cambrian. Even the pre-Cambrian has examples of bilateral symmetry in certain fauna, with other life forms

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[46] Gardner suggests that this change from chirality could be a useful tool in prediction, as there is a regularity that would lend itself to the dating of fossils. One problem he concedes, however, is that external rigours in the immediate environment could disrupt uniform transitions.

exhibiting radial symmetry. It is not only the appendages that constitute symmetry; most body plans also conform to such regularities. Consider the head, thorax and abdomen of insects, the cephalothorax and abdomen of *Chelicerata* (arachnids, horseshoe crabs and sea spiders) or the arrangement of the anatomy of vertebrates. Colour can manifest itself bilaterally (think of the butterfly wing, chiclid fish, the zebra, the tiger, a peacock's tail and so forth). The organs of perception, be they auditory, olfactory or visual, nearly always come in pairs located bilaterally. Further, are there any examples of asymmetric dentures? One is hard pressed to think of a creature that does not have teeth aligning both sides of the mouth. Even the shapes of tongues, tails and flagella conform to this topology. Also, the vast majority of plant leaves are symmetrical when folded along the centres. Despite this prevalence of different forms of symmetry in nature, this topology is not universal. Why is it, then, that most organisms conform to some form of symmetry but a few do not? Trees and bushes are often ascribed symmetry to their overall form but it does seem to invite the criticism that this ascription goes beyond any meaningful definition of symmetry. Many trees take quite irregular overall shape, especially the deciduous, either temperate or tropical. A hedge loses symmetry all too soon after trimming. The asymmetries of life and some of the explanations put forward for them will now be considered, before a discussion of consistent growth patterns, including phyllotaxis.

## Asymmetries in Nature

Just as one begins to think there are some underlying universal laws that might account for a variety of phenomena, one discovers in nature an anomaly that seems inconsistent with the observations. The narwhal provides such a case. First, it best be noted that the narwhal's 'horn' is not a horn at all, but a tooth of great size, reaching up to eight or nine feet. It manifests itself in the male, but also, very rarely, two tusks have been found on both male and female narwhals. The anomalous feature of these dual tusks is that they are not symmetrical: the screw-threaded nature of the tusk runs the same way in each – they are not mirror images of each other. (See Thompson next chapter).

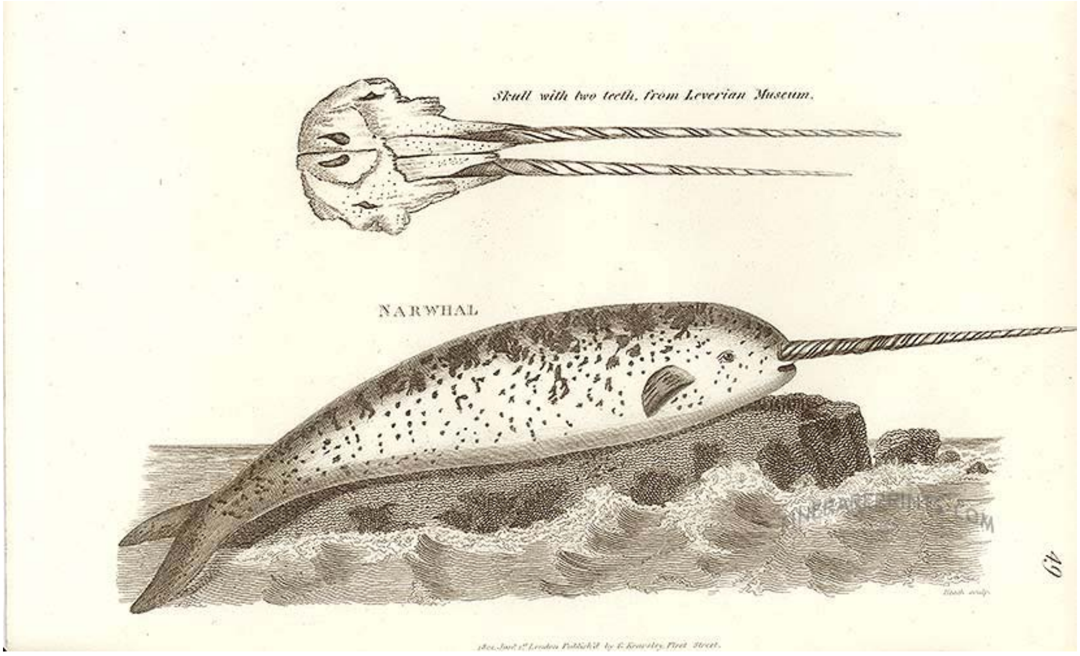

Figure 5

Source: http://www.curiousexpeditions.org

Second, all ordinary teeth in other creatures have a natural curvature, which becomes evident with growth. Not so the narwhal: its tusk remains straight, albeit with a right-handed, low-leaning screw or helix with several threads. Furthermore, these tusks are seated in the socket or alveolus of the upper jaw and are protected from many external physical forces. So how does one explain these singularities? Thompson (1961) suggested several hypotheses but admitted none was conclusive.

(The details in the following paragraph are summaries from Gardener 1990, Riehl 2100) *Porifera* is the phylum of the sponges which inhabit mostly the marine, but some 150 species have taken to fresh water.[47] They first appeared up to 650 mya, surviving the five great mass extinctions. Their bodies are without distinct tissue or organ, taking the form of an asymmetrical sack with an internal cavity. Their porous bodies admit water and nutrients. Fungi and lichen both manifest irregular form in many instances, lichen invariably so. The popular image of the mushroom or toadstool obscures the many asymmetrical forms of fungi, as illustrated by the fungi that live on tree trunks, such as *Pleurotus ostreatus*, often referred to as the oyster mushroom. Truffles and morels from the group *Ascomycota* rarely exhibit symmetrical features and members of the group *Chytridiomycota* take a form very similar to that of a plant with branching at regular angles. Coral exhibits similar form to both fungi and sponges, branching in some instances. These sessile creatures seem not to have acquired bilateral symmetry. Among the molluscs, many of the *Gastropoda* shells curl, twist and spiral, often taking the most delightful shapes. The shell of the nautilus has intrigued and tantalised both biologists and mathematicians with its logarithmic spiral and fidelity to the golden number. However, one must remember that the creature living inside retains symmetrical proportions whilst the shell builds by uneven incremental deposits.

Similar to the narwhal, the male fiddler crab displays an unusual asymmetrical feature, this time in the form of a rather extraordinary front claw. This disproportionate claw is unique in its size amongst crabs, but the ghost crab also sports an asymmetrical, although smaller, front claw. Another peculiar feature of the fiddler crab is that if the large claw is lost, then another large claw grows on the opposite side, although not necessarily as large as the original. (Zhong 2009)

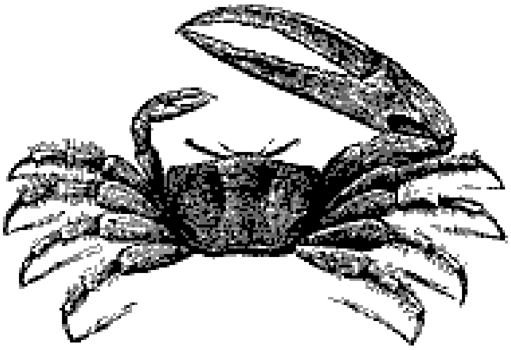

Figure 6

Source: http://etc.usf.edu/clipart/8200/8250/fiddler_crab_8250.htm

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[47] *Porifera* is taken from the Latin *porus* for 'pore' and *ferre* for 'to bear'.

Following this rather brief sketch of the features in this investigation, one can reasonably ask why it is that the varied forms of symmetry are so pervasive in nature, with asymmetrical forms being very much in the minority. One explanation draws on the influence that gravity exerts upon all forms. This argument was articulated by Thompson (1961), but here Gardner picks up the thread:

> On another planet, as on earth, the same factors would operate to produce such symmetry. Gravity would provide a fundamental difference between up and down. Locomotion would create a fundamental difference between front and back. The lack of any fundamental asymmetry in the environment would allow the left and right symmetry of bodies to remain unaltered (Gardner 1990 p59).

Gravity influences the vertical but has no influence upon the horizontal, or at least not directly. There is no bias here, so one would expect both sides of a body to result with similar features. It is argued that the relationship between locomotion and gravity partly determines the form. Gardner does not state whether he believes this manifestation of bodily form to be a direct adaptation (following Thompson), caused by gravity or an adaptation caused by natural selection. It is apparent that groups such as the *Porifera*, lichen and certain fungi (mentioned above) share sessile and asymmetric qualities. Their stationary status means they are susceptible to physical forces other than gravity that may act upon them. Water turbulence in the form of currents, erosion or rainfall is an obvious example. A creature not anchored to the ocean floor would find itself swept along with the ebb and flow, assuming a more spherical symmetry which conforms to the radial. Indeed, the empirical evidence supports such relationships in many cases but not quite all. The free floaters of the seas – such as jellyfish and members of the *Eleutherozoa*, including starfish – all conform, but the sea anemone is sessile and yet of radial symmetry. In the quotation above, Gardner says that 'locomotion would create a fundamental difference between front and back.' However, it could also be argued that the causal chain was the other way around, with the advent of front and back facilitating locomotion, as sessile organisms such as the phoronids possess a front for feeding. The colonisation of land that followed the emergence from the marine was thought to endorse the bilateral status of motile life. On land, the effects of gravity are not mitigated by buoyancy as they are in the sea; any directed locomotion requires appendages and hence particular forms of anatomy. As an illustration of this point, consider the whale, a mammal that returned to the sea some 50 million years ago. [48]An examination of its vertebrae shows how disproportionately small the bone structure is in relation to overall body size. (Thompson 1961 p25) Compare this with the whale's closest living relative, the hippopotamus, or the whale's ancestor *Pakicetus*, both terrestrial and under the influence of gravity without any counteraction from buoyancy. Their proportion of bone relative to overall size is far greater. Further, the whale has retained certain vestigial features such as the pelvis, hind legs and hands; these too are all disproportionately small.

If gravity is a plausible explanation of bilateral symmetry, how does one explain the asymmetry of the narwhal or the fiddler crab? One could argue the claw of the fiddler crab resulted from female sexual selection. Assumedly, the female crab noticed a small increment in size of the particular claw, which itself was the result of a mutation, and gave preferential mating to the mutated male. This in turn allowed the feature to be passed on to later generations. At some stage, another mutation led to a further increment in size

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[48] An excellent site for quick reference of evograms: http://evolution.berkeley.edu/evolibrary/article/evograms_03

and this too was seized upon by the female … and so forth, resulting in the asymmetry that is manifest today. However, there are several problems with this explanation. Why, for example, does the crab grow an asymmetrical claw on the opposite side if the original claw is lost? Also, why is the second growth rarely as large as the first? Is there a well-documented fossil record of crabs with claws at the intermediate stages of evolution? A further constraint seems not to be explained by sexual selection: the asymmetrical claw grows in accordance with the laws of allometry. (The subject of allometric growth and scaling will be considered in Chapter 10.) There is also a deeper problem for advocates of sexual selection, if it is argued that both sexes strongly select for symmetry rather than asymmetries, which deviate from the norm and may not promise reproductive success. Why does the female crab break from the safer option of symmetry? Trying to explain the asymmetry of the fiddler crab claw by means of sexual selection unfortunately raises more problematic questions than it solves. The situation of the narwhal is even more bizarre and elusive of explanation, for it is sometimes the female that manifests the second asymmetrical horn-like tooth. Is there then a more satisfactory explanation?

Maybe the reasons behind these asymmetries are not known. Sessions and Ruth (1990) had become perplexed by the fairly sudden occurrence of limb anomalies amongst both frogs and salamanders. In some extreme cases, the asymmetry included three limbs to one side and nine to the other. Examination of the pond water demonstrated that adulteration from toxins could not be held responsible. It was discovered later that both species were infected by a parasitic flatworm, leaving metacercarial cysts that interfered with the normal development of limb buds.

> A wide range of limb abnormalities are seen, including duplicated limb structures ranging from extra digits to several extra whole limbs. We hypothesize that these limb abnormalities result from localized regulatory responses of developing and regenerating limb tissues to mechanical disruption caused by the trematode cysts. We have tested this idea by implanting inert resin beads into developing limb buds of frogs and salamanders. Since this treatment can cause supernumerary limb structures, our hypothesis is sufficient to explain the naturally occurring extra limbs. (Sessions and Ruth 1990 abstract)

It is not, of course, being suggested that the asymmetries of the narwhal and the fiddler crab are the result of parasitic infection, but merely that physical causes from perhaps environmental factors can precipitate morphological changes. Indeed, other studies have witnessed similar rapid asymmetrical limb developments but without any evidence of the presence of the trematode flatworm.

Another difficult problem for both the structuralist and the selectionist is that although most external features of *Animalia* conform to bilateral symmetry, some internal features do not. Many vertebrates have their organs distributed asymmetrically – in humans, for instance, the heart and stomach are to the left and the liver to the right. This arrangement contrasts with that of invertebrates whose organs follow the central line, the famous *drosophila* being entirely symmetrical but for its penis which rotates clockwise during development. McManus sums up the evolutionary stages of symmetry:

> The body plans of animals have therefore evolved in three distinct phases. The first stage, the simplest, shows only radial symmetry. The second stage shows bilateral symmetry, the organs being arranged symmetrically to right and left of the mid-line. The third stage, characterised by the vertebrates, involves an external symmetry coupled with a gross internal asymmetry of the viscera. (McManus 2002 p95)

How does one explain asymmetries such as the heart being located to the left in humans? Further, how was symmetry broken internally in the evolution of vertebrates? One cannot argue that the human heart functions with advantage to the left side, for a few people have their internal organs in the opposite mirror position and they live quite normal lives, with their fitness unaffected. However, it is more difficult to explain why asymmetrical positioning for some internal organs is the norm for vertebrates but not for invertebrates.

In summary, one can conclude, that symmetry is pervasive, featuring in a range of fields from mathematics to complex biological forms. It is the asymmetries that provide the mystery and the challenge. What should be taken as evolutionarily significant are the internal asymmetry and chirality, which is a fundamental constraint and determines how our handed bodies interact with external handed molecules.

## Patterns in Nature

It can be argued that entropy rebuts evolutionary changes, but this assertion seems to rest upon a misunderstanding that biological entities operate within closed systems. In fact, there is only one closed system and that is the entire cosmos. So, to the contrary, entropy is a necessary ingredient for evolutionary change and complexity.

> A useful way to think about symmetry is in terms of structure and complexity. The more symmetry a system possesses, the simpler and less structured it is: compare, for example, the symmetric figure of a circle with an irregular polygon. Raising the temperature of a physical system reduces structure and destroys complexity: think how much simpler a glass of water is than a tumbler full of ice cubes. (Davies 2007 p183)
>
> The very early universe was so hot that everything we know was literally in the melting pot (well, the vaporization pot). All the richness, diversity and complexity of the universe we now see lay in the future: uniformity was the order of the day. (ibid. p184)

The universe at its origins was at its most symmetrical but, as the second law of thermodynamics dictated, temperatures decreased, entropy ensued and expansion was inevitable. Although symmetry was broken, it did not mean there would be no further symmetries; neither did it mean there would be an absence of regularities. In fact, in the complexities that followed, there are many patterns and regularities, but they are not necessarily symmetric. Consider the spirals that exist at the macro level with galaxy formation or at the micro level with the helical structure of DNA. A brief outline of some of the major pattern formations in nature will help elucidate the structuralist thesis.

### *Phyllotaxis*

Phyllotaxis is derived from *phyllon*, a Greek word for leaf, and *taxis*, meaning arrangement or order. The diversity of plant life can be quite surprising, considering that the leaves around a stem are nearly always arranged in one of only four basic ways. In distichous phyllotaxis, leaves or other botanical appendages grow successively, each at 180 degrees from the previous one. This is common amongst grasses. A more frequent pattern consists of whorls (circles), two or more of which grow at the same point on the stem. Their number can vary from species to species, but can also vary within a species or even within an individual specimen. In some instances, there can be clusters of six at one point and up to twenty at another point. These outgrowths are evenly spread and the next layer always situates midway between the earlier configurations. Multijugate phyllotaxis includes two or more appendages that grow at the same point. These parts of a whorl are spread evenly around the stem and each whorl is at a constant divergent angle from the previous one, which can give a misleading appearance of spiral patterning. The most common formation is the spiral. Leaves or other elements are sequentially placed, normally at a consistent divergent angle of 137.5 degrees. This is close to the 'golden angle' giving rise to the Fibonacci sequence. The golden angle has special importance for mathematicians but also has implications for biological structures. For a seed head to maximise available space and retain energy efficiency, sequential numbering such as the Fibonacci sequence is requisite. (However, nature is not confined to this sequencing; the Lucas sequence can also occur, but more rarely.) The Fibonacci sequence contains the numbers 0 1 1 2 3 5 8 13 21 34 55 89 144 and so forth. Each number is achieved by adding the two previous lower numbers: as an example, 13 is the sum of 8 and 5; then 13 added to 8 produces the next number in the series, 21. Significantly, these numbers occur in many structures in nature not by chance but as an integral part of the topology. Many plants conform to these numbers with the arrangement of their petals within the flower. The lily and iris always have three petals, the primrose and buttercup five, and so forth.[49]

> Fibonacci numbers are not an accident; they are consequences of universal geometry, the crystallography of plant structures. Indeed plants can no more avoid Fibonacci numbers than salt crystals can avoid being cubical. (Stewart 1998 p130)

[50]This is probably not quite strictly true because the Fibonacci sequence is not universal to all plant life, but what is important is that once a plant begins its growth, say, with three buds then any further buds at the same locus will conform to an arrangement of five, eight, thirteen and so forth. Smaller pine cones begin with a spiral bud arrangement of five in one direction and eight in the opposite direction, whereas a larger pine cone will always conform to eight and thirteen spirals. Once a plant is locked into a Fibonacci or, for that matter, a Lucas sequence, it always conforms to the numbers dictated by the laws of topology. Some observers have extended the importance of Fibonacci numbers within nature to a relationship with proportions related to what is known as the 'golden section'. Dividing any Fibonacci number by the number immediately below it in the sequence always results in 1.62 (rounded up). This is known as *Phi*, the 'golden number' (1.6180339887…), which has almost mystical connotations in some circles. More significantly, the number has a widespread presence, permeating geometry, mathematics, music, cosmology, architecture and design. The biological world also feels its influence, with some arguing that morphology often follows proportions related to *Phi.* Are these relationships simply correlations with *Phi*, or is there an explanation for its great frequency but not universal occurrence? To date, no one has solved this question satisfactorily, but it is generally accepted that the answer lies outside any genetic explanation. The formation of the spiral shells of molluscs such as the nautilus can be seen to follow a patterning that includes the golden angle and an expression of *Phi* through the 'golden section'. Ball (1999) noticed that the physicists Douady and Couder also demonstrated how spiral patterns could be achieved by dropping tiny droplets of magnetic liquid onto a disk with a film of oil covering it. Depending upon the speed of dispersal, the droplets formed the same divergent angles that one sees in rare leaf formations or spiral phyllotaxis. Ball said of these experiments:

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[49] See Jean (1994) for an in-depth view on the subject from a mathematician.

[50] The details for this paragraph, unless quoted otherwise, are summarised from Vajda (1989)

> Their findings imply that a plant need not somehow ‘know’ from the outset that the 137.5 degree spiral phyllotaxy is the best choice – on the contrary, the *dynamics* of the growth process automatically select this angle. (Ball 1999 p108)

Ball also discounts a genetic explanation for phyllotaxis:

> Phyllotaxis, therefore, contains a hidden mathematical pattern for which we are unlikely to find an explanation by rooting around in the genetics of plant developmental biology. It seems there is some more universal basis to these observations. (ibid. p107)

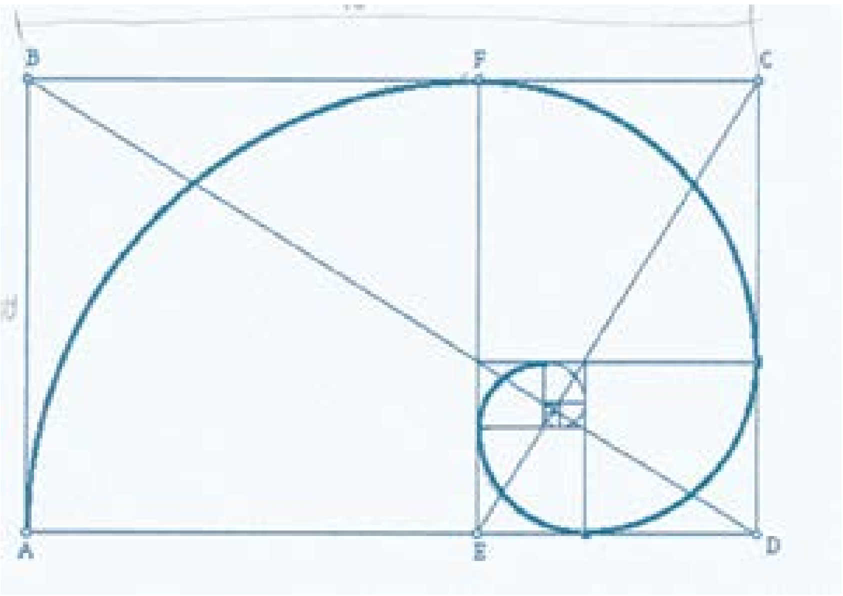

Figure 7

Source: http://ceng.calpoly.edu/

*When a golden rectangle is progressively subdivided into smaller and smaller golden rectangles, a pattern is obtained. From this, a spiral can be drawn which grows logarithmically, where the radius of the spiral, at any given point, is the length of the corresponding square to a golden rectangle.*

Early in the twentieth century, Thompson sought to provide explanations of form that could be understood through mathematics and physical forces. He was sceptical that Darwinism and explanations based upon genetic considerations were sufficient to explain many of the structures in nature. One of the many examples he employed was the explanation of the formation of the spiral shape of the mollusc shell. The shell is dead organic matter but its shape conforms to the golden number that the spiral shape can be plotted on the intersections of a series of rectangles conforming to the golden section (see Figure 7).

*Stripes, spots and dappling*

Much has been said by zoologists about the value of animal colouration and its advantages of camouflage and physical attraction. However, these considerations do little to illustrate how stripes, spots and dappling originated. In the 1950s, Turing, famous for his work on mathematics and computation turned his attention in that direction. He sought to provide a ‘mathematical theory of embryology’ that would explain gastrulation, polygonally symmetrical structures such as the starfish, leaf arrangement, colour patterning and the patterning of near-spherical structures such as radiolaria. To Turing, the diversity of patterns was a challenge, a code hidden in nature waiting to be deciphered and broken. Strongly influenced by Thompson's *Growth and Form* 1917 edition, and appreciative of Schrodinger's contemporary contribution *What is Life*, Turing wanted to complement these works with a mathematical account of how chemical solutions might diffuse and react with each other to form a pattern.

Turing produced a paper entitled 'The Chemical Basis of Morphogenesis' (1952) to answer the mysterious question of what he referred to as 'gastrulation'. Turing thought that the principles involved could also explain the phenomenon of phyllotaxis and its relationship with the Fibonacci sequence. This is of interest because Turing also discussed and incorporated symmetry – how it may be broken and the patterning that follows.

> The purpose of this paper is to discuss a possible mechanism by which the genes of a zygote may determine the anatomical structure of the resulting organism. The theory does not make any new hypotheses; it merely suggests that certain well-known physical laws are sufficient to account for many of the facts. (Turing 1952 p37)

Turing's 'reaction–diffusion model' was more of a theoretical contribution rather than a workable model. It postulated, for example, morphogens that represented the chemicals involved without being able to identify them; these could include enzymes, genes and skin pigments. Similar to the processes involved in crystallisation, a chemical substance P is able to produce more P auto-catalytically. Substance P can also produce, under the same principles, substance S. Substance S, however, will inhibit the continued production of substance P at some point. Turing applied some complex mathematics to give the model predictive power concerning areas of high or low concentration of substances and subsequently pattern formation. After Turing's death, the reaction–diffusion model suffered its own demise. Biologists could not distinguish the proposed morphogens, and attentions were taken, with the new understanding of the double helix in 1953, in the direction of genetic fundamentalism. The hypothesis languished in obscurity for over thirty years, but revival of interest began in the 1990s with the advancement of both chaos and complexity theory. Advances in computer technology had enabled Turing's complex mathematical equations to be realised, at least in patterns of simulated images. In 1998, Meinhardt (see Gilbert 2003) successfully applied Turing's principles to reproduce a computer model of patterns that bore a remarkable similarity to those found on the snail *Oliva porphyria*. Today, morphogens are recognised as physical entities and employed in the vocabulary of developmental biology. For a more in depth portrayal that goes beyond the parameters of this thesis see Tabata and Takei (2004).

There were more surprises. Researchers within developmental biology had dissected the embryos of mice and frogs at a very early stage of development. They then put them back together but not in the original order – where the component for the head had been, the legs were now placed, and vice versa. Much to the amazement of all, the embryos developed with the normal arrangement of limbs. Somehow, the cells involved had arrived at a regular body plan despite the jiggling of their inherent order, but how was this so? One explanation put forward by Wolpert (1996) suggested that cells contained 'positional information'. This 'information' comes in the form of gradients of chemical concentration, a revised version of Turing's morphogens. There is still debate over this explanation and what morphogens actually are. Stewart (1998 p154) agrees that there is very good circumstantial evidence but doubts if Wolpert's interpretation could explain the complicated patterns of a zebra. Nevertheless, Gilbert (2003) argues that, with the use of computer simulations, certain patterns can be predicted if one engages the Turing reaction–diffusion equations. This can explain the stripe patterns of the three known zebra species; further, by altering the parameters, the pigmentation patterns of angelfish can also be predicted. Evolutionary developmental biology now employs the term 'morphogen gradient' to refer to specific amounts of soluble molecules and the term 'morphogen' to refer to the particular soluble molecule. Commentators seem to be of the opinion that, although the Turing reaction–diffusion model in its original form lacked specific details, it was correct in principle and is supported by some quite compelling recent research. The mathematician Stewart (p138) endorses this view: 'Turing's equations do not match biology precisely; they are best viewed as a particularly simple example of the *kind* of mathematical scheme that must govern pattern formation in animals.' Both Ball and Stewart see Turing's contribution as a synthesis of mathematics, chemistry, physics and genetics that can explain diversity of patterning across a wide spectrum of species. In some ways, it answers some of the manifestations of convergence that perplexed Mivart. Stewart sees explanations purely based on DNA as quite inadequate:

> In the same manner, an organism cannot take up any form at all: Its morphology is constrained by its dynamics – the laws of physics and chemistry – as well as by its DNA instructions. Still, the DNA instructions can make arbitrary choices among several different lines of development that are consistent with the dynamic laws. The new mathematical models are finally beginning to put these two aspects of development together. DNA alone does not control development – nor do dynamics alone. (Stewart 1998 p157)

These views represent a revision of the neo-Darwinian thesis, moving from a genetically determined perspective to a perspective that recognises a greater role for mathematics and physical laws. The problem for such a revision, however, is being able to quantify the extent that the latter perspective erodes the province of explanation that endorses accumulated genetic mutation through heredity and natural selection. In fact, Ball in a later work demonstrates just how difficult a task this is:

> In other words, seeking a 'biological' (which is to say, an adaptive) explanation for all patterning and collectivity in animal populations runs the risk of invoking a contingent evolutionary explanation for something that is in fact an immediate consequence of the 'physics' of the situation. (Ball 2004 p152)

## Conclusions

It has been observed that the shapes and forms in all aspects of nature conform to symmetries, regularities and patterning, much of which can be measured mathematically. Nothing escapes the influence of the fabric of space, and when irregularities or asymmetries occur, an explanation is sought within physical causation. The cell, the chromosome, the gene and the protein – all important players in the story of life – must conform to the dictates of the physical dynamics of the situation. Ball and Stewart presented compelling arguments for this. However, they diverged in opinion from the structuralists to be considered in the next chapter.

## Chapter 9: D'Arcy Thompson and Lima-de-Faria

### Beyond Natural Selection: The Structuralist Alternative Takes Shape

Ball and Stewart sought to accommodate natural selection within their thesis; in contrast, an examination is imperative of those who see little role for this feature of Darwinian interpretation. At the outset, it is perhaps best to say that the entire Darwinian programme is not rejected; the principles of descent with modification, for example, are accepted but seen more as a given rather than something that illuminates explanation. It is the factors that cause and constrain the modification part of the theory that prove controversial. Just how far are these modifications canalised by natural laws? A short summary of D'Arcy Thompson's major contribution will be followed by an outline of the major work of Lima-de-Faria. Both see physical law as primary in evolutionary explanation. Interestingly, both are polymaths but whereas Thompson sees no explanatory place for the gene, Lima-de-Faria sees the gene as explanatory necessary.

Thompson (1860–1948) produced what some believe to be one of the great classics of English written scientific literature, *On Growth and Form*. Unfortunately, this work never received the full recognition those familiar with it thought it deserved. His academic background was unusual in that he was a Greek scholar, a mathematician and a naturalist, a combination that yielded unorthodox insights. It has been suggested that he should be considered the father of the fairly recent discipline of biomathematics. Thompson's ambition was to explain the many forms in nature through the use of physical causation and ultimately mathematics. This ambition did, however, recognise its limitations. The introduction of the first edition of *On Growth and Form* states:

> Consciousness is not explained to my comprehension by all the nerve-paths and neurons of the physiologist; nor do I ask of physics how goodness shines in one man's face, and evil betrays itself in another. But of the construction and growth and working of the body, as of all else that is of the earth earthy, physical science is, in my humble opinion, our only teacher and guide. (Thompson 1917, reprinted 1942, extracted from http://www-groups.dcs.st-and.ac.uk/~history/Biographies/Thompson_D'Arcy.html)

Thompson's priority was to distinguish the relevant physical causation behind morphologies. He despaired at the tendency amongst so many biologists to replace religious teleology with the teleology of the survival imperative. The finger of God had been replaced by dictates of 'fitness'. Teleology, whatever form it may take, was seen as an obscurant of the mechanistic processes that offered such rich explanation. It was not that teleology should be expunged in its entirety – there was a place for it – but the mechanics of the situation should be sought and addressed first. 'In Aristotle's parable the house is there that man may live in it; but it is also there because the builders have laid one stone upon another.' (ibid. p6.) Final causes and the physics could then be appreciated and evaluated to discover whether they were commensurable. However, if Thompson did see a place for teleological considerations, it seems highly unlikely that that he considered 'fitness' the appropriate candidate, as he treated natural selection and all its implications with extreme scepticism. Typical of his concerns are the following passages. The first addresses the fact that the same form of shell has manifested itself independently on several occasions; the second passage casts doubt upon the explanation by natural selection:

> It leads one to imagine that these shells have grown according to laws so simple, so much in harmony with their environment, and with all the forces internal and external to which they are exposed, that none is better than another and none fitter or less fit to survive. It invites one also to contemplate the possibility of the lines of possible variation being here so narrow and determinate that identical forms may have come independently into being again and again. (Thompson 1961 p198)

> Again, we find the same forms, or forms which (save for external ornament) are mathematically identical, repeating themselves in all periods of the world's geological history: and we see them mixed up, one with another, irrespective of climate or local conditions, in the depths and on the shores of every sea. It is hard indeed (to my mind) to see in such a case as this where Natural Selection necessarily enters in, or to admit that it has had any share whatsoever in the production of these varied conformations. Unless indeed we use the term Natural Selection in a sense so wide as to deprive it of any biological significance … (Thompson 1942 p849)

The last sentence anticipates Popper's dichotomy discussed in Chapter 2. These concerns also echo those of Mivart (1871 & 1876), who some fifty years earlier thought natural selection inadequate to answer the problems posed by convergence. Moreover, both Mivart and Thompson had recognised those biological attributes that lack any apparent adaptive value. But whereas Mivart could not supply an answer to those missing factors that shaped evolutionary change, Thompson takes a slightly different tack: explanations of form and growth need not necessarily take an historical perspective. For example, he notes that amongst the unicellular microscopic organisms, the radiolaria, there is a great multiplicity of forms and yet, despite these complex configurations, there is an unusual appearance of geometric regularity. He draws comparison with the snow crystal, which also boasts many thousand forms but also conforms to a symmetrical repetition of one single crystalline form. Furthermore, there are skeletal similarities between snow crystals and the radiolaria. Thompson considers the geometrical forms of many unicellular organisms and arrives at this conclusion:

> We begin by an easy and general assumption of specific properties, by which each organism assumes it own specific form; we learn later that throughout the whole range of organic morphology, there are innumerable phenomena of form which are more or less simple manifestations of ordinary physical law. (Thompson 1961 p171)

However, there are organisms that do not conform to the above view and the physical forces that might influence form are, for the moment, kept locked as a secret by Mother Nature. 'Many a beautiful protozoan form has lent itself to easy physio-mathematical explanation; others no less simple and no more beautiful prove harder to explain.' (Thompson 1961 p171) Throughout *On Growth and Form*, Thompson gives many physio-mathematical accounts of the structure of biological characters, arguing that these explanations (even if often incomplete) give more explanatory satisfaction. However, he does not entirely rule out a place for modification by descent:

> It would, I dare say, be an exaggeration to see in every bone nothing more than a resultant of immediate and direct physical or mechanical conditions: for to do so would be to deny the existence, in this connection, of a principle of heredity. (Thompson 1961 p265)

Despite this concession, Thompson's focus is directed like the engineer's, recognising that any construction must take account of certain factors, such as the relevant stresses and strains, the compensations necessary amongst the proportions of the components of a body, and the effects of velocity upon growth in any dynamic system. Conversely, the engineer or the aeronautic designer can glean many lessons from the study of nature, such as the shape of the wing or the construction of load-bearing limbs. Indeed, it was this engineering approach that led to Thompson's novel work on transformations, which many consider his greatest contribution. With the ingenious use of a Cartesian grid, he painstakingly plotted out the structure of an organism by hand and then, by changing the mathematical coordinates, was able to demonstrate related forms (see Figure 8). This method of coordinates Thompson called the 'Theory of Transformations'. Its significance was not only that form could be interpreted and understood mathematically but also that the method demonstrated the range and limits to possible configurations. Thompson thought this methodology could be of value to the palaeontologist. For example, if one was seeking to identify an intermediate form between two specimens that were considered to be related, then transformations within the Cartesian grid could predict the morphology of any intermediates. Interestingly, Thompson could not produce a transformation from a *Homo sapiens* to a *Homo neanderthalensis*, an issue of relationship that has vexed anthropologists. Another aspect of significance was that he felt that the transformations he was able to demonstrate were an endorsement of homology: nature was continually using the same materials and methods over and over again.

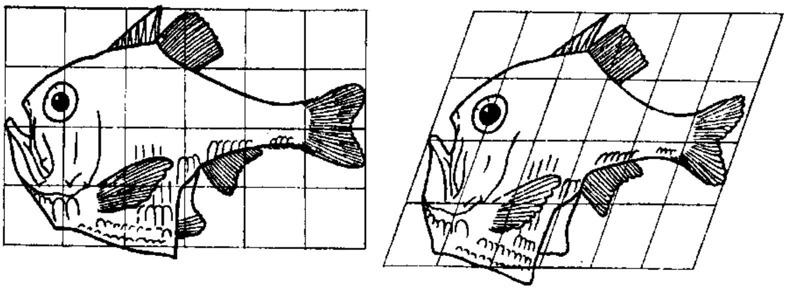

**Fig. 146.** *Argyropelecus olfersi.* **Fig. 147.** *Sternoptyx diaphana.*

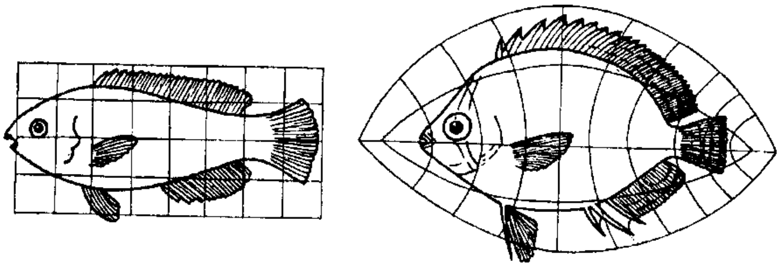

**Fig. 148.** *Scarus* sp. **Fig. 149.** *Pomacanthus.*

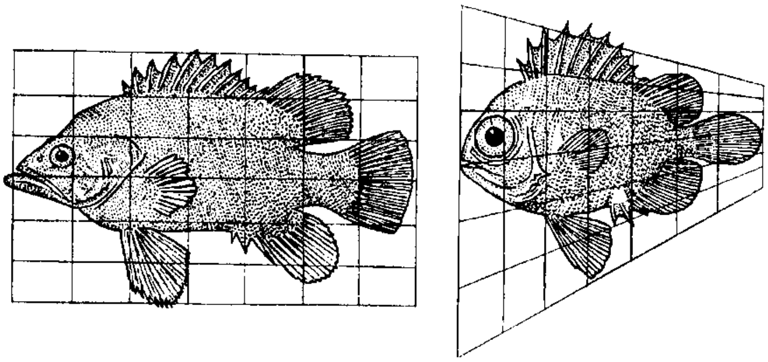

**Fig. 150.** *Polyprion.* **Fig. 151.** *Pseudopriacanthus altus.*

Figure 8. Transformations on fish

Source: Thompson 1942 p299

Thompson's claim was that if one pursued the mathematics of the situation rigorously, then one could unlock many secrets of nature and move beyond mere description and the act of categorisation. However, he recognised suspicion and reluctance amongst naturalists to embrace mathematical methodology and that they preferred to explain things through adaptive terminology. In some ways, this could be understood because the task of the biologist was so much more difficult in an arena of complexities where one is forced to look at the specifics. Whereas the physicist could describe and elucidate a wave in general terms, Thompson thought it was another kettle of fish when it came to describing a particular wave. Nevertheless, he was dismayed by many of the adaptive explanations purporting to 'explain' a wide range of biological phenomena, perceiving them as rather fanciful, unscientific and little better than the theological attempts of earlier times. In many ways, Thompson anticipated the reforms of Gould and Lewontin some sixty years later, in the now famous paper alluding to the spandrels of San Marco. This paper sought to exorcise what have become known as the 'just so' stories of biological explanation. To Thompson, any appeal to adaptations required that the adaptation went beyond mere hypothesis and faced the 'questions of mechanical efficiency where statical and dynamical considerations can be applied and established in detail.' (Thompson 1942 p961) Aerodynamic flight of birds and the streamlined bodies of fish were examples of adaptations that passed such criteria. Many of the adaptive explanations that sought to explain the colouration of insect, bird or mammal were, to Thompson's mind, little more than speculation:

> With regard to coloration, for instance, it is by colours 'cryptic,' 'warning,' 'signalling,' 'mimetic,' and so on, that we prosaically expound, and slavishly profess to justify, the vast Aristotelian synthesis that Nature makes all things with a purpose and 'does nothing in vain.' Only for a moment let us glance at some few instances by which the modern teleologist accounts for this or that manifestation of colour, and is led on and on to beliefs and doctrines to which it becomes more and more difficult to subscribe. (Thompson 1942 p958)

In an examination of the different structure and form of birds' eggs, Thompson gives an example where adaptive explanations can be quite contrary. The pointed conical egg of the guillemot is said to be an adaptation because its shape is less likely than a spherical egg to run or roll from the bird's preferred laying area, such as a narrow stone ledge. However, when considering the pointed conical egg of the sandpiper, who lays her eggs in a different environment without the spectre of the egg rolling into danger, the supporter of adaptation 'elicits another explanation, to the effect that here the conical form permits the many large eggs to be packed closely under the mother bird.' (ibid. p936.) Thompson saw these as speculative explanations and obscurant when determining the physical causes of the shape of the egg. To understand the egg shape, one has to consider the journey from conception through the oviduct. At the early stages, the membrane is a soft pliable tissue that is shaped by the muscles of the oviduct pushing the egg along the passage. As the membrane slowly hardens, the result is the rounded end of the egg proceeding with the pointed conical shape at the rear. Oviducts, however, vary in size and the more spacious oviducts, relative to the size of the transit egg, can give rise to more spherical final eggs. Thompson notes that, in general, smaller birds produce more spherical eggs than larger birds. Further, a young bird laying an egg will produce a more spherical egg than the egg she might produce when she is older. The asymmetry is determined by the relative size of the oviduct.

The importance of this example is worth deeper consideration. Thompson is arguing that the question 'Why are eggs of a particular shape?' is answered by explanation in terms of physical forces. The adaptationist outlook, however, seems to bypass the immediate chain of physical causation and provide an answer to a slightly different question. The question the adaptationist is addressing seems to take the form 'Why are eggs of a particular shape preserved through history?' Some have defended this subtle adjustment to the original question, claiming that the adaptationist account provides a more 'fundamental' or 'primitive' explanation in ancestral terms, and thus an evolutionary explanation. If we overlook, for the time being, all the problems involved in testing such explanations, there is still little detail provided as to how the particular shapes of birds' eggs originated, before natural selection is said to operate. While examining this dichotomy of explanation, it may help to look at a recent example that also concerns birds' eggs. There has been controversy for some time over what some have called the 'paradox of the speckled egg'. In traditional adaptationist terms, the phenomenon was explained by suggesting that the speckled colouration in the eggshell provided the advantage of camouflage in certain environments where the predator risk was high. The 'paradox' was said to arise because speckled eggs were also laid in areas where the predator risk was very low. Gosler observed the white and reddish-brown speckled eggs of the great tit (*Parus major*), suggesting that the distinctive colouring did little for protection and even that a 'blind weasel could not miss them'. Following an intuition on egg thicknesses, Gosler and his research team conducted an intensive study:

> This, together with more detailed investigations undertaken with students, has revealed that the spot darkness is inherited on the female lineage only, that spots mark thinner areas of eggshell and the degree of thinning is reflected in the spot darkness, that the overall spread of pigment is related to eggshell thickness, and that both are closely related to calcium availability (reflected in soil calcium and snail abundance) near to the nest-site. (Gosler 2008)

In this instance, the research suggests that the colour and thickness of the eggshell are determined by diet and the availability of calcium. Such determinism should not be too surprising: Carson (1962) brought it to attention that the often profligate use of DDT was having disastrous effects on bird populations. This pesticide proved to be a teratogen causing birds' eggs to become thin and brittle, preventing successful reproduction. The lesson to be appreciated, at least according to Thompson, is that when explaining the nature and form of organisms and their characters, one should always examine the local causes before invoking ancestral causes. The latter, being so much harder to identify and then test in an objective manner, are also apt to distract from scientific procedure. In his classic work to explain features of the biological world, Thompson also gives other accounts, such as the Fibonacci numbers and phyllotaxis (now mainstream botany), the role of symmetry and the mathematics behind the equiangular spiral. These features were discussed in Chapter 8, so now consideration will be given to other aspects of his work that further illustrate the influence of constraints.

## The Shapes of Horns, Teeth and Tusks

Once again, the shapes of the various types of horn, teeth and tusk are determined by physio-mathematical laws. Three types of horn are examined by Thompson. The horn of the rhinoceros is the most simple, being physiologically akin to a mass of consolidated hair, which is non-living and added by increments. Its elliptical shape is easily accounted for:

> Its longitudinal growth proceeds with a maximum velocity anteriorly, and a minimum posteriorly: and the ratio of these velocities being constant the horn curves into the form of a logarithmic spiral in the manner we have already studied. (Thompson 1961 p202)

The sheep, goat or ox horn is essentially the same shape but shorter. These horns are paired and hollow. The structure has a bony core covered by skin, which is fed on its internal side with nutrients from blood vessels, whereas the external side of the skin (the epidermis) is formed from a fibrous material similar to consolidated hairs, the result being a sort of horny sheath. The growth of the horny sheath is symmetrical in the pair but not continuous. It is the periodic production of the hair-like chitinous material that leads to the formation of rings and Thompson says that some have claimed that it is possible to tell the age of the animal by counting the rings. Deer antlers are much more complex in shape and it is therefore much less easy to explain the direction of growth and the forces that determine the final outcome. They are also different in nature from the mollusc shell, for when the material is first laid down in forming the horn, it is slightly flexible so it can still bend, fold or wrinkle, whereas the deposit that makes up the shell is calcareous and immovable during growth. The symmetry of horns is essential in accommodating the weight: the head of the ram *Ovis poli* has to bear 50 to 60 pounds in weight; any imbalance would render this task nigh impossible. The heavy horn can also have a bearing upon the set of the head. For example, an Indian buffalo tilts his muzzle higher than a cow and a stag carries his head higher than a horse (Thompson 1961 p.214). Thompson continues in great detail to explain the complex curvature of the various horns, which is fascinating in itself but not necessary to elaborate on here. The main point of interest is that the formation is a product of physical forces acting upon biological deposits, each variation requiring its own particular elucidation. The difficulty is summarised:

> The distribution of forces which manifest themselves in the growth and configuration of a horn is not simple nor merely superficial matter. One thing is co-ordinated with another; the direction of the axis of the horn, the form of its sectional boundary, the specific rates of growth in the mean spiral and at various parts of its periphery – all these play their parts, controlled in turn by the supply of nutriment which the character of the adjacent tissues and the distribution of the blood vessels combine to determine. (Thompson 1961 p213)

After all this investigation, elucidation and appreciation of the complexity behind the issues of form and growth, one senses the frustration and dismay Thompson felt. Consider the following statement, which concerns the explanatory power of natural selection and carries over from the previous quotation:

> To suppose that this or that size or shape of horn has been produced or altered, acquired or lost, by natural selection, when so ever one type rather than another proved serviceable for defence or attack or any other purpose, is a hypothesis harder to define and to substantiate than some imagine it to be! (ibid. p213)

Concerning tooth, beak and claw in general, these structures follow the growth and form described earlier for shell and horn. Once again, the equiangular spiral is implicit, with its asymmetrical growth leading to fine curvatures. The curvatures are slight and less easy to detect in short growth but they manifest themselves as the structure grows. For example, as a 'bird grows older, or the beak longer, the spiral nature of the curve becomes more and more apparent, as in the hooked beak of an old eagle, or in the great beak of a hyacinthine macaw' (Thompson 1961 p215).

Thompson was familiar with Bergmann's Rule, a topic to be discussed when biological scaling is examined in Chapter 10. Importantly, Thompson gives many examples of the limitations to sizes and the implications that sizes have for function and behaviour. For example, the smaller the animal, the greater is the heat loss, which must be compensated by greater calorie intake. In a day, a human male requires a fiftieth of his own body mass in food whereas a mouse requires half its own body weight.

> A warm blooded animal much smaller than a mouse becomes an impossibility: it could neither obtain nor yet digest the food required to maintain its constant temperature and hence no mammals and no birds are as small as the smallest frogs or fishes. (ibid. p26)

Thompson was not quite correct about the smallest possible animal;[51] however, the principles of heat loss relating to body size and respiration are generally thought to hold. Insects are also constrained by maximum sizes; the following is a modern endorsement:

> The respiratory system of insects comprises a network of fine ducts (tracheae) that deliver air directly to all parts of the body. Although the system works well on a small scale, it cannot be expanded to serve the respiratory needs of large animals. The size constraint imposed by the tracheal system explains why insects have been unable to exploit the advantages of gigantism during their long evolutionary history. (McGowan 1999 pp13–14).

Returning to summarise Thompson, amongst mammals, size also has its consequences. The larger the animal, the larger is the proportion of bone: a mouse skeleton makes up 8% of the bulk, whereas a dog skeleton comprises 14% and a human approximately 18%. One of the major determinants here is gravity. Growth in marine creatures is facilitated by the buoyancy that is afforded by the fact that water is 800 times denser than air, thus counterbalancing the gravitational effect. (Thompson suggests that the earlier large reptilian fauna were semi-aquatic.) Thompson asks what would be the effect of gravitational changes:

> Were the force of gravity to be doubled over, bipedal form would be a failure and the majority of terrestrial animals would resemble short-legged saurian, or else serpents. On the other hand, if gravity were halved, we should get a lighter, slender, more active type, needing less energy, less heat, less heart, less lungs, less blood. Gravity not only controls the actions but also influences the forms of all save the least of organisms. (Thompson 1961 p32)

Arguably, gravity is a phenomenon that is rarely discussed in biology textbooks. There might be a short recognition of its influence concerning bilateral symmetry or the occasional reference to insect navigation. Botanists have accorded it some importance regarding plant growth (geotropism) and developmental biologists have recently realised its force during gastrulation. However, one could argue that evolutionary biologists have paid it little regard, probably because gravitational forces are seen as a constant or a feature in the background that has no direct influence on evolutionary changes. There is an interesting division between the perspectives of Ball/Stewart on the one hand and Thompson/Lima-de-Faria on the other. The former do not seem to include gravity as a factor of evolutionary change, whereas the latter two see gravity as more than a constraint but also a determining factor. To add spice to this debate, there is a group of scientists who contend that gravity is not a passive bystander of evolutionary change but an active ingredient. The scientists of the NASA research centre have obvious reasons for studying the effects of gravity and they have arrived at some unusual perspectives on this subject. This research will be scrutinised later, but now consideration is given to Lima-de-Faria.

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[51] The smallest known living mammals now are the bumblebee bat from 29mm across the wings and the pygmy shrew from 52mm nose to rear, both at 2.0 grams. The smallest reptile, *Jaragua sphaero* or dwarf gecko, measures just 1.6 centimetres and from 129 milligrams. The frog species *Paedophryne amauensis* is the smallest amphibian, measuring a mere 7 millimetres and weighs from 20 milligrams.

## Form, Function and Evolution

It was observed earlier that Thompson attempted to explain form by way of a physics/mathematics perspective, which was essentially an ahistorical account. The exclusion of any reference to genes can be seen as a weakness of the overall thesis. Although Thompson greatly adds to the understanding of growth and form, the thesis still lacks an account of the *changes* that take place within different lineages. This indeed can be seen as a serious omission and challenges the coherence of the overall structuralist argument. An examination of the work of Lima-de-Faria is indicated, to see whether this gap can successfully be plugged. The following two quotations represent the direction of the next few pages:

> One of the central themes of this book is that all non biological and biological phenomena are homologous. There are no accidents in nature; neither are there analogies. All processes represent homologies. It is only the degree of homology that varies. In other words, every biological pattern and every biological function has its predecessor in the mineral, chemical and elementary particle world. (Lima-de-Faria 1988 p21)

> The gene and the chromosome do not create. Their intervention is important but only at a secondary level, deciding only what variant of form and function will become fixed. The roles of the gene and the chromosome appear mainly in locking a condition that has arisen from a series of a limited number of combinations. (ibid. p30)

Lima-de-Faria has spent most of his academic career at Lund University as a geneticist and is a leading authority on the subject of the chromosome. His principal and most important work is arguably *Evolution without Selection*, published in 1988. Regretfully, this work has received little attention in Anglo/American circles but is more widely acknowledged in Scandinavia and on the Continent. The volume is erudite and scholarly, with over 600 scientific references, drawing on not only genetics but also physics and chemistry to explain evolutionary change. The task ahead will be to extract the underlying principles of relevance from this, perhaps controversial and difficult work whilst maintaining a fair appreciation. If Lima-de-Faria is correct or even partially correct, then our perspectives on evolutionary change will never be quite the same. Much of Lima-de-Faria's thesis is in accordance with Chapter 8, which outlined some of the fundamental constraints. The universe is seen as homologous, deterministic and affording patterns and regularities that pervade not only the particle and chemical realms but also the more complex biological. For this reason, biological evolution cannot be divorced from general evolution, for here it is firmly embedded. Failure to consider the evolutionary transition from the chemical elements of the primordial soup to the first biological structures, and all that went before, will result in a limited understanding of evolutionary change.

## The Relationship between Symmetry, Form and Function

Lima-de-Faria observes the experiments first carried out by Pasteur (see Chapter 8) that demonstrate how crystals can be altered from their symmetric form to asymmetric forms, one left-handed and the other right-handed. It then followed that the left-handed crystals would rotate the plane of polarised light to the left and the right-handed crystals would do the opposite. The rotation would not occur if the symmetry were maintained. This fundamental observation has wide-reaching implications. Pasteur went on to observe that functions such as fermentation required asymmetry, as quoted by Lima-de-Faria:

> This evidence leads me to postulate that asymmetry creates function whereas symmetry creates form. In other words, when a phenomenon is in its *symmetric* state, it appears as form, when the same phenomenon is in an *asymmetric* condition, it appears as function. (Lima-de-Faria 1988 p86)

Nothing in nature has perfect form or function. Lima-de-Faria notes that we never observe a perfect sphere in nature or a fully symmetric insect or snow crystal, because life is dynamic with function always present. ‘The symmetry is continually being made asymmetric and the asymmetry is continually reverting to the symmetric condition. Matter, minerals and living organisms are the products that are being squeezed out of this original and permanent dilemma’ (Lima-de-Faria 1988 pp86–87). In a cautious tone and as a preliminary approach, Lima-de-Faria suggests there may be a relationship with energy-

> Function is energy in a state of flow between two or several structures. It results in a canalization of dynamic processes. Asymmetry appears as an obligatory component of this state. All matter is plunged in an energy-exchanging system. This is why form and function cannot be easily separated. (Lima-de-Faria 1988 p87)

Lima-de-Faria introduces the term ‘isomorphism’. Concisely, this is the underlying patterns, shapes and form that pervade not only biological phenomena but also subatomic particles, crystalline structures and minerals. In fact, it is argued, all forms are homologous, form is not analogous, and there is only variety within homology. All biological form arose from earlier non-organic form but not in a random or accidental process. This is essentially an evolutionary account of the structure of form. To Lima-de-Faria, there are four stages of evolution, each autonomously following or obeying physical laws. The first of these stages saw the establishment of elementary particles, providing a physical imprint. The second stage resulted in combinations of elementary particles to create more complex forms, beginning with hydrogen and furnishing a chemical imprint. Third, one can witness the mineral imprint based on crystallisation systems, which are relatively few. Each evolutionary stage determines the subsequent evolutionary stage, culminating in the fourth stage – biological evolution. Lima-de-Faria gives many examples of the same, or extremely similar, forms occurring in nature, with each having a completely different chemical composition. One example of such regularity is horn formation. This manifests itself in the vertebrate as the horn of the wild sheep *Ovis ammon*, in the invertebrate as the shell of the mollusc *Vermetus dentiferus*, in the plant as a unicellular hair of *Althaea rosea* and in the mineral as curved stacks of chlorite crystals. The argument is then that isomorphism pervades nature. There are distinguished shapes that appear in crystals, minerals, viruses, plants and animals. Even in plant cells, crystals are common. Further, crystalline patterns occur in the plant membranes of the chloroplasts. Whole chromosomes, at certain stages of their development, assume crystal shape.

> … living organisms are using the simple chemical processes used in the organic world to build their crystals during the initial stages. The bio crystals are formed in the cell following the same atomic principles which lead to the crystallisation of calcium carbonate and phosphate on a Petri dish. It is only later in development that the cell uses the molecular messages from the nuclei to transform the crystals into novel configurations. (Lima-de-Faria 1988 p94)

The last sentence in the quotation above also illustrates Lima-de-Faria’s contention that the cell’s molecular material is constrained, playing a secondary role in organisation. Further, many of the shapes and forms in the biological world can be seen earlier manifested in the inorganic, constructed prior to and without any influence of genetic material. Moreover, it is argued that DNA, often seen as unique and peculiar to the biological world, itself has its own antecedents of shape and replication processes.

> One usually thinks of DNA replication, i.e. the growth of a new DNA molecule, as a strictly biological phenomenon. However, the molecular analysis has revealed that DNA replication is preceded by the formation of an RNA primer, i.e. a small piece of RNA that is formed first and later discarded and which allows the DNA growth to start (Dahlberg 1977, Kornberg 1980). Hence, DNA is a prisoner of the process of crystal formation that occurs at the underlying level of evolution. (ibid. p121)

In fact, Lima-de-Faria claims that mineral evolution must have occurred for cell evolution to occur, i.e. it is a necessary condition. Biological evolution is facilitated by an earlier general evolution, but this general evolution always maintains a presence, constraining and shaping the evolution of life. (Stevens (1974) observes, as discussed in Chapter 9, that the patterns of nature follow only a few formal themes, restricted by three-dimensional space but nevertheless producing great variety.) It was also argued earlier that form and function are two aspects of the same phenomenon. For a function to occur, however, an asymmetry in molecular arrangement is necessary. This pervades not only the mineral world but also the biological. Functions are the results of evolution. Lima-de-Faria gives the example of insulin, whose molecules changed their functions over time.

> The evolution of insulin represents a similar shift in organ type. Insulin was present in nerve cells before it became produced by an endocrine gland (Faulkner et al 1984). Moreover, insulin has changed its function during evolution. It occurred in insects before it appears in vertebrates. In *Drosophila* it is present in the larval haemolymph where it functions as a hormone that enhances cell differentiation, whereas in mammals, it regulates glucose metabolism (Seecof and Dewurst, 1974). (ibid. p151)

Not only do functions change their roles over time but also old functions can combine to produce novel functions. Lima-de-Faria gives the example of the stapes bone found in fish and amphibians. At one stage of its evolution, this bone is part of a gill and used for respiration; at a later stage, it is part of a jaw and functions in food ingestion; then again, it is part of the hearing system. ‘This means that this one, by combining with other organs, acquired completely new functions’ (Lima-de-Faria 1988 p151).

Lima-de-Faria (1988) continues that eukaryotes have telomeres at the ends of their chromosomes, which enable single strands, whereas prokaryotes have no telomeres and the chromosomes are circular.[52] The telomeres together with centromeres determine the organisation and position of DNA sequences within the chromosome. This ordering was further canalised with dependence upon protein and RNA. None can function without the other. This canalisation means that the gene has a limited number of alternatives that follow an order already observed in minerals.

> The basic shapes of leaves are already found in minerals, just as the basic shapes of animal vertebrae are found in minerals. The gene only fixes and perpetuates one of the alternatives, making the vertebra long or short. (ibid. p319)

To Lima-de-Faria, the symmetries and asymmetries in life forms are already canalised in the physiochemical forms of minerals. This self-assembly of elementary particles, atoms, molecules and cell organs is the basis of ‘auto-evolution’. This is broadly a deterministic account and would include such auto-catalytic processes as were considered earlier in Turing’s reaction–diffusion model. Also, ‘self-assembly’ – a ‘term created by biochemists to describe the ability of macromolecules to organise themselves spontaneously’ (Lima-de-Faria 1988 p179) – is thought to pervade at all levels, from the particle to the society. Subsequently, there is no

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[52] Recent research has discovered bacteria with linear chromosomes and telomeres.
See: http://www.sci.sdsu.edu/~smaloy/MicrobialGenetics/topics/chroms-genes-prots/chromosomes.html

privileged status for any biological components: the gene, the chromosome, the protein etc. are all locked into a symbiotic relationship and heavily, although not entirely, canalised.

Lima-de-Faria rather surprisingly thinks that it is the physicist who must change approach to biology rather than the biologist who should change approach to physics. Many physicists, it is suggested, have misinterpreted Heisenberg's uncertainty principle, introducing an unnecessarily random or probabilistic aspect to all levels of nature. However, the situation is changing:

> Physicists are now recognising that randomness does not occur in nature. They are coming to the conclusion that in physics, like in biology, randomness is synonymous with ignorance of the phenomena involved at levels lower than those accessible to experimentation. (ibid. p300)

The second law of thermodynamics does not escape criticism either. Lima-de-Faria notes that unlike other laws of physics, this second law has a most ambiguous nature and he lists three different formulations.[53] As understood by Nicolis and Prigogine (1977, quoted by Lima-de-Faria), the law contains randomness that fails to explain the ordered properties of living organisms. Organisms are built by self-assembly, Lima-de-Faria continues, and energy transportation is canalised within open systems, processes incompatible with the second law of thermodynamics as it stands in its three interpretations.

### Critical evaluation

What does one make of this unique work? Does this account provide the answer to the problem that was levelled against Thompson – the lack of any explanation for evolutionary changes? One of the difficulties here is that very few biologists and philosophers have encountered this work and the seemingly one review of the book is rather short and superficial (Korthof 2011). This might be expected, as the project draws on a mass of detailed genetics together with an understanding of chemistry, mineralogy and physics, both Newtonian and quantum. The implications are clear: if Lima-de-Faria is correct, then the brand of Darwinism that seeks to explain evolutionary change primarily through natural selection and adaptationism is under threat. Indeed, he states this as his target in the opening chapters. Kauffman has for many years held an interest in self-organising systems and may agree with many of Lima-de-Faria's arguments. Kauffman too steps outside a purely biological perspective and embraces auto-assembly, together with the concept of 'free energy' in Schrödinger's thermodynamics, but nevertheless retains natural selection. Lima-de-Faria contends that nature is an ordered affair and to support this argues that physicists are 'recognizing that randomness does not occur in nature' (p200 1988). However only one example of such physicists is referenced and one might easily doubt this claim. Another contentious claim concerns the second law of thermodynamics; it could be argued that the open systems identified in biological processes are indeed compatible with this second law. In the later stages of 'Evolution without Selection' (p291) there is a chapter that argues in favour of Sociobiology but from the perspective of 'autoevolutionism'. This consideration goes beyond the parameters of this work. Nevertheless, sociobiology is a controversial subject and one has to question whether sociobiology is worthy of being rescued. [54]

One fundamental question that comes to mind concerns the term 'auto-evolution' employed by Lima-de-Faria to describe the physical basis of evolution. How does 'auto-evolution' differ from the plain word

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[53] Some commentators have listed 21 variants to the law. See Čápek and Sheehan (2005).

[54] See David Stove's (1995) critique of the relationship between neo-Darwinism and Sociobiology for a lively account.

‘evolution’? Would anyone deny that evolution has a physical basis? It will be argued later that the explanation of evolution is better characterised in terms of ‘natural processes’ rather than ‘auto-evolution’ or ‘natural selection’.

## Conclusion

The foundations to the structuralist alternative were laid out and elaborated in a bid to answer that which lies beyond the scope of natural selection. Thompson and Lima-de-Faria share a deep scepticism over natural selection and adaptive reasoning. Symmetries, for example are seen as phenomena that precede and constrain biological form. This contrasts with the view that symmetries exist in animate nature because they are beneficial to the function of organisms. For instance, mobility is easier for an organism with an even number of legs or wings than an uneven number. Any organisms possessing such asymmetries would be at a functional disadvantage and selected against. This purports to explain why bi-lateral symmetry is so pervasive amongst *Animalia.* The simplicity of such lines of reasoning are easy to apprehend and can be quite seductive. However, there are serious questions that face the selectionist. First, is there any evidence within the fossil record to suggest that a selection process took place? In other words is there any evidence of extinct fossils with an uneven number of legs? Second, when asymmetries do arise in nature, as with the fiddler crabs, why is it that such an asymmetric creature manages to survive and reproduce seemingly just as well as their symmetrical colleagues? Third, for any selection to take place there must by definition be some variations of fundamental form. How does the selectionist account for fundamental form? Is it that space, gravity and the laws of topology constrain nature tightly or is it that things are not so invariant as a Structuralist might claim?

Both men also see a wider role for the physical forces, with Thompson providing many mathematical explanations and Lima-de-Faria giving novel explanations from a detailed genetic base. Where Thompson seems to lack an account of evolutionary change, Lima-de-Faria presents a bold prognosis that biological evolution is embedded within general evolution. Despite a few quibbles the account is found to be a coherent one that does not require any selectionist import. Moreover, the account provides an important continuation between general evolution and biological evolution, consolidating a causal relationship between physics, chemistry and biology. The evolution of the universe can be considered to be of four stages, with each stage leaving an imprint in the subsequent stage. Under these circumstances, convergence, which so perplexed Mivart (Ch.1), can be perceived to be less surprising. The ordered imprinting is also said to explain the recursive patterns and regularities that manifest in the biological and non-biological realms. The deterministic nature of the thesis, which embraces such concepts as canalisation, auto-assembly and an understanding of the relationships between form and symmetry on the one hand and function and asymmetry on the other, does seem consistent with much of modern physics. However, denial of randomness conflicts with the Copenhagen interpretation of quantum mechanics. The perspective concerning the relationship between form and function is intriguing and deserves further consideration. Stephen J Gould once said, counterfactually, that if one were able to re-run the story of life starting from the same origins, one would probably witness biological forms quite unlike those of today. Both Lima-de-Faria and Thompson, one suspects, would take the converse view and expect to see the same forms, or nearly so, given the same conditions. Conway Morris, in a more recent contribution, goes so far as to argue that “something like a human is an evolutionary inevitability". *Life's Solution* (2003) is probably the most comprehensive study of convergence to date, going far beyond the scope appreciated by Mivart (Ch.1). Although Conway Morris considers himself a neo-Darwinist there is a remarkable absence in this work to explanation in terms of selection. There is no appeal or index to adaptive reasoning, natural selection or selection pressures which one would expect in a neo-Darwinian text. In fact all explanation to convergence appeals directly to natural law, an essentially structuralist approach. Indeed he states that the explanation to the main principle of evolution is beyond selection and adaptation and found "relying on the tried and trusted building blocks of organic architecture" (Morris 2003 p8). Contrary to Gould's randomness, Conway Morris considers that the ordering within nature allows opportunity for prediction, a view shared by those who work closely with scaling laws and discussed in the following chapter.

So far, consideration has been given to constraints at the fundamental level, including symmetry, geometry, topology and the mathematics behind patterning. Now this thesis will outline proposed further constraints, before committing to any philosophical assessment.

## Chapter 10: Constraints or Determinants: Gravity, Temperature, Nutrition and Size

### Gravity

In the previous chapter, it was observed that both Thompson and Lima-de-Faria saw gravity as a determining factor for form and hence subsequent related functions. Thompson even claimed that the direct and permanent effect of doubling the gravitational power would be that previously upright organisms would be resigned to quadrupedalism, with heavy bone structures and large hearts, whereas a reduction in the gravitational pull would facilitate slender bipedal bodies with lighter frames and smaller hearts. Is there any evidence to support this claim and, if there is, what are the implications for evolutionary changes? One person who supports this hypothesis is Morey-Holton of the NASA Ames Research Centre:

> As species on land increased in size, they required support structures appropriate for the loads imposed. Species that crawled along the ground didn't need the same mechanisms for countering gravity's effects as those species alternating between horizontal and vertical positions. The latter species required more complex systems for balance or gravity sensing, fluid regulation, and locomotion. So, gravity, though constant, may have played a major role in evolution as species crawled from the sea and began to populate the land. (Morey-Holton undated)

To understand how these conclusions were arrived at, it is necessary to elucidate the physiological changes that take place in micro or reduced gravity, such as in the weightlessness of space. It is important to recognise, however, that the astronauts floating within their spacecrafts are not entirely free of gravitational influence. At 400 kilometres up, gravity is almost 90% that at the Earth's surface. This height corresponds to the usual orbit of a space shuttle. The force of the Earth's gravity at an altitude of 100 kilometres is only 3% less than it is at the Earth's surface. [55]Even with these small reductions in gravitational pull, the physiological changes that take place in organisms can be quite dramatic. Take humans in space. The first symptoms observed by those entering space are of nausea, headache, vomiting, vertigo, body ache and general malaise. Vision can also flip temporarily 180 degrees. This is known as space adaptation syndrome (SAS) and normally lasts for little longer than 72 hours. The long-term effects, however, are much more serious and of interest here. These include muscle atrophy, loss of body mass, osteopenia (loss of bone mineral), slowing of the cardiovascular system, reduced heart size and reduced production of red blood cells. To minimise and prevent further such adverse effects, a regular daily regime of intense exercise is necessary. Conversely, astronauts returning to earth suffer orthostatic intolerance, unable to stand unassisted, fainting after only 10 minutes. Under the Earth's gravitational pull, breathing and locomotion are very difficult for them. These symptoms take several weeks to disappear fully and it is said that astronauts age more quickly even in a short period in space (Versari et al 2013). It is not clear that a prolonged existence in space would be conducive to survival on return to earth. It is important to recognise here that all the major long term physiological adaptations, both in space and when returning to earth, have taken place without altering the astronaut's genetic constitution.

The biochemical reactions in altered gravity are an area of active research within the field of gravitational biology. NASA is keen to appreciate the implications of extended space flight and for the viability of colonising other planets. Astrobiologists take an interest in evolutionary forces and the necessary conditions

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[55] All the empirical details concerning physiology in space were extracted from Lujan and White (2009) unless otherwise referenced.

to sustain life. The impact of gravity is seen as fundamental, as it plays a crucial role in convection, nutrient availability, sedimentation and waste control. It was once believed that the gravitational force was too weak to influence the behaviour of cells, but studies of many organisms in space and on earth, by using centrifugal force, indicate a different story.[56] It seems there are limits to the amount of gravitational strength that life can withstand, and this differs according to the type and size of organism. Micro-organisms, for example, can survive at much higher gravitational strengths than do rats, with humans being even more sensitive, expiring at strengths one-third those that rats manage to survive. Morey-Holton considers whether life can exist on planets with greater gravitational fields:

> The ability to evolve under increased gravity appears related to size. Single cells and nematodes withstand105-G for brief periods, young plants easily cope for 10 minutes at 30–40-G without noticeable structural changes, rats withstand 15-G for 10 minutes while 20-G is lethal, and humans are capable of tolerating only 4–5-G for 10 minutes. Gravitational levels, like other physical environmental factors, appear to determine the boundaries for life. (ibid.)

The measure for the Earth's gravitational field is given a benchmark of 1-G at sea level. Morey-Holton observes that it is not only organisms that respond to gravitational changes; as much as 40% of equipment on initial flights failed to function as expected. This too suffered from convection problems and other factors such as air bubbles impeding fluid flow in piping. Morey-Holton sees the insights gained from research conducted in 'weightlessness' as highly significant for understanding the factors that shape evolution, maintaining that the influence of gravity had previously been masked, as it was always seen as a constant and neutral. Her perception endorses that of Thompson in appreciating that gravitational factors had a bearing on life emerging from the aquatic and becoming terrestrial:

> Gravitational loading acts on all masses at the Earth's surface and defines the weight of each object. Weight is the product of the object's mass times the force of gravity, which on Earth is equal to 1G. Weight drives many chemical, biological, and ecological processes on Earth. Altering weight changes these processes. Given these facts, one should not be surprised that changes in gravity could alter life, as we know it. If gravity causes changes to biology, then gravity, per se, must be a major physical environmental force shaping life on Earth. (ibid.)

The lessons to be gleaned here demonstrate that an environmental feature, such as increased or reduced gravity, can have a very dramatic impact directly on the organism, but more so on those of larger mass. Moreover, any organism that remains within that changed environment will maintain those physiological changes and this will also apply to any offspring. One can predict that if humans of the future were to seek out an existence of continuous space travel, then they would look morphologically quite different from at present. The principle establishes that the environment can determine biological form directly in a non-Darwinian and non-Lamarckian manner. In light of this, we can better understand the vestigial features of creatures, such as the whale, that swapped a gravity-strong terrestrial environment for an aquatic environment with reduced gravitational effects afforded by buoyancy.

Morey-Holton talks of gravity as being a constant force, omnipresent and unchanging. However, this requires some qualification. It has already been observed that an organism migrating to or from the sea or a large body of water will experience different gravitational effects. In this sense, the gravitational field varies because of

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[56] Of the four fundamental 'forces' of nature, the nuclear weak force is measured as $10^{-14}$ whereas gravity is a mere $10^{-40}$.

the buffer that water affords. But what if an organism migrates from one part of the globe to another? It was assumed that the gravitational field was only stronger at the poles than at the equator, but recent very accurate measurements have demonstrated that matters are much more complicated. Figure 9 reproduces an illustrated gravitational field map produced by two GRACE (Gravity Recovery and Climate Experiment) satellites. The dark blue areas show where the gravitational field is at its weakest, through to the dark red representing areas where it is strongest. The observed anomalies are a measure of the mass beneath the Earth's surface. The measurement is achieved by the deployment of two satellites following the same orbit around the globe. The first satellite speeds up when it approaches an area beneath of greater gravitational strength, putting a greater distance between itself and the following satellite. Constant circumnavigation enables the researchers to plot an amazingly accurate map of the Earth's gravitational anomalies. This has been extremely useful in locating different metals and sources of energy such as coal and oil (http://science.nasa.gov/missions/grace/ 2009).

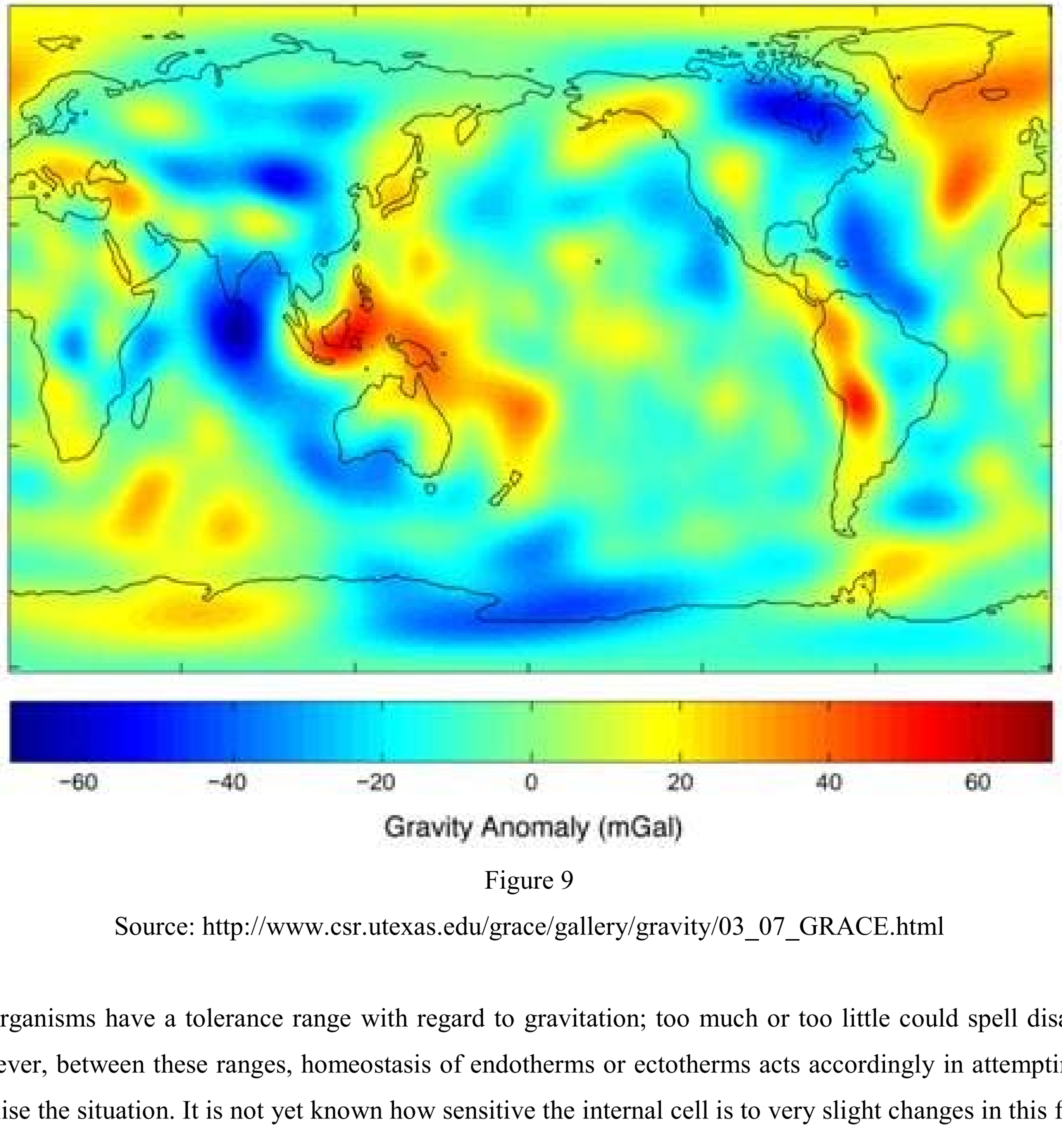

Figure 9

Source: http://www.csr.utexas.edu/grace/gallery/gravity/03_07_GRACE.html

All organisms have a tolerance range with regard to gravitation; too much or too little could spell disaster. However, between these ranges, homeostasis of endotherms or ectotherms acts accordingly in attempting to stabilise the situation. It is not yet known how sensitive the internal cell is to very slight changes in this force, nor is it fully understood how gravity triggers a response. Morey-Holton thinks that rather than a 'direct' response, 'reduced gravity more likely initiates a cascade of events – the altered physical force leads to an altered chemical environment, which in turn gives rise to altered physiological response.' In more recent work, Ingber (2011) has demonstrated that the skeletal structure of cells feels the effects of gravity and responds in unexpected ways. Moreover, cytoskeletons give cells their shape, help cells move and hold the nucleus in place, but they respond to gravity through the interface with proteins known as integrins. ‘Tickling’ the cytoskeleton can make cells switch between different genetic programmes. Moreover, there is a relationship between the topology of cells and their functions. Cells that are flat and stretched tend to divide, cells that are round and cramped tend to die. Changing the shape of the cytoskeleton serves as a switching mechanism. Ingber (2011) argues that, ‘By pursuing the question of [how cells sense] gravity we’ve uncovered entirely new aspects of cell regulation’.

Research into the effects of a gravity-free environment upon the development of zebra fish demonstrated that the critical period was disrupted, producing serious and permanent functional deficits (Moorman 2011). It is also now known, from research in developmental biology, that 1-G gravity plays an important role in axis formation in the chick embryo. Here the radially symmetrical blastoderm is converted to a bilateral symmetric structure. (Gilbert 2003 p360.) More evidence of cell sensitivity is observed in the cells of plants: there is a positive gravitropic response in downward root growth and a negative gravitropic response in upward stem growth (Chen et al 1999). Plant roots placed horizontally in a contrived environment grow towards the earth even if a nutrient and moisture rich soil is arranged above the root to prompt upward growth. It is not clearly understood why this is the case. However, the statolith theory postulates that plants ‘sense’ gravity in special cells (statocytes) located at the tip of the root and containing heavy particles of starch called amyloplasts. (Kumar et al 2008) At one stage, it was believed that the primary factor determining the upward growth of a stem was phototropism, which could include attraction to some forms of artificial light as well as sunlight. Charles Darwin and his son Francis (1880) conducted some early experiments that demonstrated that stem growth would incline toward a light source even if the source were set at an angle and not directly above the plant. However, they also discovered that if they cut and removed the tip of the stem, the plant would grow vertically and not towards the light source.

It may very well be the case that gravitational influence has been grossly underestimated. One has only to consider that small variations in the Earth’s gravitational field can have the effect of accelerating a satellite 500 kilometres above sea level. Therefore it does not seem outrageous to consider whether small anomalies in the gravitational field have an impact upon the deposition within cells during the early stages of development. This question is not to be answered here obviously, but the potential explanatory power of such a theory would be enormous. There would also be a downside. One of the things gleaned from operating GRACE satellites for many years is that anomalies in the gravitational field are not constant but shift over time.

> Gravity anomalies are often due to unusual concentrations of mass in a region. For example, the presence of mountain ranges will usually cause the gravitational force to be more than it would be on a featureless planet – positive gravity anomaly. Conversely, the presence of ocean trenches or even the depression of the landmass that was caused by the presence of glaciers millennia ago can cause negative gravity anomalies. (http://earthobservatory.nasa.gov/Features/GRACE/page3.php)

If gravity were an important factor for evolution, then there would be many problems historically correlating any relationship between impermanent gravitational anomalies and nature most diverse.

### *Gravity and altitude*

Before the relationship between gravity and altitude is considered, one point requires slight clarification. It is not the case that the proportion of oxygen changes, it remains at just under 21% whether measured at sea level or atop Everest. If there is a compositional change, then it's the isotopes that change, Oxygen16 is more prevalent at higher altitudes than Oxygen 18 owing to the small difference in masses. (Helfand 2009 Ch.4) What does vary, however, is the air pressure, which changes with height, following Boyle's Law. The cause of the differential pressure is gravity: air pressure increases with gravitational pull, which is greater nearer the centre of the Earth. These physical laws have implications for the physiology and structure of any organism.

> If you were to analyze the body shape and composition of a Peruvian mountain dweller you'd find some striking differences from someone who has lived all his or her life at sea level. For one thing, the mountain dweller would be somewhat short, have a barrel-chested appearance, have more red blood cells, more blood in the circulation, and more blood vessels in his lungs. (Widmaier 1998 p62)

To summarise Widmaier: The less pressure there is, the harder it is to drive air into the lungs and then force it across the lungs into the blood capillaries. The shorter stature and expanded chest of a mountain dweller facilitate larger lung capacity, which in turn facilitates increased blood cells, which in turn offers greater haemoglobin and hence the ability to derive oxygen from a less pressurised environment. Such mountain dwellers also have proportionately larger hearts. Moreover, cells contain more mitochondria, which in turn contain more of the enzymes that are required to produce energy. Widmaier observes that similar capacities to cope with oxygen deprivation are present in diving mammals and concludes that 'without these remarkable abilities, all mammalian life would be confined to a narrow range of terrestrial altitudes' (Widmaier 1998 p64). This is undoubtedly true, but one must be careful when universalising biological attributes. Beall (2007) points out that the physiological characteristics of the high-altitude Andean are not the same as the characteristics of the high-altitude Tibetan. It seems that the Tibetans have evolved through different pathways and are able to cope with diminished oxygen pressure:

> In summary, measures of oxygen transport reveal that Andean and Tibetan populations have large quantitative differences in numerous physiological and molecular traits involved in oxygen delivery. The hypothesis is that evolutionary processes have tinkered differently in the two founding populations and their descendents, with the result that the two populations followed different routes to the same functional outcome of successful oxygen delivery. (Beall 2007)

This study illustrates how pluralistic evolution can be. The search for a fundamental mechanism that underlies all evolutionary change may prove as fruitful as the search for El Dorado. Nevertheless, the gravitational biologist has witnessed that rapid changes to form will occur *universally* under changed conditions of gravity. These changes are permanent as long as the individual remains in that environment.

### *Gravity and the relationship of parts*

The previous chapter mentioned that Thompson had recognised that gravity plays a determining influence over the size of physiological features, bone structure, organs etc. Some recent observations by Lavers (2000) have expanded this perspective concerning the relationship between different parts of the body. For instance, Lavers notes that no animals with big heads can have long necks. Because of gravitational forces, large heads such as those of the elephant and the hippopotamus can only be supported by a short neck. Animals with long necks, such as the giraffe or the huge dinosaurs from the past, all have relatively small heads. The relationships go deeper still: the giraffe's head is further from the ground than that of most animals; therefore the energy required to pump blood to it is greater. To counter gravity, the giraffe must have a heart that is capable to pump the blood the longer distance. Indeed, the giraffe has evolved a heart with much thicker wall on the left ventricle and an increased blood pressure. The important lesson here is that one cannot adjust or alter one part of a body significantly without a corresponding adjustment elsewhere in the body. As the giraffe evolved a longer neck, it was not only the heart that changed; longer legs evolved to facilitate access to water at ground level and the longest known nerve cells stretch from its brain to its limbs. One must be wary if one is given to explaining features by recourse to the selection of particular traits, such as the long neck. For traits are rarely particular and any analysis, selectionist or structuralist, must bear this in mind.[57]

## Conclusion

The influence of gravity in evolutionary matters has been little discussed until recent years. On the rare occasions it has been discussed by those of a neo-Darwinian persuasion, gravity has been perceived as a constraint that set the boundaries for an arena for natural selection to work within. However, in the quest to understand how life might endure for long periods in space, it was witnessed that profound changes to the form of any organism are induced very quickly under conditions of reduced gravity and the weightlessness of free-fall. Moreover, those non-genetic, physiological changes prove permanent whilst those conditions remain. Interestingly, the full impact of gravity can be softened by continuous exercise of bodily parts – in other words, 'use it or lose it'. Gravity, then, has a direct impact upon *every* organism's physiology and constitution. The precise causal processes are little understood but increasingly of interest and under study. For the purposes here, it is important to recognise that gravity must be a key factor when it comes to understanding form. It impinges upon overall body size, the skeletal structure, the convection and distribution of fluids, the size of the heart and other tissues, the relationship between parts, the external bilateral symmetry, the nature of the cell and production of proteins (Blaber et al. 2010). Gravity may also play largely in self-assembly self-stabilising structures that form spontaneously at every scale (Bhattacharjee 2012). One must remember the importance of gravitropism in plants and the influence of gravity upon the configuration and formation of the body axes in the development of the embryo.

One might accept that gravity does indeed have an influence over the form of organisms but still wonder why it is that organisms take on all manner of sizes, from the microbe to the blue whale. If gravity is so significant, why are organisms not all the same size? Well, apart from differential effects of gravity, such as the marine and the terrestrial, there are many other factors that impinge directly upon the organism. Temperature and nutrition will now be considered and appraised as important parts of the jigsaw puzzle of life. The pieces, however, are not distinct and unrelated: gravity, size, temperature and nutrition all go hand in hand and form an evolutionary perspective which may come to life when considered in the context of development.

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[57] For a modern holistic account of form in reference to the giraffe see Holdrege (2005). Holdrege asks, did the giraffe evolve longer legs first? (Which facilitated faster fleeing from predators.) If so, did the evolution of the long neck follow, which enabled the giraffe, now with long legs, to reach essential water?

## Temperature

The last section demonstrated that gravity is a major determining factor of an organism’s form. From the perspective of this work, this is an important consideration because gravity impinges on *all* members of any population directly. However, gravity alone leaves many unanswered questions, so it is essential to consider other factors that might also have a direct influence upon the organism. The influence of ‘temperature’ will now be considered, in particular its relationship with homeostasis and the scaling of body size. The implications of scaling and size for aspects of general behaviour and the importance of nutrition will then be examined. The particulars are diverse and complex, but the aim is not only to demonstrate that gravity, temperature, scaling and nutrition are factors that impinge upon the overall form and behaviour of all organisms but also to demonstrate that these factors are inextricably related. To elucidate all of this, however, one must go back to the earliest forms of life.

Prokaryotes have dominated the planet since the first proto-cell four billion years ago. It took over two more billion years before a new life form emerged in the shape of a eukaryote and it was this later group that gave rise to some cells combining and forming multicellular organisms (Smith and Szathmary 1995). Prokaryotes, it seems, are not normally conducive to multicellularity, although it is not entirely unknown (Russell et al., 2008 p535). The transformation from the single cell to the multi-cell is one of the major evolutionary steps in the formation of life as we recognise it, but how this came about is still a mystery and subject of much research and speculation. Attention here, however, will be directed to the consequences that face multicellular organisms, the avenues that are opened and those that are closed. Our focus here will be on mammals and the rigours of homeostasis.

One could argue that, whereas the single cell is largely governed in its geographical location by the elements – wind, tide, current etc. – the advent of appendages, facilitated in most instances by multicellularity, allows these organisms freedom from such restrictions. Moreover, this new freedom required precise internal interactions and coordinations. Locomotion opens new vistas for the multicellular but is dependent upon specialised cells, tissues and organs. These specialised features must themselves be protected from the elements if they are to function and produce locomotion. It is further suggested here that the formation of protective skin or shell enables a safe internal environment for cells to interact. However, internal operations can never be entirely divorced from external events: the proteins, which are the workhorses in the mammalian body, are themselves influenced by physical and chemical conditions. These include such conditions as salt concentration, carbon dioxide levels, oxygen concentration, the acidity or alkalinity of solutions (pH) and, as is central for the perspective here, temperature. The internal temperature of a human, for example, must fall within strict parameters, between 36 and 39°C, if it is to survive and function.[58] How, then, is this narrow constraint achieved and what are the consequences? Certain mechanisms, which will now be examined, are required to achieve thermal homeostasis.

[59]Generally, biochemical reactions within an organism work at a faster rate in warmer temperatures and slow down as temperature cools. If the temperature becomes too high, then enzymes will expand and unfold, ceasing to function. Further, membranes will become more permeable, losing protective advantage. On the other hand, if the temperature drops dramatically, the whole biological machinery could come to a halt as the cells literally freeze. One can draw the analogy for thermal homeostasis with a heated room or office. To maintain a fairly constant temperature, a thermometer is needed to obtain current information; in biology, this is known as the receptor. The receptor is not an organ but the chemical processes that slow or speed in response to temperature change. These chemical changes lead to further chemical changes known as the comparator; in the room analogy, this is the thermostat. The thermostat (comparator) will activate the ‘effector’, which could be the biological equivalent of a heater or a cooler. In an animal, it works something like this: Beginning with normal body temperature, there is an increase in the external temperature which begins to speed up the chemical activities in the body. This causes an area at the base of the brain, behind the mouth and known as the hypothalamus, to activate cooling mechanisms, such as capillaries close to the skin surface filling with warm blood and sweat glands activating to help evaporative cooling. As the body temperature cools, the comparator (thermostat) turns off the cooling mechanisms. On the other hand, if temperatures drop, then slowed activity in the hypothalamus leads to muscle contraction, shivering and blood vessels constricting until things warm up again. It is important to appreciate that these are all inevitable chemical processes interacting with changing thermodynamics. ‘Inevitable’, that is, until something goes awry. For instance, it was discovered that animals with a damaged hypothalamus cannot enjoy the benefits of homeostasis. Chemical changes in the hypothalamus can also be caused by bacterial invasion. A part of the defence within the immune system is to raise body temperature when under attack from pathogens.

Creatures that possess the homeostatic system outlined above are typically endotherms. The maintenance of such a system is dependent upon metabolism and the conversion of sugars to energy. Ectotherms, such as fish, amphibians and reptiles, have a more direct relationship with the external environment; their internal body temperatures do not have the same constancy as those of endotherms but reflect external temperatures. The ectotherm can gain part of its energy directly from various sources of heat including the sun, with its metabolic rate increasing as temperatures rise and dropping as temperatures fall. Endotherms also see an increase in metabolic rate when external temperatures increase. The ideal external temperature for an endotherm is for it to be the same as its normal body temperature because then the extra work involved in metabolism is not necessary. Because ectotherms have a direct relationship with external temperature, their range of behaviours and geographical locations is constrained. If the temperature is too high, ectotherms must seek shade or water to avoid overheating. If the temperature is too low, they fail to function; persistent severe cold leads to death. Both ectotherms and endotherms have evolved a few other physiological means of controlling temperature; take the example of icefish:

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[58] This range is similar for most active lizards, snakes and larger flying insects. Passerines, however, only survive in a higher temperature range of 40–42°C. The parameters are 34–36°C for marsupials such as the kangaroo and 30–32°C for monotremes such as the duck-billed platypus. (See Akin 2011).

[59] The empirical details concerning thermoregulation and homeostasis are a summary from Locker (1973).

> The fish completely lacked red blood cells, the pigmented oxygen-carrying cells that, until the discovery of these Antarctic icefish, had been found in every living vertebrate. Indeed, no other case of bloodless vertebrate has ever been discovered outside the fifteen or so species of the icefish now known. (Carroll 2009 p22)

The icefish do have a nearly transparent liquid in their veins but it lacks the haemoglobin molecule that gives the normal red appearance. Carroll explains this novel feature by the loss of one globin gene and the erosion of another that has left it useless, 'similar to a fossil'.[60]

*Metabolism and scaling*

> Life is amazing. Even the smallest bacterium is far more complex in its structure and function than any known physical system. The largest most complex organisms, large mammals and giant trees, weigh more than 21 orders of magnitude more than the simplest microbes, yet they use basically the same molecular structures and biochemical pathways to sustain and reproduce themselves. (Brown, West and Enquist 2000 p1)

Interest in scaling began at the start of the twentieth century with Thompson (1917) and Murray (1926). The theme was developed further in the 1930s by Kleiber (1932) and Huxley (1932), the latter introducing the term 'allometry'. Interest declined after this, with the focus directed toward molecular sciences, but it flourished again in the early 1980s, only to stall once again. The arrival of the twenty-first century has seen a revival of the study. Why is biological scaling important when understanding evolution? To answer this, one must consider the two familiar themes in evolutionary explanations – function and form. Sometimes, these themes have been perceived as antagonistic, sometimes as divorced and irrelevant to each other. Scaling biology, however, demonstrates relationships between them, illustrating some of the physical constraints on evolutionary variability. Further, the size of an organism requires that its components observe proportional relationships. If the relationship is not 'correct', with one of the components becoming too large or too small, then the risk is that the organism in question will no longer be able to function.

> Even the simplest organism is an extremely complex system, which depends for its existence and reproduction on the integrated performance of its many component structures and functions. As organisms vary in size, these structures and functions, and the integration of all of them, must be preserved within narrow limits. (Brown, West and Enquist 2000 p9)

The scaling of organisms does not follow simple geometric scaling such as one might see in a series of Russian dolls. Metabolism – the conversion of external sources to provide energy for the organism – plays an essential role in scaling. The metabolic rate for all mammals scales as the three-quarter power of body mass ($M^{3/4}$), which indicates that smaller mammals have disproportionately faster metabolic rates than larger mammals (Brown et al 2000 p87, 114). Another example of differentiated scaling is that as a mammal increases in size, its bones must become disproportionately larger to provide the necessary mechanical support (ibid p1, 14, 299). Biological scaling is not confined to mammals but stretches across all the kingdoms of life. For example, as a tree increases in size, its trunk grows not at a geometric rate of 2M/3 but

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[60] However, this may be an oversimplification of the events, as other researchers discovered 'surprisingly, a phylogenetically derived icefish species, *Neopagetopsis ionah*, possesses a complete, but non functional, adult αß-globin complex'. This icefish retains the genetic material thought responsible for haemoglobin, but this remains unexpressed, and an example of two pseudogenes. It is something of a mystery why expression does not take place. (Cocca et al. 1995)

at a faster rate of $M^{3/4}$ (ibid p167, 199). This applies to all trees. Failure to conform to this pattern of growth would result in the tree buckling under gravity or strong wind.

*The implications*

Imagine taking a cake from the oven and placing it on a cooling tray. Half an hour later, the cake is cool on the outside but still warm at the centre. Now imagine taking a cake from the oven, cutting it into quarters and placing it on the cooling tray. This time, the cake is evenly cool half an hour later. The simple laws of thermodynamics dictate that a large body retains heat and energy better than a smaller body. Cutting the cake into quarters greatly increased the surface area, facilitating heat loss.

All living systems must keep their temperature within a certain range to function; failure to do so could lead to death. Large endotherms (warm-blooded animals) such as elephants living in the tropics run the risk of overheating and have to continually seek shade or cool themselves in water. At the other end of the endothermic scale, a mouse or a shrew has the opposite problem (McGowan 1999 p65). Like the quartered cake, these small creatures suffer a much faster heat loss relative to their size. In order to maintain their temperature, they must replace the energy lost through the surface with energy from consuming food. This conversion determines the metabolic rate (ibid p18, p22). The smaller the organism, the disproportionately faster is the metabolic rate (ibid p28). Smaller endotherms are unable to accommodate large hearts within their bodies, so their hearts must beat faster to supply the whole body with blood. A shrew's heartrate is 700 times a minute compared with an elephant's 35–40 beats per minute. Humans have a heartrate of 65–70 beats per minute (ibid p8)

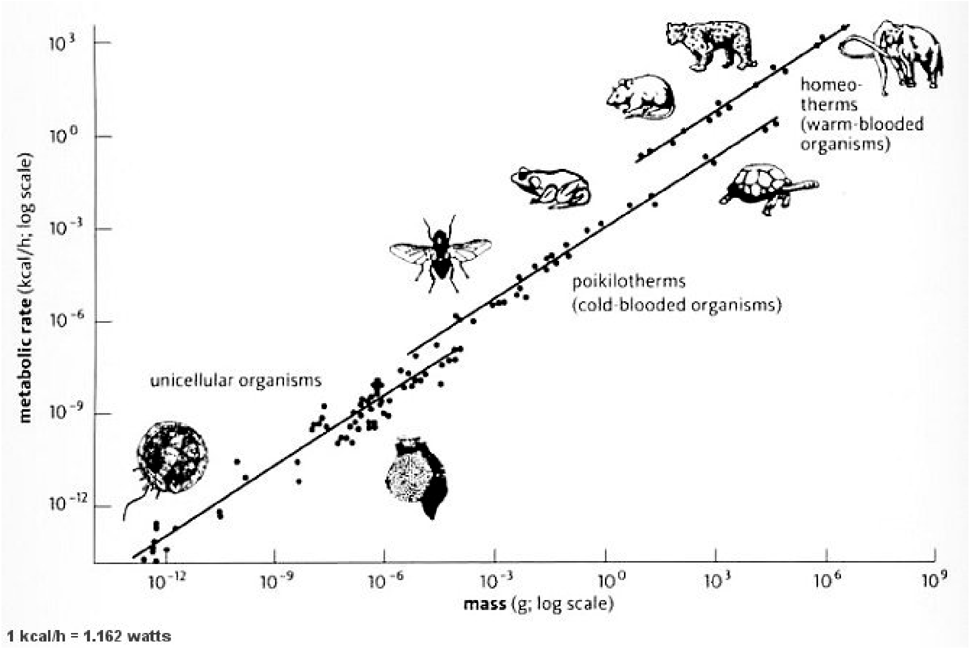

Figure 10

Source: http://universe-review.ca/R10-35-metabolic.htm

In 1932, Kleiber drew graphs to demonstrate allometry across a wide taxonomic range, from unicellar organisms, to vascular plants, to poikilotherms (ectotherms) to endotherms. See Figure 10 for a more recent illustration. Later, it was noticed that this same power of scaling could apply to the components of the cell:

> When extrapolated back a further twenty orders of magnitude, this fit coincides with the respiratory rate not only of mammalian mitochondria but even with that of molecular respiratory complex and terminal oxidose molecular units within mitochondrial membranes! (Brown, West and Enquist 2000 p88)

The authors above claim allometric scaling laws provide one of the rare examples of universal quantitative laws in biology. Indeed, their model extends to explain the circulatory and respiratory systems of both mammals and vascular plants. They argue that, fundamentally, the architecture of all the transport systems that provide essential nutrients is linear with hierarchical branching. Within the physical and geometric constraints these systems must observe, the energy required for transportation is minimised.

> Thus, for example, the architecture of both mammalian arteries and plant xylem are both fractal – like branching 'trees' even though the former is driven by a pulsating pump (the heart), which propels blood through vessels of decreasing size, while the latter consists of an osmotic pump, which draws fluid through many parallel micro capillary tubes (ibid. p92)

The authors claim that the evolution of both large mammals and trees has been largely influenced by the hydrodynamic and biochemical constraints imposed by resource networks. Brown et al.'s prediction within mammalian cardiovascular and respiratory systems has correlated remarkably well with the empirical data. If these patterns of scaling are held to be correct, then many predictive possibilities arise. This biological/mathematical approach has not escaped the attentions of physicists working in the fields of complexity and chaos theory. Indeed, Strogatz (2008) is convinced that the fractal nature of organs such as the pulmonary arteries, the heart and the smallest capillaries lends itself to mathematical scaling and perhaps even explaining some of life's biological mysteries when considered in a relationship with metabolism and mass. Some enigmatic questions arise. Why is it that species have the life spans they have and not a longer or shorter life span? Why is it that a mouse, composed of a very similar set of molecules and genetic make-up to a human, only lives for one or two years but a human for 70 or 80? Indeed, this whole area of research touches on some very curious regularities and correlations that have deemed to be unrelated in the past. For example, take any animal, be it an ectotherm or an endotherm, and given its normal number of years, all will enjoy the same number of heartbeats: 1.5 billion in fact, *Ceteris paribus* (McGowan 1999 p57-59). It was mentioned above that the scaling model promises predictive advantages. One is that once the average mass of an organism is known, its probable lifespan, its metabolic rate, its necessary calorific intake and even perhaps the limits to any reproduction rates can be inferred. Brown et al. postulated that the scaling model could predict the minimum size for a mammal, which they suggested would be approximately 2 grams – a figure that was established in Chapter 9 when consideration was given to Thompson. Another prediction resulting from the model that has recently been confirmed was that a mammalian cell's metabolic rate is related to the geometric size of the organism (West et al 2002).

However, one needs to be cautious and not be swept away seductively by these promising symmetries that seem to both explain and predict facets of biology and a range of evolutionary possibilities. There are asymmetries that do not conform so neatly. For example, humans live for longer than the model would predict and this cannot be dismissed as simply the 'noise' to be expected with some statistical compilations.

A similar problem arises with micro-organisms: the model predicts that the smaller the organism, the lower its longevity, and this does seem mostly true. However, in a recent study, Stewart Johnson et al. (2007) collected soil samples in the permafrost of the Yukon, Canada and found bacteria that were half a million years old. These cells still maintained metabolic functions, clearly contrary to what one would expect from the scaling model. Should the scaling model be cast aside on this evidence? Supporters argue no, saying that one would expect to find such anomalies in the biological world and the model should be seen as a tool for prising out asymmetries. Furthermore, it is the asymmetries uncovered in nature that are of interest and should be the focus of further research. This does seem a reasonable response and when one sees the mechanisms behind the unusual behaviour of other microbes that induce dormancy, it is clear why there is an anomaly. The example of the human anomaly is more difficult to explain and no doubt subject to debate. However, it must also be respected that the presence of any such anomalies does render any predictive powers less assured and here one must tread with more caution.

### *Temperature, size and the distribution of species*

> This scaling has some interesting and unexpected effects on human society as well. For example, the grain storage buildings constructed by the Inca civilization at low altitudes were fashioned from rocks that had been laboriously shaped by pounding with river rocks until they could be fitted tightly together. On the other hand, the grain storage buildings at high altitudes (up to 5.5 kilometers, or 18,000 feet!) were simply rough shelters covered with a roof. Why the difference? One reason was that small, warm blooded, grain eating animals such as rats and mice can not survive at high elevations because they lose body heat too fast. Therefore there was no need to construct buildings with closely fitting stones to keep these animals out. (Barnes 2009)

The considerations of temperature, size, scaling and the distribution of species are inextricable. It is arguably uncontroversial that climatic conditions determine the scope and quality of the flora and fauna globally and not by accident that a disproportionately large number of species occupy the equatorial regions compared with the cooler climes. The rainforests make up only 6% of the land surface and yet are home to half of the world's terrestrial plants and animals (Cox and Moore 2010 p149, 1311). One striking example is that in a single square mile of rainforest, there can be 1,200 species of butterfly, which is more than the number of butterfly species in the whole of the USA and Canada combined (Raven 2010). The marine is an example of temperature limitations on life: in warmer waters, oxygen levels decrease, limiting the abundance of life (Kaiser et al. 2005 p281). In the depths of the abyssal, where there is no light, nothing exists; but at depths of 2,500 metres, an entire ecosystem exists independently of photosynthetic processes. The thermal energy of the rocks heats the surrounding waters to 350°C and bacteria are able to practise chemosynthesis within the tissues of the clams, mussels and large red-plumed worms that cluster around the heated vents, providing energy in a symbiotic relationship (ibid. p58-60).

[61]On land, the abundance of life decreases dramatically, for example, to the far north and the form of organisms is affected. Apart from the wood frog and the common garter snake living in the most southerly part of the Arctic, there are no known amphibians or reptiles. In the Arctic itself, there are no trees; some shrubs can exist, but they never reach more than two metres in height. The pioneers of terrestrial life – mosses and lichen – can be found in the tundra, but vascular plants are largely non-existent; only a few survive, living in close proximity to each other, near to the ground, their growth checked by the harsh winds.

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[61] The details of arctic biodiversity outlined in this paragraph were extracted and summarised from Huntington (2001).

The arctic willow has very small roots and its leaves turn a curious crimson colour in late summer, giving the appearance of a large carpet. No adaptive advantage of colour is present here. This plant is the food of the hare, the Peary caribou and musk oxen. Small mammals are a rarity. As indicated in the quotation above, heat loss is a major factor, and the smaller the mammal, the higher is the proportion of body exposed to the elements. These smaller mammals operate homeostasis by hibernating in the coldest periods or, in the case of lemmings, by burrowing underground. Characteristic of larger animals are smaller extremities and shorter and often thinner limbs than those of their relatives in warmer climates. One interesting example is the comparison of foxes' ears. The arctic fox has the smallest ear, the fox of temperate region has a middle-sized ear and the desert fox has a much-elongated ear. Arctic foxes also have denser, shorter, softer hair than their relatives in warmer climes. Snowshoe hares, lynx, mink and baby seals have similar hair.

Are these differences explained sufficiently by the relationship between the homeostasis of the organism and the long- or short-term temperature? Is it necessary to posit explanation through appeal to some form of adaptationism? Can a more parsimonious explanation be achieved by simply examining the physical causality outlined above? Prior to Darwin, many naturalists had accredited variations to changes in environmental features such as climate, humidity and the importance of diet (Kropotkin 1995 reprint). Bergmann's Rule (1847) considered some of what is said above concerning the relationship between form and homeostasis, whereas Gloger's Rule (1833) considered the role of humidity in relation to pigmentation in endotherms. Whilst Darwin was still alive, Allen's Rule (1877) was posited to explain the relationship between heat loss and the length of bones and other appendages such as the ear. One could argue that these 'rules' appealed to few biologists, being seen as rule-of-thumb curiosities whose generalisations were not without exception. Explanation through adaptation was the popular ideology of the twentieth century and any research that suggested direct physical causation was thought by many to be evolutionarily insignificant.[62] However, this new century has already witnessed some radical changes to our thinking and researchers have looked again at the importance of temperature and Allen's Rule. Serrat, King and Lovejoy (2008) discovered, both *in vitro* and *in vivo*, that the growth of appendages of mice was directly sensitive to temperature differences:

> The mechanism by which environmental temperature modulates extremity growth has remained elusive. Understanding growth plasticity is critical to basic evolutionary analyses, because many characters that have long been hypothesized to be adaptations may instead be partial or even entirely effects of ambient temperature. (Serrat, King and Lovejoy 2008)

This research is consistent with work from the 1960s in which two groups of pigs were reared at different temperatures, 25°C and 35°C. At the higher temperature, the pigs developed longer extremities and less hair than the controls, even though body weights were similar (Weaver and Ingram 1969). Weismann, back in 1875, (Quoted in Gilbert 2005) observed the effect of temperature upon the colouration of the wings of the butterfly *Araschina levana*. Such was the difference between the eclosing of spring and summer that Linnaeus believed two separate species were evident. It is now known that changes in day length and in temperature trigger the amount of the hormone ecdysone in the larva. Gilbert (2005 pp66–72) sees this as one example of several that illustrate how the environment can induce differentiation in gene expression, leading

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[62] See Kropotkin's collection of articles reprinted in 1995 for an insight into the evolutionary debates in the Victorian era.

to phenotypic variation. Temperature does not only induce the activity of the gene but can also affect the final protein in other ways. Gilbert provides the following example:

> When discussing environmental regulation of gene expression, it is important to keep in mind that gene activity does not necessarily mean gene transcription. The regulation of the gene product can occur at other points along the pathway to make a functional protein. One of the best-documented cases of temperature affecting protein activity and normal phenotype production is the temperature sensitive tyrosinase found in Siamese cats, Himalayan cavies, mice, and guinea pigs (see Schmalhausen 1949). Some families of humans also have this condition, caused by a temperature sensitive tyrosinase enzyme. Under normal (high) body temperatures, this enzyme is folded in a manner such that it becomes unstable and remains in the ER-Golgi apparatus to be degraded. However, at slightly lower temperatures – that of the ears, nose and extremities of the limb – the enzyme folds properly and is able to function. (Gilbert 2005 pp68–69)

Indeed, it has been demonstrated that if one were to shave the white fur of a Himalayan rabbit and then apply an ice pack on the naked skin, the resulting regrowth of fur would be black.[63] The term 'phenocopy' was coined by Goldschmidt in 1935 and is illustrated by much of the above.

## Size, Speed and the Correlation of Parts

One can argue that the size, shape and mass of an organism have consequences not only for its metabolism, longevity and reproductive rates but also for its locomotion and aspects of its behaviour. One must remember that organisms are constituted of smaller components, down to the smallest of particles, and continuously interacting with the extrinsic. Just like the electron or the neutrino, they are subject to laws that determine the relationships between mass and motion, and it is worthwhile giving a brief overview of such relationships. The smallest of particles, the photon, travels (in a vacuum) the fastest; as particles increase in mass, their potential velocities slow accordingly (Close et al. 1986). This pertains through to the molecular, but very large objects such as planets and stars proceed at enormous speeds, far greater than those of any molecules or living organisms (Bonner 2006). Movement within molecules is determined largely by temperature: high temperatures excite the atoms, with progression to gas, whereas cooler temperatures lead to less activity, retaining solidity. At the point of the smallest of organisms and of the largest of molecules, there is a curious equivalence in motion (ibid. p137-146).

It is generally true with organisms that the smaller the organism, the slower the speed. The smallest microbes are the slowest movers and the virus, if it can be considered an organism, is a virtual non-mover (ibid p137-146). Fortunately for birds, most travel at greater speeds than insects, and penguins are generally faster than most small fish.[64] The general rule does not always hold: the elephant cannot muster much more than 15mph, the anomaly here being the effect of gravity. Compare this with the blue whale, a creature that can outstrip a speedboat (Reisner 2009).Is it not the case that size and speed are major considerations for behaviour? Take again the blue whale: its source of food is largely krill, which it engulfs in the manner of a trawler, mainly because it is faster than its prey. Although larger sea life would provide a welcome diet, the size of the blue whale means that momentum in one direction precludes any quickness in changing direction that would be needed to catch smaller fish of lesser speed but greater mobility.

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[63] For a detailed modern exposition of the genetic explanation see Baum el al. (2010).

[64] The world's fastest animal is the peregrine falcon, diving at speeds of 200mph, with the swift reaching lateral speeds of approximately 100mph. This compares with the 80mph of the cheetah. (Reisner 2009)

[65]The largest dinosaurs were all vegetarian, too cumbersome for mobile prey to be of any interest. This is not the case with the smaller *Tryannosaurus rex* or *Spinosaurus*, both massive creatures coming close in weight to the elephant but, unlike the elephant, carnivorous and dependent upon speed. This was achieved by counteracting the gravitational force through enormous and powerful hind legs, but the dynamics of this inevitably resulted in compensatory much reduced forelimbs. One might wish to consider this as an example of Darwin's correlation of growth or as a more modern author suggests:

> It is clear that size, from the pure point of view of physics, has an enormous effect on living organisms. It constrains, or even controls, the shape of an organism, including its internal structure. It determines what is possible and what is impossible. And as we have also seen, it can effect the behaviour of animals as well as their locomotion. (Bonner 2006 p49)

Arguably, the amount of energy an organism can take in is limited to its size; therefore the conversion of Adenosine-5'-triphosphate (ATP) can only fulfil certain tasks. It follows that an individual cannot be a fast runner, adroit swimmer and soar in flight amongst the clouds. Energy constraints ensure that specialisation in one area entails deficiency in another.[66] If the size of an organism changes, then other matters must follow. Therefore, does one need only explain this by parsimonious means of direct causality? Neo-Darwinists would disagree, perhaps even arguing there is a *Prima facie* 'no' here. Structuralists do however argue in favour of direct adaptations. Taking a unique perspective on this point Reiss (Ch.12) argues that we should abandon the concept of 'adaptation' altogether, but more on this later.

There is another form of constraint that can be observed at the macro level. If predators are dependent upon their prey then this has implications for the distribution of species. There can never be more carnivores than omnivores. There can never be more omnivores than plants or fungi. All of these groups are also completely dependent on micro-organisms, but these micro-organisms can survive, and did so for many years, without the existence of multicellular life. None of this ordering necessitates adaptive explanations or an appeal to natural selection.

### Nutrition – We Are What We Eat

It can be argued that life as we know it is composed of stardust, where all the components of an organism are the products of the Sun. The dominant constituents are carbon, oxygen, nitrogen and hydrogen, plus a little phosphorus, potassium, sulphur etc. (Gribbin & Gribbin 2009, Berkowitz 2012, Hazen 2012). Altogether, there are thought to be 30 elements that constitute the human body, for example. (See Appendix 2.) What contributes to the various forms of life is the quality of the elements taken in by an organism through breathing, absorption and diet. For instance, the mineralisation of soft-bodied animals to those of skeletal animals could only have taken place if the minerals were available for acquisition. As an example, the quality of human bone and teeth is determined largely by the quality of the materials consumed. In fact, by analysing the isotopic ratios in a bone, forensic palaeontologists can discover not only the organism's diet but also the elements absorbed from the environment (Lewis 2007). From this, these elements can even be matched to particular environments. Such acquisitions are fundamental therefore for a complete understanding of form.

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[65] The details concerning the physiology and behaviour of the dinosaur were extracted from Colbert et al., (2001).

[66] For a recent consideration of the importance of the correlation of parts, see Lockley (2007) and Schad (1977).

Changing the quality of the acquisition could also have evolutionary consequences. It is worthwhile considering other examples, one of which has a relationship with a scaling model.

One form of scaling not mentioned so far is the relationship between body size and brain size. Brain size has been found to reflect body size: elephants have the largest terrestrial brains on the planet and the mouse lemur (*Microcebus murinus*) of Madagascar, which weighs 2 grams, the smallest (Hart et al. 2001). However, the scaling is not directly proportional but follows a 2/3 power law ($Ew(brain) = 0.12w(body)^{2/3}$). The correlation holds well as a general rule but, as one might expect in biology, there are anomalies. The encephalisation quotient (EQ) measures any divergence in brain size from the expected norm (Foley and Lewin 2004). Porpoises, dolphins and humans have high EQs because their brain mass exceeds the $^{2}/_{3}$ scaling with their respective body mass. So why is it that humans have a much greater EQ than their closest evolutionary relations? How does one explain this phenomenon of great evolutionary significance? Just how did the human cerebral neocortex come to be the mass it is?

Anthropologists have sought to explain this rapid evolutionary novelty in two distinct ways. The first explanation focuses upon the importance of bipedalism, which facilitated freedom of the upper limbs to engage in social activities such as tool-making and hunting (Foley and Lewin 2009, Stanford 2004), In turn, these activities would exercise neural cells, leading to more complex neural connections and development of the frontal lobes. This has certain plausibility but one must recognise that the mechanism described here is essentially Lamarckian. It follows from Lamarck's ideas of use, entailing the activation of organs which, if continued over many generations, would result in acquired characteristics. Darwin also posited this type of explanation on many occasions if he felt there was no evidence of Malthusian struggle or sexual selection at play (Ch.1). The second anthropological explanation postulates that the quality of the nutritional intake can change an organism's form. Focus here is placed upon the diet of our hominid ancestors. (Striedter 2005) One explanation is that the meat appropriated on the savannah provided the energy necessary for cortex growth (Bunn 2006). An alternative explanation is that fish was the important protein factor, for it contained docosahexaenoic acid (DHA), a major chemical substrate for the brain (Crawford 2008). Crawford and Marsh (1989) perceive evolution as 'substrate driven' where a change in diet leads to an evolutionary change in brain architecture in a way that is not dependent upon the chance mutation process. Again, Darwin (1868) saw that nutrition could produce evolutionary change but carefully distinguished such a process from his Malthusian natural selection.

Researchers are quoted in Gilbert and Epel (2009) as saying that a particular diet can 'cause changes in jaw structure of mammals and fishes' without any alteration in the genetic sequencing of the individuals under study. This type of morphological change and many others are referred to as processes of 'phenotypic accommodation'.

Another contrast between the direct effect of diet explanation and the chance mutation explanation can be seen with flamingos and other birds such as the house finch (*Carpodacus mexicanus*) and the canary, which is the domesticated form of the serin (*Serinus canaria*) originating in the Canary Isles (Hill et al. 1994). How does one explain the plumage colouration of such birds? Take the flamingo: the chick default colour is white, but within three years or so the bird becomes the striking pink. However, this is not always the case; certain zookeepers found that their flamingo chicks remained white when they developed into adults. This was discovered not to be albinism or genetic mutation but simply the result of changing diet. For such birds require a carotenoid-rich diet such as shrimp, seeds, vegetables, fruit and insects that contain the necessary pigments (ibid Hill et al). It does not follow, of course, that if birds of other species were fed such a diet, they too would change colour. For a colour change to manifest itself, certain genes must be present. The important point here is that, to understand form fully, one must consider any possible environmental interaction with an organism's biochemistry. A permanent change in environmental factors could produce a permanent change in an organism, so it is very problematic to assume any default position. One classic example to illustrate these considerations further is that of the queen honeybee: a diet of protein-rich 'royal jelly' is required to increase hormone levels to the levels necessary for the formation of fertile queens; if the diet is insufficient, then the larvae become sterile worker bees (Seeley 1996).

## Conclusion

There are many factors, other than heredity and changes in gene sequencing, which shape the form of living things. Indeed the structure of DNA itself is subject to the laws of physics and topology. Temperature, gravity and nutrition are factors that have been discussed here, but this list is far from exhaustive. Consideration could also be given to the influences of humidity, precipitation, the cycles of light and dark that come from a revolving planet and electromagnetic interactions, to name a few. Organisms are not divorced extrinsically: changes in external factors can effect changes in the organism and these could subsist from generation to generation. This direct causality could also impinge upon the biochemical changes that lead to mutation in the chromosome. The subtle but influential relationships between gravity, size, temperature, homeostasis, growth, locomotion and behaviour have perhaps been under-appreciated. These factors combined impinge upon the organism constraining and determining the products of the cell and its components. The interactions are complex and difficult to elucidate, the variables are many and unfortunately do not conform to a convenient equation. One might argue that all the phenomena above could be addressed from the perspective of selection. Indeed, one could do so but then the question arises- would such an approach be parsimonious? What is the point of icing a cake twice?

## Chapter 11: Explanation in Evolutionary Biology

In this chapter, explanation in evolutionary biology is considered. There are many difficult obstacles, for explanation in general is a live philosophical issue with little consensus. There will be no pretence to resolve this situation here, but existing arguments within evolutionary biology will be assessed for validity. The type of explanation employed within evolutionary theory and where it is that natural selection can be legitimately engaged are of particular interest. There have been many advances empirically within evolutionary biology during the last 15 years or so. The recent evidence impacts upon the issue of natural selection and it is valuable to examine new interpretations or refinements that have been suggested. It is of paramount importance to be clear as to what exactly the explanandum is. Without this, the spectre of anomalous selection is lurking and predisposed to undermine evolutionary theory.

What counts as a good explanation in evolutionary biology? Is explanation in evolutionary biology of the same form as explanation in other parts of biology or the physical sciences such as physics and chemistry? What counts as an explanation in ordinary day-to-day life? The issue is a vexed and complex one that has occupied the minds of philosophers and scientists probably since the pre-Socratics of ancient Greece. Would it be that unfair to suggest that the issue is still open-ended with no likelihood of an imminent consensus? Needless to say, perhaps, there will be no attempts within this work to add anything novel to this debate, for this would transcend far beyond the chosen parameters. Nevertheless, it is important to consider some of the principal ‘explanations of explanation’ in the context of this study.

Generally speaking, when one asks for explanation one is indicating that there is some matter not understood, perhaps partially or fully. The explanation that follows is intended to clear the matter so that it can be understood. This may take several forms. A school teacher may be asking for an explanation from a boy who is late for class and the pupil’s explanation takes the form of a description of events that led up to his being late. Or perhaps the pupil explains that the bus broke down and that ‘caused’ him to be late. Explanations can also take the form of definitions: one may not know what a bachelor is, but the definition ‘unmarried man’ may be more familiar. Translations from one language to another can explain also, if one is not familiar with a particular language. The use of analogies can illustrate a difficult point; Darwin (1859) used the analogy of artificial selection to explain his concept of natural selection. Use of analogy can be misleading, however, as an analogy is not a simile and, under closer examination, some purported analogies are actually in part disanalogous. ‘Models’ can also be developed to simplify complex situations, particularly where mathematics is not easy to comprehend or visualise. This method of explanation can also be misleading on occasions, sometimes purely because of a poverty of language to represent abstraction. If one cannot understand the drawings of an architect, then a small cardboard model of the project will help illustrate or explain what is intended. Nevertheless, the model will lack many of the details contained within the drawings and one has to take care.

Traditionally, in scientific explanation there have been two main approaches to explanation, with other approaches deemed more peripheral. The first major recourse is an appeal to causality, often embodied in

Mill’s method (1843). The causes need not be singular in origin, but several factors could combine to produce a phenomenon. One could argue that this recognition is often cited within complexity theory. The alternative to causal explanations is the empiricist approach. Following the problems Hume (1777) exposed with ‘necessary connexions’, regularities and uniformities are sought in nature and then, in some instances, treated as universal laws. The formal structure of this approach was laid out by Hempel (1942) and is famously known as the Deductive-Nomological Model, or *DN* model. After the rise of quantum mechanics, some laws became of a probabilistic or stochastic nature. The *DN* model, however, has been much debated, one of the major problems being that a strict application accommodated explanation in the ‘hard’ sciences, such as physics and chemistry, but failed to accommodate the explanations emanating from ‘softer’ sciences, such as evolutionary biology and psychology. The ambition has been to discover universal or invariant laws that are conducive to accurate and reliable prediction (Popper 2007). Cartwright (1980) and others have alternatively argued that universal laws are hard to establish and if they are to work, do so only under highly specified conditions. The view is controversial and there are concerns that one might overly idealise the structures of scientific explanation (Feyeraband 1975, 1978). One thing that can be assumed, even if there are concerns over universalisation, is that the ‘hard’ sciences are more likely to come within reach of this ideal than the ‘softer’ sciences. This is largely because there are far more variables within biology, for instance, than within physics or chemistry. With quantum mechanics or the periodic table, one can get good mathematical handles on the material, which in turn provide highly accurate predictions. Ironically, quantum mechanics is the most precise science mathematically and yet it is extremely difficult to conceptualise and describe in words. For instance, it is very difficult to conceptualise a photon as both particle-like and wave-like or to conceptualise a universe of 10 dimensions. Biology, however, struggles to achieve the advantages that mathematics has to offer, despite some recent advances in systems biology. Evolutionary biology is even more disadvantaged, having to carry the weight of history with subsequent recourse to semantic narrative. How then does biology explain matters when the nature of the beast restricts the advantages available to the hard sciences?

Another concern of philosophers is that science should deliver more than mere description and taxonomy. There should be, one might argue, ‘structure’ underlying such explanation. Without it, there is a concern that pseudo-sciences may qualify equally alongside the established sciences: astrology could compete with astronomy and creationism could compete with evolutionary theory and geology. (One might argue that creationism would contradict all science.) On the other hand, it could also be argued that too much ‘structure’ in explanation could lead to teleology, a sensitive issue in evolutionary biology. Of course, the call for structure is not without difficulty itself, especially when it comes to demarcating what counts as structure and what does not. Perhaps it is the case that there is no single method of scientific explanation but several. If this is so, then what are these methods? Unificationists, such as Kitcher (1989), have argued that scientific explanation should provide a unified account of a range of different phenomena. However desirable this suggestion, it seems that biologists employ a wide variety of explanatory devices, with very little consensus as to which approach is the most suitable. One recent approach that may be accessible to evolutionary biologists is that suggested by Salmon (1984). If universal laws are unavailable for this discipline, then one might consider Salmon’s causal mechanisms or processes, sometimes referred to as the *CM* model. The idea is of causality having a physical nature – one of spatio-temporally continuous causal processes and interactions. In theory, one could identify all the relevant factors and describe any interactions that may have taken place in a chronological manner.[67] For Darwin and Wallace, this would unfold as a population of organisms increasing in numbers but faced with diminishing food supplies; only the fittest secure enough food, while the unfit fail to survive. These interactions between growing populations and scarcity of resources would persist over the generations etc.

One can see that the *CM* model might be attractive to evolutionary biologists, but even this is not without problems. There is biological explanation that does not fit the *CM* model: for instance 'scaling laws'. Although 'scaling laws' are not laws in the sense required by the *DN* model, they nevertheless play an important role in explaining many relationships and also offer rule-of-thumb predictions. Another issue is how to explain the prevalence of the different forms of symmetry. The neo-Darwinist might appeal to explanations of functionality or sexual selection, but the structuralist might argue that symmetry is more fundamental than biology and appeal to physics for an explanation. However, it is not clear that the physicist can provide an explanation for symmetry or would even attempt to do so. A strictly empirical physicist would not attempt to answer such 'why' questions and might say that is just the way the universe is. But is such a negative response better than that proposed by the neo-Darwinist? However poor the structuralist believes that neo-Darwinian explanation to be, is any explanation better than no explanation?

The structuralist does have another explanatory card to play and this involves what one might call 'negative prediction'. This concerns the issue of constraints and what can be said of form and function. An example of negative prediction could be 'no creatures with neck length *x* could support a head size *z*' or 'creatures of size *y* could only function and survive in environment *w*'. One can continue to build upon these constraints imposed by the 'forces' considered in Chapter 10 – gravity, temperature, nutrition, magnitude, metabolism etc. One could also include the intrinsic constraints associated with phylogeny, genetics, development etc. When considering these in totality, the window of opportunity for selective explanation diminishes. In a logic puzzle, one might follow and build upon one negative clue after another. There comes a point when only one possibility is left. Astro-biologists[i68] do indeed employ such methodology when calculating whether a planet supports life. The 'habitable zone' is determined not only by considering the necessary conditions but also by delineating the negative factors. For instance, the gravitational pull may be too great or too small, or the prevailing temperature extreme.

The idea of negative prediction may tie in well with Schaffer's proposal of 'contrastive causation'. This takes the form: c *rather than* c* *causes* e *rather than* e*. To understand the significance of this, one can draw relations with the selectionist first; that is, that c *rather than* c* *causes* e. To make this less abstract, *c* could be an organism with certain qualities that organism *c** does not possess, therefore leading to *e*, which is greater reproductive success. If this is so, then it could be that *e** need not be considered. However, the tension from the structuralist is represented by *e**. To make this less abstract too, *e** could represent all the constraints and direct impact of physical forces that may impinge upon an organism and/or its components. Now it may be the case that *e** is so strong (negative constraints and/or direct influences) that c *rather than* c* is no longer an option for *e* or that only *c* is applicable or only *c** is applicable. In other words, the

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[67] See Weele (1999 pp49–53) for a discussion and comparison of Salmon with other philosophical perspectives on explanation within evolutionary biology.

[68] See Woodruff T. Sullivan III and John Baross (2007) for an exposition of exobiology and astrobiology.

selectionist is so constrained by what physics and chemistry put on the table that there is little or no work for natural selection. On the other hand, it could be argued that *e** is not relevant in some circumstances and that matters can be settled by simple application of c *rather than* c* to determine *e*. One does need to be clear also about what c *rather than* c* is to entail. For instance, does it entail that one organism is fitter than another through virtue of some particular trait or might it entail that an organism is able to survive rather than not survive? Clarity is important here; one has in mind the application of the term ‘selective pressure’ and its ambiguous nature. One might also be alluding to c *rather than* c* as competition between groups or populations for resources.

Another concern to be aware of is the chronological nature of the aetiology. It must be remembered that before one can consider c *rather than* c*, one has to account for *c* and *c**.These do not appear by magic and any causal account must begin with *e**. In neo-Darwinian terms, variation must precede selection. Therefore, it is stressed that the particular aspect of evolution must be clearly identified and its place in the causal chain ascertained prior to assessment of contrastive causation; otherwise, conflation of causes may ensue.

One can conclude that there is no simple or singular mode of explanation that fits either biology or, especially, evolutionary biology. Explanations such as the *CM* model or contrastive causation can only be touched upon lightly here. To give full justice to their significance requires deep analysis but may open a new philosophical enquiry in its own right.

## The Explanandum and the Explanans

In evolutionary theory, it seems there are two main issues to be addressed. The first is what is it that is to be explained, what is the explanandum? Once this is identified or established, the second issue is how does one explain the explanandum, what is the explanans? It is important here to draw this distinction and address both issues, for there seems to be a tendency to commit oneself early and discuss the explanans before the explanandum has been established. This oversight can cause much confusion and two interlocutors in disagreement might simply be talking at cross-purposes. What, then, is to be explained here? With the exception of a fringe group of religious scientists, there is a broad consensus that naturalistic evolution has occurred over billions of years and explanations for this should be sought. But what aspects of naturalistic evolution are to be addressed, what are the main foci? Speciation? Adaptive traits and behaviour? Demographic changes in population numbers? Extinction and fitness? The great diversity of forms of life that has emerged? The origins of life in the primordial soup? The periods of stasis when no significant evolution is said to have occurred? The bilateral body plan? And so forth; the more one examines evolutionary theory, the more one appreciates the number of evolutionary issues to be explained. Should all of these issues be addressed or just some? The first question to ask, however, is ‘Is there one broad explanation to all of these distinct phenomena or does each phenomenon require its own distinct explanation? Or is it even that one explanation covers some phenomena but not others?’

One might argue that when one is introduced to evolutionary theory, one gains the impression that ‘the’ explanation for all aspects of evolutionary theory can be put down to natural selection. If this is so, then one could argue further that an oversimplification of natural selection has proved enormously popular and has permeated many areas outside evolutionary theory, including the 'hard' and the 'soft' sciences. Looking deeper into the matter of natural selection, one realises the complexity involved. How is it, for instance, that the term 'natural selection' was introduced by its creator as a metaphor to explain a limited range of biological phenomena (Ch.1) but that it can also be seen by some to explain such diverse things from aspects of cosmology to aspects of ethical theory? (Ch.5). Under these circumstances, one needs to disambiguate the term 'natural selection'. The main ambition of this work has been to establish first the ontological question of natural selection and only then to attempt to provide guidelines as to what one can legitimately explain. What is of interest is the historical analysis presented earlier. This illuminates how the explanandum has changed over time. It was observed that the proto form of natural selection, prior to Darwin and Wallace, recognised that favourable traits could spread through populations and unfavourable traits would not survive. All of this occurred without any consideration of speciation, or transmutation as it was then known. All was within the concept of the fixity of species advocated by Linnaeus, Paley et al.[69] and accepted by virtually all the scientific community and the general public. At least, this was so in Britain, even if it was not so consolidated on the continent. Darwin and Wallace went boldly, arguing that the explanandum was principally transmutation or the origin of *de novo* species and characters and also their eventual extinction. The explanans was the earlier concept of favourable traits spreading through a population but now coupled with the Malthusian element. Darwin coined this process 'natural selection' (Ch.1). The 'mystery of all mysteries', on page one of the *Origin*, was the principal explanandum but the issue of adaptation was a secondary explanandum. Further, Darwin (although not Wallace) thought that some adaptations, such as the giraffe's long neck, could not be explained exclusively by natural selection (Darwin 1900 p279). Darwin also invoked Lamarckian processes (Appendix 2). By the mid-twentieth century, arguably this situation was inverted: adaptationism was the principal explanandum and many neo-Darwinists argued that natural selection was the exclusive explanans (Block and Kitcher 2010, Coyne 2010, Futuyma 2006, Pigliucci, 2009) Speciation became the secondary explanandum. Problems arose, however, with evidence from palaeontology indicating that the fossil record demonstrated mass extinctions followed by periods of speciation, which in turn were followed by long periods of stasis (Gould and Eldredge 1977). Episodic evolution was a new explanandum but what was the explanans? Natural selection had been devised by its creators to explain a gradualist perspective of evolution, step by step, small incremental changes scrutinised every second, every minute. How does one explain the long periods of stasis when there was little of evolutionary significance? Seemingly, neo-Darwinists were loath to abandon the cherished principle of natural selection that they had championed with almost ubiquitous explanatory powers. Rather than accept the possibility that evolutionary explanation could be pluralistic, new variants of natural selection were termed to 'explain' new phenomena. 'Balancing selection' and 'stabilising selection' are terms used to explain the long periods of stasis. The terms 'relaxed selection' and 'lifted selection' are employed to explain evolutionary radiations or periods of fairly rapid evolutionary change. (See below). The situation has grown bizarre: this latter addition completely inverts the rationale of Darwin and Wallace, who proposed natural selection as an explanans for evolutionary change. Under the new terminology of lifted or relaxed selection, evolution is said to occur when natural selection is absent.

Putting aside, for the moment, this problem of anomalous selection, focus will now be directed to evaluating the argument that natural selection is the best and even the only explanation of adaptation.

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[69] See Bowler (2003) for an excellent discussion of the problems of fixity for early evolutionists.

Cain – Selection is Everywhere

To Cain (1997 pp132–134), many of the examples that purport to demonstrate the instantiation of evolutionary drift are, under closer inspection, really the subject of selection. Traits or characters that, on the surface, seem to have no functional value do, in fact, have a value if the researcher is prepared to investigate long enough. This perspective clashes with the earlier views of Dobzhansky (1937). Part of the problem, according to Cain, is that researches in the laboratory do not embrace the full rigours of selective forces; therefore fieldwork is essential when testing for drift or selection.

> Looking at skins of closely related species of bird reposing on a museum tray, one might well be at a loss to produce an explanation for some of their interspecific differences: but a stuffed bird on a museum tray is not in the best position to show what it does with its characters. Extensive field work may be necessary before their significance is realized, even if it is great. In fact, every case which has been carefully examined, the supposed influence of random drift, postulated on the basis of insufficient knowledge, has been greatly reduced or actually disproved for the characters under consideration. (Cain 1997 p132)

To Cain, it is selection alone that determines gene frequency. He admits there are studies that seem to suggest that random processes affect frequencies.

> But these studies do show, as do so many other studies on genes in the wild, that merely to fail on a casual inspection to see any selective significance in a particular variation does not licence the observer to proclaim that there is none. (ibid. p133)

However, Cain recognises that not all characters selected are adaptive. Some characters are by-products of those that are selected for, and in themselves of no selective value or even somewhat deleterious. Moreover, genes being pleiotropic are ‘likely to produce all sorts of changes throughout the phenotype’ (p133). Dobzhansky (1937) had argued that the usefulness of a trait must be demonstrated, it cannot just be taken for granted. In a long career of laboratory research, he had noticed that many differences between *Drosophila* species have no claims to being directly useful. Moreover, some traits that one might consider important, such as orbital bristles, were missing in some individual flies but their absence did not cause the mutant flies any inconvenience. Dobzhansky concluded that the supposition that all or even most of them are directly useful to their possessors stretches one’s credulity too much. Here is Cain’s reply to and criticism of Dobzhansky:

> But equally, its uselessness cannot be taken for granted, and indirect evidence on the likelihood of its being selected for and actually adaptive cannot be ignored. In any case, the argument that flies in cultures do not seem to be affected by the loss of a bristle is inconclusive, a few per cent selection, enough to fix the character in a short time, would not have been noticed, or selection might be more stringent in the wild. (Cain 1997 p134)

*Evaluation of the arguments*

So what does one make of this debate between two eminent neo-Darwinists? Is it really the case that all traits, apart from those that piggyback, are the product of selection? Some of the arguments Cain put forward to establish what he sees as near ubiquitous selection will now be looked at a little more closely.

Is Cain arguing that all laboratory tests are inconclusive or that only the tests that do not support his preference for selection are inconclusive? For one could argue the converse: that laboratory tests that suggest a selective component may not transfer such a confirmation if tested in the wild. If there is doubt about the efficacy of laboratory work, then it could cut both ways, being inconclusive about drift and selection. Cain favours research in the wild over work in the lab, but does this overlook that fieldwork itself is not always without problems? A laboratory environment has more control than a fieldworker over factors that impinge on the studied organism. In the wild, there are many more variables – different and unforeseen predators, irregularities in food supply, changing climatic conditions etc. The results of a field study are therefore contingent on a changing environment and different field studies of the same subject can give quite different results. A classic example of this is the study of the peppered moth, which catalogues such contrary results (Sargent 1976 and Sargent et al. 1998). How the presence of melanism becomes established is still an open question and one of ongoing research (Majerus 1998).

Another concern over Cain's argument is that some researchers simply have not found evidence of selection at work in their studies. If one follows the submission of papers on this topic, then one appreciates that a steady stream of researchers have evidence of drift or other mechanisms independent of selection (Gherman et al. 2007, Lynch 2007, Venditti and Pagel 2010). Of course, there are also many papers that support an adaptive or selective interpretation, so one has to be careful not to seek out exclusively papers that favour one's own hypothesis. It would also be disingenuous to claim that researchers had not completed their work, insisting, for example, that selective 'forces' were present but that those researchers had just not looked hard enough. What if the researchers were to go back, carry out further tests and still maintain there was no evidence of the presence of selection? Could one say, 'Well, you still haven't looked hard enough; if you look harder, then you'll find it'? If one were to demand such strictures, then of course one could never demonstrate any evidence of drift. Under such circumstances, the selectionist will have built a fail-safe into the theory and one could never demonstrate there was no evidence of selection at work. Imagine a person who maintains there are custard pies floating around the universe; such things have never been witnessed but, by the logic above, that simply means that not all the corners of the cosmos have been searched and that one should continue looking until floating custard pies are found.

The issue of adaptive traits is an old one[70]. Explanations that appealed to adaptationism have suffered from any clear criteria to distinguish 'genuine causal' explanation from 'just so' explanation. Elton, one of the founding fathers of ecology, appreciated the difficulties involved in identifying adaptive traits. For instance, it was common to assume that the dimorphic colour of the coats of arctic foxes (*Alopex lagopus*) was an adaptation. White coats conferred advantage in the snowbound environment and blue/grey coats an advantage in the warmer snow-free environments. However, upon closer inspection, Elton noticed several anomalies in the details: within these colour morphs, there is a wide range of colouration and, moreover, in the snowy environment of Iceland, blue/grey morphs exist frequently alongside the white morphs with no loss of fitness.

> Although the ordinary theory of natural selection appears at first sight to explain almost all the phenomena produced by evolution, the two greatest arguments in its favour being the existence of so many perfect adaptations in animals and the difficulty of imagining how any useful characters could spread in a

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[70] See Robson and Richards (1936) for an early, extensive but critical discussion of adaptive reasoning.

> population; yet there are certain cases of colour dimorphism among animals which cannot be explained on the hypothesis of natural selection. Of these one of the most striking is the arctic fox, with its blue and white phases; another example is the white-eared cob of the Sudan. In fact it seems very likely that most so called adaptive colours in mammals are not actually adaptive at all. (Elton 1927, reprinted in 2001, p179)

Contrary to Cain, Elton argued that one could not necessarily explain the existence of particular traits by means of adaptation through natural selection. Elton is not arguing that there are no cases of successful explanation by adaptive reasoning, the argument is against universal application. Saunders (1994) has argued that not everything that is to one's advantage is the product of selection. Instead, he argues, many things may just be the consequences of natural causes, coming directly from physics and chemistry. Saunders constructs a mathematical variation of Watson's and Lovelock's 'Daisy World Parable' (1983), a model that demonstrates how two species of daisy, distinct in colour only, on an isolated planet can have their respective reproductive fortunes determined mathematically by simple regulations in physics. Constructions can come together through complex interactions that are simply of the natural order. Perhaps, if one is unaware of these interactions, then one can be tempted to explain the phenomenon in question in terms of selection. Saunders is following the traditions of Thompson and Lima-de-Faria here (Ch.9). This discussion brings us back to the debate that raged at the beginning of the twentieth century. Are the facts of evolutionary biology attributable to selection processes or to the direct actions of the environment? Or to a mixture of both? A hundred years on and similar considerations have resurfaced; the appreciation of phenotypic plasticity has led to enquiries that seek to discover what triggers the expression of particular genes or networks of genes. Arguably, researchers have pushed back the boundaries to discover the causes of such expression; consideration is now given to the epigenetic, the epigenomic and the different types of interface with the external environment.[71] What is most important with the last point is that interfaces with the environment can, but do not necessarily always affect whole populations. Some examples might include temperatures that determine the sex of reptilian offspring (Georges et al 2010); diets that change the colour of flamingo plumage (above) or the colour of chicken eggshells (Gosler 2008), population density that can determine the length and colour of the locust wing (Lester et al.2005, Song 2005), and gravity that determines the density and overall size of the skeletal bone (Ch.10).

### *Phenotypic Plasticity and Natural Selection*

It has been argued that without a singular and formal definition of natural selection confusion will ensue concerning the demarcation between evolutionary factors; those that can be assigned within the province of natural selection and those that are not. Phenotypic plasticity is an example of this confusion. On the one hand it is argued 'To the best of our knowledge, no one has ever suggested that plasticity plays a role in evolution as a mechanism `on a par with' natural selection' and concluding the paragraph, '….. selection acts on developmental plasticity, and the two simply cannot be considered alternatives from a logical standpoint' (Pigliucci et al 2006). On the other hand, 'Models of population divergence and speciation are often based on the assumption that differences between populations are due to genetic factors, and that phenotypic change is due to natural selection. It is equally plausible that some of the differences among populations are due to phenotypic plasticity', and later, 'Phenotypic plasticity is widespread in nature and may speed up, slow down, or have little effect on evolutionary change'.(Price et al 2003) Clearly, both assessments cannot be

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[71] See Hall, Pearson and Muller (2004) for a compendium of essays that seeks to link together the environment, development and evolution in a revised synthesis.

correct. What is odd about this is that both sets of researchers agree broadly over what phenotypic plasticity involves and that it is evolutionarily significant[72]. The difference in interpretation seemingly comes from the different senses of natural selection employed. Pigliucci et al see natural selection as evolutionarily important in a more narrow sense, alluding to natural selection as ‘an ultimate cause of adaptation’, whereas, Price at al seemingly have a wider perspective of evolutionary change where phenotypic plasticity is a source of variation for natural selection to act upon. One cannot say if either of these views is correct because there is no formal definition of natural selection, in fact the fluidity of the term allows contradictions to remain.

In Chapter 10, consideration was given to the effects of micro gravity on the physiology and morphology of all organisms. If humans were to remain in space for prolonged periods and were able to reproduce – something unknown at the moment but hypothesised for the sake of this argument – after generations they would look very unlike the humans they had left behind on Earth. Osteopenia would result in highly reduced skeletal frames, the cardiovascular system would alter dramatically, the heart would be much smaller, muscle tissues (unless actively exercised) would diminish and so forth. These adaptations to life in space are the direct result of the combined effects of micro gravity and free – fall. It would not be unreasonable to suggest that, in such circumstances, humans would look different, more akin perhaps to sea creatures, which exist where the effect of gravity is reduced by buoyancy. If one did not know the full history and came upon these later generations of humans, one might even conclude that they were of a different species and well adapted to their environment. The point of this illustration is not to suggest that this is a future scenario but to demonstrate how a changing environment would affect *all* the members of the spacebound population and in a directional manner. In such circumstances, differential reproduction does not enter the explanatory equation. This does not mean that differential reproduction is therefore redundant as an evolutionary explanation, but merely demonstrates that evolutionary explanations are pluralistic. One must not assume that every trait, adaptive or not, is the product of differential reproduction and differential survival.

### Fodor and Piattelli-Palmarini – Selection is Nowhere

Opinions of late have polarised once again over the extent of explanatory power natural selection is thought to possess. Fodor and Piattelli-Palmarini (2010) have argued antithetically to the pan-selectionism of those sympathetic to Cain’s views outlined above. In *What Darwin Got Wrong*, F&P develop several arguments against the principle of natural selection. The first argues by analogy that natural selection faces the same type of criticisms that Chomsky employed to refute Skinnerian behaviourism. Little consideration will be given here to this argument, as it is obscure and its validity rests upon a faithful analogy between the biology of natural selection on the one hand and the psychology of behaviourism on the other. The strength of the analogy is open to interpretation and the understanding of psychological behaviourism transcends the current work. In a review, Dupre (2010) argues that the analogy employed is difficult to justify.

Overlooking the uncertainty of this particular argument, the second line of attack employed by F&P rested on an argument that is an extension of that famously put forward by Gould and Lewontin (1979) in ‘The spandrels of San Marco and the panglossian paradigm’. Essentially, this argument was an attempt to

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[72] See also Larsen (2004).

demarcate between genuine explanations attributable to natural selection on the one hand and to non-scientific explanations or pejorative ‘just so’ stories on the other. F&P take this argument one step further by suggesting that there is no demarcation and natural selection is attributable only *post hoc.* If two novel traits are correlated – that is, *x* develops with *y* – then which is subject to natural selection? One would not know for many generations which, or even whether either, trait is selected, as all is contingent upon the environment. The problem is that the environment is changeable and therefore not easily predictable. F&P argue that natural selection cannot act counterfactually, meaning that if two correlated novel traits emerge, natural selection has no means of detecting at the point of emergence which is to be the fit.

That summarises part of F&P’s argument but one could go further however. In fact, one could argue that it would be difficult to predict whether any novel trait, correlated or not, commands fitness. One could only wait and observe whether the trait, over time and generations, later proved to aid reproduction. It is only at that point that one can claim ‘selection’ has taken place. There is a further pragmatic problem for any researcher: how to determine which particular trait is advantageous for reproductive success or fitness. In any population of sexually reproducing organisms, all the individuals vary in characters and most of this variation is subtle. Among humans, characteristics are all slightly different: there are differences in weight, height, skin colour, hair colour and texture, not to mention the intrinsic differences in organs, tissues etc. Even a single character such as the human nose can vary slightly in numerous ways; De Rijke et al. (2000) have written a book on the variation in nose topology. The epistemic problem is obvious: no one could possibly identify which, and (more importantly) whether any, of these subtle differences between traits conferred reproductive success. Hull (1999) has argued that individuals possess an enormous collection of traits and it would be almost impossible for natural selection to single out and favour particular features. Moreover, an individual’s success in reproduction, if one wants to think in those terms, depends on the overall performance of all these traits combined, ‘useful’ and ‘non-useful’, functional and non-functional. Hull has a fair point, is it not the overall performance that matters? The individual does not even have to be the fittest; it only has to suffice, satisfying whatever are the conditions of existence.

There is a further complication in identifying ‘advantageous traits’ and that concerns how organisms behave collectively. Take the differences between the lion and the hyena. The lion outstrips the hyena in almost every physical comparison – size, speed, strength and so forth – yet the hyena successfully competes against the lion, often in the same environment. What the hyena lacks in physical strengths, it makes up in collaborative group behaviour[73]. Taking ‘behaviour’ into consideration adds a whole new dimension when it comes to identifying what it is that leads to fitness, in the widest sense.

### Emergent and Preserved Properties

It was argued earlier that it is essential to be clear about what the explanandum is before one proceeds with the explanans. Without such clarity, confusion could ensue. It is therefore important in evolutionary explanation to distinguish between properties that are newly emerged and properties that are preserved or sustained after their emergence. The issue was also discussed in Chapter 9 in relation to Thompson raising

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[73] A short video demonstrates the power of cooperative behaviour - http://museum.msu.edu/exhibitions/Virtual/hyena_kiosk/HyenaCooperation.html

the question of why are some eggs are spherical and other eggs elongated at one end. It was observed that two answers were forthcoming. To re-cap, the neo-Darwinist explained that elongated eggs were less likely than round eggs to run off the edge of a cliff. Birds that laid elongated eggs were thus more likely to see their offspring hatch and go on to reproduce in their own right. This would confer considerable advantage over the birds that laid round eggs in similarly precarious places. However, Thompson was sceptical of this type of explanation and observed that elongated eggs were also laid on flat ground where there was no likelihood of loss. This occurrence undermined the explanation put forward concerning the cliff edge, he argued. Moreover, he thought the neo-Darwinist counter-argument rather convenient. This held that, in the case of the elongated eggs laid on flat surfaces and not on a cliff edge, there was an advantage in that a clutch of such eggs arranged in a circle were easier for the hen to brood than rounded eggs. Thompson instead argued that the eggs were the shape they were because of the internal physical forces that impinged upon the formation of the shell from its beginning when it was most malleable to the egg's exit from the oviduct when the shell arrived hardened. Which explanation is better, Thompson's or the ones provided by the neo-Darwinist?

With these types of questions, a distinction between *preserved* properties and *emergent* properties is invaluable. Clearly, the shape of the egg must be initially determined by physical forces, so Thompson is correct in that respect. It is doubtful that any modern neo-Darwinist would deny this, but they would nevertheless suggest that Thompson's explanation is only an example of a proximate or immediate cause. Furthermore, the neo-Darwinist's explanation is an example of an 'ultimate' or historical/functional cause and they would perhaps claim that this type of explanation is the important 'underlying' or 'real' cause.[74] One must recognise though that so-called ultimate causes cannot apply to novel emergent properties because these emergent properties lack, by definition, a historical precedent. Ultimate or historical causes can only attempt to explain why characters or behaviours are *preserved* and not why they *originated*. At best, one might be able to say that a bird's continued practice of laying elongated eggs on precarious slopes is a behaviour that is more likely to sustain than the behaviour of any bird that attempts to lay spherical eggs in a similar position. However, one can never say that laying eggs in such a place caused them to be elongated. Chronologically, form arrives first and function follows. Croizat, the biogeographer, appreciates the order of such a causal chain, arguing that 'the structure, or instrument precedes and determines its use: for without structure, or instrument, use cannot follow' (Croizat 1981 p519). There is an underlying logic: selection, by definition, can only operate if there is already in place a variation of forms. Therefore the selective process (whatever that is) can only follow chronologically from form. The question then arises of how one accounts for the nature and emergence of such form or forms. Before addressing this question, one misconception needs to be dispelled. To say that certain characters are preserved by natural selection is not entirely unambiguous. One could ask 'how does natural selection preserve properties?' Which could be seen as similar to the question 'how does one preserve jam?'. In the latter case, the answer could be something like 'jam is only preserved by boiling particular fruit with added pectin, sugar and so forth.' But how does one explain how natural selection is said to preserve favourable traits? Or, for that matter, how does natural selection eliminate unfavourable traits? Moreover, how does natural selection distinguish between traits that would prove to be favourable and those that would prove to be unfavourable? These types of questions are

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[74] Biologists have looked for causal explanation, but what form do biological explanations take? Tinbergen (1963) suggested that biological explanation could be divided into four overlapping categories – the proximate, the ultimate, phylogeny and ontogeny. Rose (2004) offers an interesting modern discussion of these issues and, as a clear example, looks at the different ways a frog's behaviour might be explained by physiologists, biochemists, developmental biologists, animal behaviourists and evolutionists.

the result of defining natural selection loosely, as if it were some form of anomalous force or filter. This reification fallacy can be avoided, however, if one recognises that natural selection is not a force or some form of agency. All that happens, at least if Darwinism is to be internally consistent, is that one can witness in nature that favourable forms are preserved with a statistical likelihood of being passed on and thus spreading into a population. It is this long *process* that Darwinists should arguably denote as natural selection. One must also remember that interactions such as jam preservation are quite specific about quantification and the particulars involved, as are the interactions of, say, the weak or strong ‘forces’ identified in physics. With natural selection, however, things are not specific; there can be many traits that are said to be preserved and their preservation can be for many different reasons. The process of natural selection is a generalised term that covers all of these. In a nutshell, natural selection is the term one might employ that *reflects* or *denotes* that traits are preserved or eliminated; it does not itself preserve or eliminate traits.

From such an analysis, it can be appreciated why natural selection is thought to lack any predictive power. Favourable or unfavourable traits are only recognisable after they are established. A favourable trait may initially begin to spread through a population and, according to neo-Darwinism, this trait is statistically more likely to do so than other traits. However, this statistical advantage depends *ceteris paribus* upon the environment. Trait *t* in environment *e* may enjoy reproductive success, but generations later it may be that environment *e* becomes environment *x*. It may be the case that changes in climate, predator regimes, resource availability, viral infection and so forth make environment *x* no longer conducive to the success of trait *t*. Conversely, a trait that might be said to be neutral or even unfavourable in environment *e* may prove to be of advantage in environment *x*. Consider the inherited sickle cell, which can lead to anaemia, lung problems and strokes but can also confer increased immunity to malaria in areas where malaria is prevalent (Williams et al. 2005). In other words a gradual accumulation of neutral mutations could eventually prove to be advantageous (or detrimental) in changing environments. If this is the case then accumulated neutral traits could also lead to adaptations.

To summarise, the problems when trying to explain adaptive traits or adaptationism are quite formidable. A reasonably clear and uncontroversial definition of these terms must first be provided. For instance, do adaptive traits increase fitness or are they simply seen as sufficing – that is, sustaining the lineage? When considering whether a particular trait is adaptive, one has to demonstrate that it is that particular trait, and not a correlated trait or body of traits that counts. One is faced with the chronological problem: if adaptations are contingent to the particular environment of the time, then there is always a relativistic element that requires identification. One needs to be sure that the adaptive trait is genuinely adaptive, arising from differential sources and not simply as the direct effect of the environment or by drift; otherwise, one might be guilty of the construction of ‘just so’ stories. The crucial point of all the above is the distinction between the emergences of forms *de novo* on the one hand and the sustainability or fitness of such on the other. One cannot say that adaptive traits or organisms emerged because they were adaptive; one can only claim that such adaptations are identifiable because they sustained and/or demonstrated increased fitness. As discussed in Chapter 1, people such as Bateson and DeVries argued just over a hundred years ago that the salient point in evolutionary theory was to explain the source of variation. Moreover, whatever was providing the source or sources of variation was the driving mechanism/s behind evolution, at least in the sense that evolution encapsulates transformations and novel biological features. Today, biology has advanced considerably and is in a much better position to elucidate the nature of variation. But what are the consequences for natural selection? Two contrary perspectives on this will now be examined.

## A New Model of Explanation?

In the biological zeitgeist of the twenty-first century, one might perceive a growing consensus that evolutionary explanations cannot be addressed only by observing and calculating the changes in gene frequencies. This perspective of the 'new' synthesis is seen as a gross oversimplification, and an extended or new synthesis is required to embrace all of the recent discoveries and advances of this fast-moving science. Although there is a consensus over this point, two contrary views are emerging concerning natural selection. One of these still sees a place for natural selection, albeit with some modification, and the other sees natural selection as marginalised or even superfluous. The view that seeks to accommodate natural selection will be examined first.

### *Accommodating natural selection*

In the literature of evolutionary developmental biology, there are calls for change. Carroll (2007) argues that a third revolution in biology is ensuing; the first was initiated by Darwin and the second by the members of the modern synthesis, while the third is the inclusion of developmental biology within evolutionary theory. Carroll (2009) believes natural selection has important explanatory powers but suggests that explanation should be considered as more a matter of the 'making of the fittest' than of the 'survival of the fittest'. In a more detailed theoretical view, Gilbert and Epel (2009) develop a new model of explanation that includes a broader spectrum of evolutionary pluralism. This includes factors other than developmental biology and recognises symbiogenesis, epigenetics and so on. In an earlier work, Gilbert calls for a new evolutionary synthesis, to combine population genetics with developmental genetics:

> Population genetics is perceived as–
>
> a) variation within populations,
> b) genes in adults competing for reproductive success,
> c) survival of the fittest
> d) natural selection.
>
> Developmental genetics is perceived as–
>
> a) variation between populations,
> b) genes in embryonic and larval organisms building structures,
> c) arrival of the fittest and
> d) phylogeny.
> (Gilbert 2003 p779)

It is noticeable that the defining points of population genetics, according to Gilbert, include 'survival of the fittest' and natural selection as distinct entities. There is nothing in the text to explain how or why these two phenomena are perceived differently. Nevertheless, the important point is the inclusion within developmental genetics of the 'arrival of the fittest'. One assumes that the 'arrival' part of the term is equivalent to what

Carroll (2009) later called the ‘making’ in his term ‘making of the fittest’. Gilbert argues that population genetics and developmental genetics can be reconciled:

> The two approaches complement each other. While the population genetic approach focuses on the survival of the fittest, the developmental genetic approach to evolution is more concerned with the *arrival* of the fittest. (Gilbert 2003 p778)

Gilbert and Epel (2009) endorse the difference Gilbert perceived between these two models of explanation:

> In other words, while the modern synthesis could explain the *survival* of the fittest, it could not explain the *arrival* of the fittest. For that, one needed a theory of body construction and its possible changes, a theory of developmental change. (Gilbert and Epel 2009 p324)

What is meant by the ‘arrival’ or the ‘making’ of the fittest? Essentially, it is the discovery of what constitutes the material basis of variation and how variation came about. Developmental genetics, to paraphrase Carroll (2007), for instance, elucidates much detail concerning the embryo and the larva. It can explain: why and how a feather is constructed rather than a hair or a nipple; how changes in development can lead to changes in the phenotype; how the processes and interactions of genes, proteins, cells etc. can produce eyespots on butterfly wings or rippled patterns on a mammal’s skin; and so forth. The combination of development and epigenetics provides a rich source of detail that fulfils Bateson’s suggestion of focusing on the causes of variation.

The interesting point for this work is the conclusion by Carroll, Gilbert and Epel that the recently discovered details can provide what they call the ‘arrival’ or ‘making’ of the fittest. Now, the details of variation may be empirically well established but, if this is so, it is very difficult to see why there is also a requirement for natural selection within their models. *If*, from the development process, they have identified the ‘fittest’, it must then be those same fittest organisms that persist and successfully reproduce. If these identified organisms were to fail in reproductive prowess, then they could not be rightly described as arriving or made as the fittest. One cannot claim to have provided an explanation of the advent of the fittest organisms and still require the services of natural selection. One of these considerations has to go. The argument is not a new one: Bateson, all those years ago, appreciated that if a science of variation could be elucidated, then natural selection is virtually redundant.[75]

This is a messy affair and symptomatic of the anomalous selection problem. Yet more selective terminology is introduced, fuelling the charge of a biological phlogiston. To make matters worse, the authors persist in using the word ‘fittest’ when the term ‘fit enough’ is more appropriate. If it were *only* the fittest that arrived, then there would be many casualties and populations would soon plummet. These criticisms should not detract from the recognition that Carroll, Gilbert and Epel (and others) have produced some excellent empirical work; it is only their conclusions concerning natural selection that need address.

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[75] The term ‘arrival of the fittest’ was coined in 1904 by Arthur Harris, who was typical of his time in being sceptical of those who saw evolutionary explanation through the eyes of selection only. (Gilbert and Epel 2009 p324.)

### *Selection as conservative*

Reid (1985) argued that evolutionary theory was an incomplete affair. His last book, *Biological Emergences: Evolution by Natural Experiment* (2007), is of particular interest here. As the title suggests, Reid sees a rich vein of variation occurring in nature that goes far beyond Mendelian genetics, recombination and point mutations. Whereas evolutionary developmental biology has been largely confined to explanation within *Animalia*, Reid embraces all the biological kingdoms and presents a highly pluralistic account of how new forms emerge and are generated. Rather than taking the traditional view of natural selection as the causal or creative 'force', Reid sees natural selection as a more conservative phenomenon. It preserves the status quo and stultifies much of the naturally occurring biological experiments. Contrary to the interpretations of most neo-Darwinists, natural selection is seen as preventing evolution (Reid 2007 p371). Moreover, Reid is critical of 'adaptationism' as an explanation of evolutionary change; if there is such a phenomenon, then being adapted is also conservative, a foil to further evolution. Of the neo-Darwinist supporters of adaptationism, he says:

> But soon they retreat back through the mirror, proliferating more preposterous circularities such as 'wings are adaptations to flight' or 'eyes are adaptations to sight' – as if flight and sight were metaphysical absolutes that existed before the emergence of wings and eyes. (Reid 2007 p37)

To Reid, then, it is the emergent properties that explain evolutionary change and it is natural selection and adaptationism that explain stasis. This perspective is consistent with those who argue that 'lifted or relaxed' selection facilitates rapid evolutionary changes, including speciation and novel characters (Janzen and Etienne 2012, Guze 2012). For instance, lifted or relaxed selection is said to apply to the evolutionary radiations when virgin territory is colonised. Deacon (2008) has employed relaxed selection in an attempt to explain the origins of the human language faculty. The important difference between Reid and those who think in a similar way to Deacon is that Reid sees natural selection as singularly conservative, whereas Deacon sees relaxed selection as one form of selection amongst many. In fact, Deacon may have contributed to anomalous selection by introducing the terms 'intraorganismic' and 'axonal' selection to neurobiology.

Reid's unusual perspective of natural selection is challenging, as it completely inverts what the term was initially conceived to explain – that is, speciation (transmutation), adaptation and evolutionary change. Nevertheless, there is an internal logical consistency to Reid's perspective: adaptive traits are only adaptations if they can demonstrate persistence. Moreover, the fitness of a particular organism, such as the crocodile, is only considered as fitness if the crocodile remains relatively unchanged for many generations. In fact, thinking of the literal meaning of the 'survival of the fittest', it is a very conservative metaphor. If the fittest manage to survive then there is little room for evolutionary change.

It is important to recognise that Reid is not simply invoking natural selection as a filter, nor does he ascribe natural selection as causal or as a force. Furthermore, he does not perceive natural selection as a Malthusian process or a process of accumulated beneficial mutations. Actually, Reid seems to think that balancing or normalising selection could be the most appropriate attribution of natural selection. He asks, 'what if, without prejudging alternatives, natural selection were better understood as the hypostasis (or imposer) of dynamic stability?' (Reid 2007 p407) On the other hand, he also considers the possibility that natural selection is limited to the descriptive, 'that selection theory is little more than a theory of demographics, or book-keeping.' (ibid. p67) This latter perception of natural selection as 'book-keeper' is consistent with the considerations earlier, when it was said that natural selection is a term that can be used to denote where some characters have proved favourable or unfavourable, but not neutral. Normalising and balancing selection, however, seem to claim more than just book-keeping; they represent the conservative, the antithesis of evolutionary change. This phenomenon might be seen as all the processes that ensure fidelity, which could include the intrinsic self-regulating and repairing that takes place to produce faithful replication or the external mimicry and learned behaviour that is passed down the generations unchanged or even the maternal protection of the young. The situation is more like 'whatever has proved sufficient to survive and reproduce in the past is more likely to do so in the future'. One could draw an analogy with the past cultural situation of China, when Confucian ideology self-perpetuated for hundreds of years, stifling innovation or change. Analogies can be dangerous, however, and one should not suppose that normalising selection is a force per se. To consider normalising selection as an 'imposer' would be misleading and tantamount to hidden teleology. Reid, on several occasions, does taint his otherwise exceptional analysis with terminology suggestive of teleology. However, it may be that when he writes of agency in natural selection, for instance, he is merely paraphrasing the terminology of some neo-Darwinists. The term 'natural experiment' within the title of Reid's last book could be construed as slightly teleological, as it sounds as if there is some body or thing called nature that is trying out novel biological experiments. For there to be an experiment implies an experimenter. 'Evolution by Natural Processes' might be a safer and preferable title. The problem of teleology is another long and vexed one, to be tackled in the next chapter.

Defenders of the causal power of natural selection have attacked Reid. Pigliucci (2009) admires the boldness of Reid's approach and accepts there are indeed many ways in which significant variation can arise independent of natural selection. Nevertheless, Pigliucci argues that natural selection is the only explanation there is for adaptation and moreover that Reid fails to provide an alternative explanation. One might question however whether Pigliucci has correctly or fully understood Reid's take on adaptation. Whereas neo-Darwinists such as Pigliucci see adaptationism to be of crucial importance in evolutionary explanation Reid sees it as unimportant, moreover, as non-evolutionary and as an effect of evolution, not its cause. The confusion here illustrates the contention in this thesis, that natural selection lacks a formal definition and leaves open uncertainty over natural selection's proper explanandum. In the next chapter we see Reiss argue further that attempts to answer the design problem by adaptationism is an unnecessary enterprise.

## Conclusion

It was noted that any explanation of explanation was a difficult and live philosophical issue with little consensus. Nevertheless, it was suggested that the *CM* model of explanation may be the one best suited for explanation within evolutionary theory. The next step in this long argument suggested that it was extremely important to be clear what the explanandum is before attempting any explanation. The inherent danger, it was argued, was that natural selection was employed to explain more than it should. For instance, both evolutionary changes and long periods of stasis could be explained by some variation of selection. Moreover, to compound the spectre of anomalous selection, it was observed that evolutionary change could be explained also by the absence of natural selection (relaxed or lifted selection). The anomalous nature of present-day selection theories has largely been caused by the empirical discoveries and advancement within biology. The scope of natural selection has been expanded to accommodate these advances, but this has created differences between biologists as to the exact explanatory power of natural selection. An important difference was identified in the type of explanandum being explored; one must be clear about what one is explaining: is it an emergent novel property and source of transformation or is it the preservation and ubiquity of traits that are said to facilitate fitness?

## Chapter 12: Explanation, Teleology and Anthropomorphic Language

*It is the primary function of every organism to pass on to the next generation as many copies of its genes as possible.* (Mogie 1992)

*Hearts are for pumping blood, eyes are for seeing, and so on.* (Perlman 2010)

Explanations in biology often appeal to form and function: what a thing *is* and what a thing *does*. Wings are made of hollow bone and feather and wings are *for* flying. Describing the form of a scientific object is relatively uncontroversial and can be settled largely by empirical investigation. However, describing the function of a scientific object in biology can be controversial. It is not that function itself is questioned; everyone agrees that organisms must function sufficiently to survive, before replication or reproduction is considered. The stronger claim is that biological entities are *for* something. For instance, hearts are for pumping blood and that is their purpose and the reason they exist, whereas the pulse produced by the heart is considered not to be *for* anything but just one of the consequences of the heart's function that does not entail advantageousness. Cummins (2009) and Cummins and Roth (2010), in criticism, have labelled this interpretation as neo-teleology. This can be compared with the more modest claims that hearts pump blood and wings enable flight; there is no requirement for the word *for.* There is huge difference between the following two observations concerning the biological clocks of organisms:

Clocks probably evolved several times *to* perform very similar functions, so they are an example of convergent evolution.

Clocks probably evolved several times *and* perform very similar functions, so they are an example of convergent evolution.

Although the only difference is the words *to* and *and*, the meanings are quite distinct. The latter is purely descriptive, but the former makes a stronger claim that entails some form of purposefulness. The controversy rests on whether the stronger claim can be justified. When one argues, for instance, that wings and feathers are for flight, is one arguing that wings and feathers are only for flight? If this is what is being proposed, then one runs into the difficulty of universal application – for example, penguins have both feathers and wings but neither are employed to facilitate flight.

On the contrary Wright (1973) argues in favour of neo-teleology. For example, the heart functions to pump blood but it does not function to make a thumping noise or provide wiggly lines on an electrocardiogram. To support this argument Wright draws an analogy with the telephone. The function of a telephone is communication but it also does other things, such as take up space, absorb and reflect light. These latter points are not functions but accidents, at least according to Wright. However, there are problems over the analogy between the telephone and the heart in a historical context. One can argue that a telephone was purposely designed by humans to fulfil the function of communication but not designed to absorb and reflect light. With the heart, however, there is no designer or purposeful intentions in nature to provide such a biological object. The analogy is a poor one because it overlooks that telephones were designed with a function in mind but the heart was not. Supporters of Wright might accept that hearts are not the product of any form of intentional design but nevertheless argue that with the heart there is an importance qualitative functional difference between pumping blood and producing a pulse. They may have a good point but how does one categorise such differences? The problem may lay with the word "function", Wright remarks that it has a spectrum of meanings. It is suggested below that there may be alternatives that might avoid controversy.

Teleological complications are largely absent in the harder physical sciences: stars radiate energy but stars are not considered to be *for* the radiation of energy; electrons absorb photons but electrons are not considered to be *for* the absorption of photons. Historically, scientific explanation was keen to distance itself from divine explanation that considered teleological explanation universal: a star such as the Sun was held to be purposely in place for the benefit of human beings; thunder and lightning were expressions of divine dissatisfaction (Russell 1940). In the biological world and according to Abrahamic traditions, animals were created by God for the benefit of humans. Moreover, the wonderful adaptations one can witness between creatures and Mother Nature could only be explained by divine special design. Darwinists, and in particular neo-Darwinists, took up the challenge in an attempt to provide a naturalistic explanation of this apparent good design. To a large extent, natural selection was the key mechanism that underpinned the naturalistic alternative (Millikan 1984, Godfrey-Smith 2010, Perlman 2010). 'Traits have evolved to function the way they do because of a past advantage' (Perlman 2010 p53). In other words Perlman believes functions arose by means of natural selection. Contrary to the 'selectionist' perspective, Davies (2001) sees functionalism as explanatorily valuable but detaches the historical component. 'Functions are contributions to systemic capacities and, while selection can preserve or eliminate those functions, selection is not the source. I also argue directly against the attempt to understand functions in terms of ancestral selective success' (2001 preface *xiii*). Functionalism in this latter sense will be endorsed and expanded upon in this chapter and later John Reiss's solution to the 'design problem' will be summarised. Before this ensues the 'artifact model' will be critically examined.

### *The 'Artifact Model'*

Lewens argues in favour of an 'artifact model', but does not see 'selection' as a necessary condition for functional explanation (2005 p101-102). The 'artifact model' is in favour of teleological explanation and claims that the methods one might use to examine an artifact can be also a valuable heuristic for the investigation of organisms (Ibid., p42-43). This view however rests heavily on artifacts being analogous to organisms and one might question whether this holds. For instance, the molecular components and structure are different; artifacts are made of plastics, metals, fabrics etc but organisms are not. Organisms develop, grow and change over time, their cells suffer apoptosis, and eventually an organism will die. None of these characteristics applies to artifacts. Organisms can reproduce, exchange genetic material, self assemble, change their behaviour, solve problems; again there is no similarity with artifacts. Moreover, when artifacts are designed they are normally intended to be as optimal as possible but the current 'received' view for neo-Darwinism is that organisms are far from optimised. Consider the case of the human eye; 'no intelligent designer would put such a clumsy arrangement in a camcorder, and this is just one of hundreds of accidents frozen in evolutionary history that confirm the mindlessness of the historical process' (Dennett 2005). Again concerning the eye and the difference between an engineer's view of design and what is produced by nature, 'it is the principle of the thing that would offend any tidy-minded engineer!' (Dawkins 1986, p. 93) There seemingly is another important incommensurable factor, artifacts are designed to meet a particular function or number of functions, therefore it can be said that here form follows function. However, in nature new forms emerge without a designer and are the consequence of unintentional physical interactions. The change in form of an organism may alter the functions available to that organism. A simple example; with metamorphosis the caterpillar is able to alter its functions dramatically when its form changes to a butterfly. Therefore, it can be said that in nature functions follow form, the opposite of the artifact chronology. It seems therefore, that there are serious problems with the 'artifact model', with too much dissimilarity for it to be considered a suitable model in the explanation of organisms. If anything, a converse model is more fruitful; we have seen how organisms function and note their form and then apply the principles to the design of artifacts. (Thompson 1942, Williams. C. 1995, Sachs 2007)

### *Anthropomorphic language: Time for reform*

Teleology is also prevalent within anthropomorphic language: genes are said to be 'selfish', 'competitive', 'co-operative'. There are also 'regulatory' or 'master' genes (no 'mistress genes' as yet). There are also instances in the literature of gene 'strategies' or evolutionary 'strategies'. Evolution is said to 'invent' or 'experiment' and sometimes evolution is said to 'select' or 'act' upon biological characters (Rennie 2010). Under these circumstances, evolution and natural selection sound suspiciously synonymous. Putting this latter concern to one side for the moment, the question here is whether the appeal to teleology is legitimate or desirable within evolutionary biology. One can take any of several perspectives on this. For instance, one might think the employment of teleology is justified when considered naturalistically[76]. Alternatively, one might think the employment of teleology is undesirable but nevertheless inevitable[77], a sort of necessary evil. At the other end of the spectrum, one might consider the employment of teleology both undesirable and unnecessary (Reiss 2009), '….it has been found that 'purpose' is not a useful concept when we are in search of scientific laws' (Russell 1968 p17). There is little likelihood of any consensus between any proponents of the perspectives outlined above but there may be an area of agreement. For instance, following Ockham, there is a broad agreement that scientific theories are preferred in the simplest form possible, provided there is no loss of explanatory or predictive power and that agreement is found over what constitutes the simplest form possible. Furthermore, there could be agreement that it is better to use explanatory terminology that is less inclined to teleology, provided again nothing of value is lost.

The reason for pursuing this course is that teleological and anthropomorphic language can be misleading. Take the example at the start of this chapter: *It is the primary function of every organism to pass on to the next generation as many copies of its genes as possible.* This quotation represents a popular view of evolutionary theory but it is unclear what exactly the word 'primary' entails. For instance, is it that primary functions shape or control psychological motivation or is it that psychological motivations can override these so-called primary functions? There is the problem that it could be interpreted in a manner that was not intended. It could imply, for example, that organisms have a primary goal or motivation where the purpose is to reproduce or replicate. This interpretation contrasts with the interpretation that more modestly suggests that it is just that inherited favourable traits within a population are more likely in the long run to be present in future generations, *ceteris paribus.* This more modest claim does not entail intentionality. Nevertheless,

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[76] Lewens (2005) provides a good overview of what he calls the 'received view'.

[77] Haldane's (1932) famous quip: 'Teleology is like a mistress to a biologist: he cannot live without her but he's unwilling to be seen with her in public.'

there is still an empirical problem. The claim is that passing on one's genes is the primary function of every organism, but how can it be established that it is the primary function? Moreover, is it the case for every organism? The case could be made that the primary motive for organisms is to survive, or to avoid pain, or to seek pleasure. Perhaps there is no single primary function but a collection. It might come as a surprise to many humans that their primary function is to pass on as many genes as possible, especially a surprise to non-heterosexuals. Perchance the best case that can be made is something along the lines that the motive for eating may be that one is hungry but the evolutionary function of eating is surely staying alive. This may be the case in this instance but there are still problems with this view. What would be the underlying evolutionary function of an alcoholic, a drug addict or a bungee jumper? People can be strongly motivated in areas that do not conform to simply passing on genes or trying to survive. The danger here is to reduce complex human behaviour to simplistic explanations. One must also bear in mind that although it is necessary for an individual to survive before one can pass on genes the converse is not necessary. That is, that an individual does not need to pass on ones' genes in order for that individual to survive. It is sometimes the case in the animal kingdom that parents put their own welfare before that of their offspring; they may abandon all their young or even consume them (Dagg 2005). Animal sexual behaviour is also subject to surprising diversity (Bagemihl 1999). Moreover, animals sometimes care for the young if it is not their own and sometimes even adopt and help rear young of unrelated species. In the microbial world, it is not uncommon for bacteria to divest themselves of parts of their genome in order to survive (Kassen and Rainey 2004, Ponciano et al., 2009). On empirical grounds, the premise of passing on one's genes where one can lacks the universality claimed. Furthermore, a gene is not a clearly individuated biological object with an unambiguous definition (Ch.2).

It is not only that such premises are shaky but also that, when combined with anthropomorphic language and excess of metaphor, valid arguments are difficult to maintain. The concern is also that metaphors can have the habit of sliding into unestablished facts. Reiss (2009) has argued that two basic reforms are necessary for evolutionary biology. The first is to 'retire Darwin's watchmaker'. Summarising Reiss, this entails a sufficing account of evolutionary theory to replace an optimising account. Moreover, there is no necessity to take up the chalice of the creationist and try to answer the question of 'perfect design'. Natural selection, according to Reiss, was the tool employed to replace the explanations of adaptedness by divine intervention. To Reiss however, such employment is flawed.

> Why do we need to 'retire Darwin's watchmaker?' Because we don't need him and we never did. If we accept a naturalistic world view, then we must accept that all organisms we see existing on the planet today are doing so only because they are satisfying the conditions for their existence. (Reiss 2009 p353)

The second major reform, to Reiss, is to replace the teleological language that underpins the optimising account of evolutionary theory and recognise that, in order for an organism to exist, all it needs to do is fulfil the conditions for existence. The term 'conditions for existence' was taken from Cuvier's 'meeting the conditions of existence' and is seen as a replacement for the term 'natural selection'. Reiss demonstrates how the teleological overtures within selective terminology can be extricated and offers his alternatives. Perlman's premise that traits have evolved to function the way they do because of a past advantage becomes an exaggerated and unnecessary claim under the auspices of Reiss. Traits function the way they do simply because they meet whatever the conditions of existence demand. Accepting this 'sufficing' account does have other advantages.

One could argue in favour of Reiss, that some traits, such as the regeneration of limbs or even the regeneration of two halves of a body once it had been severed, could be perceived as highly beneficial to the fitness of these particular organisms. Yet this advantageous trait was lost in many of the descendants that diverged from their ancestors (Bely and Nyberg 2010). This demonstrates that sometimes creatures can exist and reproduce by satisfying the conditions for existence even though they lost, over generations, what must be considered under Darwinism an extremely advantageous trait.

The sufficing account of evolution is therefore better suited to help explain the ‘endless forms’ of biological life and avoids much of the philosophical quagmire of neo-teleology, paradox and adaptationism. Reiss has undoubtedly contributed some valuable clarification and reform of evolutionary theory, but it must be recognised that he was not the first advocate. It was observed that Butler (Ch.1) argued that the term ‘natural selection’ be replaced by the less teleological and more appropriate term ‘meeting the conditions of existence’.

> I have said that there is a practical identity of meaning between ‘natural selection’ and ‘the conditions of existence,’ when both expressions are fully extended. I say this, however, without prejudice to my right of maintaining that, of the two expressions, the one is accurate, lucid, and calculated to keep the thread of the argument well in sight of the reader, while the other is inaccurate, and always, if I may say so less ‘convenient,’ as being always liable to lead the reader astray. (Butler 1882 p354)

Butler’s observation rings true: anthropomorphic and teleological language, although intended to make difficult concepts clearer, often has the opposite effect and ‘leads the reader astray’. When constructing valid arguments in logic, there is a rule that stipulates that the premise must be as unequivocal as possible and without ambiguity; if a premise is ambiguous, it should be rewritten to remove the ambiguity. This approach should be applied to arguments employed within biology. For instance, when one says that the heart is *for* pumping blood, one is opening up a range of issues that are not there if one simply asserts that hearts pump blood when they function. One must recognise that a heart is still a heart even if it is no longer pumping blood. The function of the heart on the butcher’s cold slab, it could be said, is to provide the vendor with an income. A pack of wolves might see the purpose or function of the sheep’s heart as the provision of a healthy meal for the alpha wolf. One might argue however that function explains existence, i.e. that pumping blood explains why the heart is there. There should be some care here, more accurately one can say the heart is *preserved* as it plays the vital role of pumping blood but this gives little clue as to how the heart evolved or emerged. The importance of emergent and preserved causes is discussed in the following chapter.

When one thinks comprehensively of what an object *does*, there is rarely a singular function and usually the function is context sensitive. Rather than talk of the function of a biological object, it may be preferable to borrow some terminology from physics and refer to the *dynamics* of an object. This sidesteps the problem of teleology and respects the fact that an object’s dynamics might alter in different situations. Under such a recommendation, there is no need to describe genes as ‘selfish’ or ‘cooperative’; all one need do is describe the dynamics of genes or gene networks in the context of development stages or the relationship with the cell and its components. It may also be more desirable and accurate to talk of ‘interactions’ between biological items rather than to talk of ‘forces’. The term ‘natural selection’ also carries an element of teleology if taken literally. It might suggest to some that nature has a preference for certain biological qualities, which further implies that nature is some body or force with intention. This of course is nonsense: nature is not a force, body or super-organism; nature does not have foresight, but then neither is it 'blind'. Darwin's 'blind watchmaker' is not simply a case of extravagant metaphorical language; it is an inaccurate and potentially misleading metaphor. Watchmakers blind or sighted still have intentions, whereas nature has none. The temptation is to reify processes as objects. All the interactions, reactions, combinations, dissolutions and processes that occur in the universe result in the formation of stars, planets, black holes etc. There is not any requirement to suggest these objects are of marvellous design or selected (although one may still wish to perceive such items as marvellous).

It was noted in Chapter 5 that some people thought neo-Darwinism should be extended to other scientific disciplines. A danger with this move is that neo-teleology could also be exported to the physical sciences. One might then argue that it is not the case that *the* S*un radiates energy* but that *the Sun is <u>for</u> the radiation of energy*. Or, as another example, *black holes are <u>for</u> the absorption of matter* rather than the description currently used, *black holes absorb matter.* One might be tempted to go further still and argue that the existence of the Sun can be explained by past advantages and that it was selected from a range of other possibilities. Someone might then ask, 'Is it the Sun that is being selected or is it the atoms that compose it that are selected? Or does selection operate at all levels of cosmology?' One might think this scenario absurd, but this type of reasoning is already being advocated and applied (Ch. 5). If this propagation of neo-Darwinism is not checked, then science could be lumbered with the same confusions and lack of clarity that blight some of evolutionary biology today. All the philosophical problems that arise from neo-Darwinism, and in particular anomalous selection, would be transferred to physics et al. alternatively, this terminology, tinged with teleology, can be discarded by the neo-Darwinist without compromise to the theory. One could still argue that the series of advantageous genetic alterations eventually result in transformation. It would be less teleological to say the processes of advantage *produced* or *gave rise* to any such transformation than to say these results were selected. It is preferable therefore to talk of evolution by natural processes than evolution by natural selection.

## Conclusions

In the last chapter, an important difference was identified in the type of explanandum being explored in evolutionary biology; one must be clear about what one is explaining: is it an emergent novel property and source of transformation or is it the preservation and ubiquity of traits that are said to facilitate fitness? Most of the discussion concerning teleology is only applicable to the latter explanandum and has little or nothing to say about the sources of variation. Some have called for reform and some have argued that natural selection should only be considered as an explanation for stasis, inverting its earlier *raison d'être.* Other reformers have considered the teleological problems inherent in neo-Darwinism, suggesting alternatives to the terminology of selection. It was argued here that much of the problem concerning teleology and anomalous selection could be avoided if one thought of evolutionary explanations in terms of different processes that 'suffice' rather than optimise. Not only would this call for evolutionary pluralism be consistent with the *CM* model of explanation, but it would also open up areas of research that have previously been omitted from evolutionary theory. This idea is not new: Darwin had recognised that there were factors other than natural selection at play; Mivart (1871) had criticised Darwin for putting too much emphasis on natural selection. But Darwin and Mivart did not know what we know today. It is now time to observe how evolution by different natural processes can resolve many of the philosophical and biological problems that stem from anomalous selection.

## Chapter 13: Evolutionary Pluralism

So far, this work has surveyed many of the debates and problems that pervade evolutionary theory in relation to natural selection. The overall perspective has been rather critical and perhaps fairly negative. Now is the time to present something more positive and that is, hopefully, a more coherent account of evolutionary theory that avoids many of the philosophical problems encountered so far. It will be suggested that this can best be achieved by extending a pluralistic approach. However, this will not be sufficient. On the one hand, it is recommended that the selective terminology is replaced with the less anomalous and demanding principle of 'meeting the conditions of existence'. On the other hand, evolution and origins by means of natural selection is substituted by evolution and origins by means of natural processes.

It should be acknowledged that evolutionary pluralism is not a new concept; Darwin was a pluralist who recognised factors other than natural selection to explain evolutionary changes. Today, one has the advantage over Darwin: biological science has progressed enormously, filling in many of the gaps that were groped at by the Victorian naturalists. There was very little understanding of the causes or sources of variation that natural selection requires. Anyone who is in the fortunate position of being able to read widely across all the fields that are embraced nowadays under the 'life sciences' can appreciate the many ways in which evolution can and does occur. Apart from the major transitions, what is also striking is the diverse methods of change that can be seen at the different taxonomic levels, sometimes exclusively at a particular level. For instance, the fruit fly *Drosophila melanogaster* has been extensively examined and wider extrapolations have been made to explain how evolution occurs. However, one has to be careful for it is now known that the fruit fly does not methylate its DNA but that the honeybee, plants and placental mammals do (Carey 2012 p285). There is conjugation between prokaryotes only, meiosis is practised between eukaryotes but not by bacteria or *Archaea* (Madigan et al., 2011). Moreover, the form that initiates meiosis is different too: fungi produce spores but mammals produce sperm. Unexpectedly, female sharks and komodo dragons in captivity have produced viable offspring by parthenogenesis (Watts et al., 2006).

Allopolyploidy occurs in eukaryotes and is particularly common in plants (Soltis et al 2010); hybridisation is more frequent in *Animalia* than previously thought (Ch.7). Further to this variety, there is symbiogenesis – special relationships between members of different kingdoms that produce new forms of life. Examples of this include *Elysia viridis*, the sea slug that is able to incorporate algae and effectively photosynthesise like a plant, and the diverse forms of lichen (Trench et al 1974). 'Higher' organisms are composites that share and carry other organisms, more akin to a micro ecosystem than strictly individual (Madigan et al., 2011). Finding a singular formula to embrace such a wide range of evolutionary variety is difficult. Attempts to embrace all have resulted in a principle so wide and general that it invites criticism of vacuity. The enigma of nature is the great diversity on the one hand and the converging patterns and pathways that provide this on the other. A possible solution is therefore to recognise a plurality of evolutionary processes amenable to empirical scrutiny and testing. What should be considered? Evolutionary pluralism could embrace the processes documented during the twentieth century – drift, allopatric, sympatric and parapatric speciation etc. – but also incorporate many other features that are beginning to be recognised and included within the 'extended evolutionary synthesis'. Additionally, it will be suggested that consideration should also be given to the inclusion of the structuralist agenda.

## The Cost of Extending Evolutionary Theory

Recognising and adding these new processes to an extended synthesis is not without issue; it would arguably have its detractors and there are always conservatives who resist change. Moreover, there is a debate over which processes should be included and which should be excluded (Pigliucci 2007, Pigliucci and Muller

2010). This situation is to be expected; it was demonstrated earlier how many of the evolutionary processes or factors that were seen as being outside and even contrary to neo-Darwinism were eventually 'Darwinised' (Ch.2). Convergence, seen as a foil to natural selection by Mivart (1871) in the nineteenth century was embraced as an example of natural selection in the twentieth century. Mendelism and mutation theories were seen as non-Darwinian at first but were brought into the 'modern synthesis'(Ch.2). Wagner and Dixon (Ch.1) saw evolution in segregated or island populations as examples of evolution without natural selection; Mayr embraced the phenomenon, calling it allopatric speciation and seeing it as an example of natural selection (Ch.2). Symbiosis and symbiogenesis were perceived outside and insignificant to the modern synthesis, but they were later embraced and seen as subsumed under natural selection by its modern-day protagonist, Margulis (Ch.7). Hybridisation was discussed by Darwin as an alternative mechanism to natural selection, although eventually rejected by both Darwin and the modern synthesis architects as unimportant. Latter-day proponents of hybridisation as an evolutionary mechanism (Arnold, Mallet) see it not as Darwin saw it as a separate process distinct from natural selection but as a process where the products are subject to natural selection (Ch.7). For almost a century, developmental biology was perceived by nearly all neo-Darwinists as having nothing to say about evolution, but now it is seen by all but the most conservative of Darwinists as important (Gilbert and Epel 2009). Today, the products of development are seen as subject to natural selection, but embryologists at the end of nineteenth century saw their discipline as having promising explanation for evolution but nevertheless being distinct from natural selection (Bateson 1894).

There is something of a Kuhnian pattern here. In the last century, many novel processes of evolutionary significance were discovered or identified that were considered outside the paradigm. These were seen as anomalies and rejected, sometimes with outright hostility. McClintock, who discovered transposons, was treated with such severity, working alone and isolated from the Darwinian community (Comfort 1999). Eventually, she triumphed and won a Nobel Prize, and her work was absorbed into the paradigm as if it had always been there. This is not an atypical example; many have suffered rejection and not always with a consoling ending. Kammerer ended his life by suicide after being accused of fraudulently manipulating his experiments, which purported Lamarckian acquired characters. Today, his work is being re-evaluated more sympathetically and it is being asked whether he should be considered a founding figure of epigenetics (Vargas 2009). Waddington and Goldschmidt were two mid-twentieth-century figures who paid the price for stepping outside the perceived boundaries of evolutionary theory. Waddington found that he was not invited to major conferences and Goldschmidt[78] was mocked and his work caricatured with the adage 'hopeful monster'. Waddington today is recognised as an important figure in both the fields of evolutionary developmental biology and epigenetics (Gilbert 2000, 2003). Goldschmidt's theory is undergoing re-evaluation; it is now known that many mutations are not exclusively 'single point' and that chromosomes can be considerably rearranged without being maladaptive. The early Russian advocates of symbiosis received short shrift from the architects of the 'modern' synthesis (Khakhina 1993), and the latter-day champion, Margulis, found her attempts to reintroduce concepts of symbiosis and add symbiogenesis to evolutionary theory resisted with hostility. Today, these concepts feature in many evolutionary and ecology textbooks. Kimura's (1983) neutral theory of evolution was 'laughed out of court' (Crow 1995 p4) when introduced as an alternative to neo-Darwinism. This has now been incorporated within the paradigm but there is still discussion over the full weight of its explanatory power. The underlying reason for such hostilities seemingly

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[78] See Nature News for an overview: http://www.nature.com/news/2010/100217/full/463864a.html

is that these new insights undermined the view that evolution was explained only in terms of natural selection 'acting' upon small mutational changes. [79] As, Gould (2002) demonstrated there was a hardening within the modern synthesis around the middle of the 20th century, toward adaptationist explanation and against the evolutionary pluralism that was popular beforehand.

There are also some people who have not been accepted into the 'mainstream' but who are nevertheless evolutionists. How often does one hear the disingenuous charges from critics – 'they fail to truly understand evolutionary theory' or 'they should stick to physics'? Is it fair to apply this criticism to the following? Steele (1998), who has spent 25 years trying to convince everyone that the Weismann barrier is penetrable; Jablonka and Lamb (1989, 2005) who have also been advocates for Lamarckian behavioural inheritance; and the most intriguing omissions, the two evolutionists who have been examined in this work, Thompson and Lima-de-Faria (Ch.9). The neo-Darwinian response to these two has been quite different but in both cases quite disturbing. Thompson's *On Growth and Form* has been heralded as a classic of evolutionary biology by a wide range of academics, including some neo-Darwinists, but has never been incorporated into the literature of the paradigm. Why is this so? Fox Keller (2002) has suggested that Thompson's reluctance to engage in genetics is the main reason his work has been passed over. There could be however, another explanation. Comparing the first edition of *On Growth and Form* (1917) and the 1961 abridged edition, there are some serious but illuminating omissions in the latter; many of the references critical of neo-Darwinism and supporting direct adaptation have been removed (pages 86–87, 221–222, 537–541, 664, 888–889, 1022, 1092–1094). Two representative examples of cuts should suffice:

> In short, nature proceeds from one type to another among organics as well as inorganic forms and these types vary according to their own parameters and are defined by physio-mathematical conditions of possibility. (p1094)
>
> Our geometrical analogies weigh heavily against Darwin's conception of endless small continuous variations: they help to show that discontinuous variations are a natural thing that 'mutations' or sudden changes, greater or less – are bound to have taken place, and new 'types' to have arisen, now and then. (p1094)

Why should Bonner edit *On Growth and Form* in such a manner that it misrepresents Thompson's intentions and main arguments? One does not have to go far to discover the answer, for Bonner provides it within the editor's introduction. To be fair to Bonner, he does acknowledge that Thompson is critical of natural selection, seeing it as a negative force, and that Thompson does prefer the alternative explanation of direct adaptation by means of physics. However, without blush, Bonner states how this can be rectified: 'let me briefly show how the heterodoxies of D'Arcy Thompson can be easily transformed into orthodoxy'. Bonner then proceeds with an 'orthodox' account of neo-Darwinism that subsumes Thompson's arguments under natural selection.

The emasculation of Thompson's critique of natural selection by Bonner is a different treatment from that received by the other major structuralist considered in this work, Lima-de-Faria. How is it that such an

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[79] It is not only those that are seen to undermine the explanatory power of natural selection that offended neo-Darwinists. Woese discovered the third kingdom of *Archaea*, which is now recognised and standard textbook material. However, this recognition was not without a struggle against the neo-Darwinian establishment. 'The hostility', Woese said, 'was shocking'. 'Others soon followed, crossing boundaries of common courtesy by making fun of Woese. He was called a crank and a crackpot, being neither a microbiologist nor an evolutionist.' (Korthof 2009.) Woese's background is in maths, physics and biophysics.

erudite and prolific geneticist, who has committed his life to his work, is virtually unheard of in Anglo-American academia? Why is it that there are no scientific reviews of his books and no philosopher to date has conducted a critical evaluation? Scouring the internet, there is only one review of one of his books to be found, and that is negative (Korthof 2011). This 'review' is very concise and does not explicate the fundamental ideas involved in 'autoevolution'. Curiously also, *New Scientist* declined to publish a paper Lima-de-Faria had written on natural selection. He has said, 'when *Evolution without Selection* was published I expected a backlash because I had challenged neo-Darwinism but I was wrong, I never heard a thing, it was a stone wall of silence' (2009, private conversations).

What should one make of these treatments? Without equivocation, they are totally unacceptable. One of the worst things for a researcher is to spend his or her life in scientific enterprise, only to be humiliated by lack of recognition or to suffer personal innuendo. Moreover, this type of behaviour goes against the ethos of science. As Popper (2007) says, science must welcome new and bold conjectures that will be subject to critical scrutiny. One expects a degree of scepticism from the establishment towards new ideas – that is normal in any discipline – but one should not be party to the ostracisation of individuals or subject them to ad hominem attacks. There is also lurking the danger that genuine and valuable contributions are stifled or missed. This is another reason why evolutionary pluralism is preferable to evolutionary monism. Lima-de-Faria's early work (1983) anticipates many of the biological realisations of the late 1990s and the beginnings of this century. Briefly, for this has been covered earlier: he argued that many genes were homologous, rather than accepting the popular perception that evolution took analogous pathways; and that the gene and the chromosome were only the parts of a wider network, rather than taking the gene-centric and reductionist view. One might contend, this anticipated the core views of modern systems biology. Moreover, Lima-de-Faria argued that development of the embryo or larva was of evolutionary significance, anticipating much of evo-devo. He also provided much discussion of a major topic today, canalisation – the relationship between order and plasticity. Hedging all this is caution: Lima-de-Faria (2003) advises that there is still much that is not understood about the chromosome, especially in relation to the centromere and the telomeres.

One could argue that Lima-de-Faria is ahead of his time and this may be one of the reasons his work has never been embraced or 'Darwinised'. Moreover, Lima-de-Faria sees his work as a direct challenge to neo-Darwinism and not without some abrasion. Under such circumstances, neo-Darwinists, rightly or wrongly, are much less likely to be receptive to Lima-de-Faria's novel hypothesis. Moreover, it may not be possible to incorporate these ideas into a selectionist framework. For whereas structuralists see a fundamental ordering in nature, with patterns and regularities the direct result of physical law, the neo-Darwinist postulates unpredictability[80] behind the variation for natural selection to 'work on' (Mayr 1984, Gould 2002). Nevertheless, there may be scope for some form of reconciliation within a new concept of evolutionary pluralism. Mendelism, for instance, is an *ordered* system of inheritance that at first was seen as a challenge to Darwinism because of its deterministic nature[81], only to be incorporated at a later date in the 'modern' synthesis. Evolutionary pluralism should recognise that many of the structures in the biological world are

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[80] Gould (2002) argues that if the ticker-tape of life was re-run then life would in all probability look very different because of randomness. He argued further that randomness thwarted prediction, a view challenged later by Conway Morris (Ch.4)

[81] See Wallace letters to Read 1909, reprinted in James Marchant, 1916. Letters and Reminiscences (New York: Harper & Brothers, p. 340. Wallace expresses his concerns over the 'rigidity' of Mendel's mechanisms of inheritance.

founded directly from physics, chemistry, topology and even complexity theory without recourse to selectionist hegemony. Kelly (2010), a proponent of convergent evolution, illustrates this point:

> But a hundred, or thousand, cases of isolated significant convergent evolution suggest something else at work. Some other force pushes the self-organization of evolution towards recurring solutions. A different dynamic besides the lottery of natural selection steers the course of evolution so that it can reach a remote unlikely destination more than once. It is not a supernatural force, but a fundamental dynamic as simple in its core as evolution itself. Evolution is driven toward certain recurring and inevitable forms by two forces of convergence: 1) The negative constraints cast by the laws of geometry and physics, which limit the scope of life's possibilities. And 2) The positive constraints produced by the complexity of interlinked genes and metabolic pathways, which generates a few repeating new possibilities. (Kelly 2010)

A proponent of natural selection might retort that convergent evolution is actually a product of natural selection, where environments are similar one would expect similar features and this is best explained by natural selection at work. The difficulty with this reply however is that even if it were true it overlooks the fact, as demonstrated by Conway Morris, that convergence occurs also in environments that are quite dissimilar. Moreover, many convergent features of unrelated organisms are neutral as to fitness. What then is the casual factor in these instances? Again, another defender of natural selection accepting that convergent evolution is the product of physical law might say that natural selection is secondary, and acts on the products of convergent evolution. Of course without a formal definition of natural selection one does know if convergent evolution is caused by natural selection or if natural selection simply acts on the products of convergent evolution. Or perhaps natural selection is both the producer and the filter?

The danger to be thwarted is that every biological phenomenon (and physical phenomenon) becomes subsumed under natural selection, which does not strengthen the explanatory power of natural selection but dilutes it. A theory that explains everything is likely to explain nothing. For example, what is to be avoided is that the explanations for the *Bauplan*, other symmetries, auto-assembly and autocatalytic processes become subsumed under natural selection. The 'explanation' for bilateral symmetry would then be that bilateral symmetry was selected because of advantage and therefore one could coin the term 'symmetry selection'. When asymmetries arise, as in the case of the fiddler crab or the narwhal, one could coin the term 'asymmetry selection' as the alternative explanation. This would be explanatorily vacuous and symptomatic of anomalous selection. One might think this practice of subsuming order under natural selection absurd, but it has already taken place. Orthogenesis was conceived as a direct intrinsically evolutionary process that was immune from natural selection, but this did not stop the coining and application of the term 'orthoselection'(Ch.4).

Darwin divorced natural selection from other processes. Sexual selection accounted for the traits that could not be construed as advantageous; use, disuse and habit accounted for traits that materialised in the absence of Malthusian struggle; Lamarckian mechanisms could assist natural selection or work independently; and so forth. (Ch.1. Appendix 1) The important point here is that Darwin advocated a plurality of processes, each independent and not necessarily subsumed under natural selection. Today, there is knowledge of many more processes of modification, some through descent and some through reticulate evolution, not to forget speciation through various forms of symbiogenesis. There are many advantages to be had from recognising all of these documented processes as processes in their own right and not confusing them with natural selection.

## Why Evolutionary Pluralism Could Be Desirable

It is demonstrated here how the problems that have afflicted natural selection can all be avoided by some simple changes to terminology and our conceptual framework.

### *Two key stages of evolutionary theory*

There is no tautology problem within pluralistic evolution. Research is firmly on empirical grounds or within competing hypotheses. Causal processes can be identified that lead to evolutionary changes. These changes then prove at later stages to be sustainable or not. To break the charge of tautology one must regard the points of address in two stages. The first explanandum is the cause or causal processes responsible for an evolutionary change to the status quo; the explanans for this can then be identified – for instance, it could be mutational change/s, an epigenetic effect or a hybridisation event. The second explanandum regards the sustainability of these new evolutionary changes; the explanans in this instance provides an account of why the change might improve or decrease fitness, or simply meet the conditions necessary for continued existence. Such an account might include considerations of predator–prey relationships, sexual selection, climatic conditions, resource availability and so forth. What is important here is that the explanantia are not conflated. The explanans that addresses the ‘second’ stage – that is, the ‘sustainable or not’ stage – should not be employed to explain the first stage, which is the origins of the emergent property or properties. As an example, sexual selection should not be addressing emergent properties. Sexual selection is a second-stage explanans that endorses (or perhaps sends to extinction) any first-stage emergences. A long-tailed bird, for instance, might appear attractive to members of the opposite sex and this may indeed lead to increased numbers of birds with long tails in subsequent populations. However, this does not and cannot explain how the long tail emerged originally, which thus cannot be explained by sexual selection.

It is recommended, then, that this aspect of evolutionary theory recognises two important and distinct phases, first the question of origins and thereafter the question of sustainability. Both stages require their own particular and relevant explanans and they should not be misappropriated. To do so is to commit to the fallacy of correlation and to confuse the causal chain. Thus the charges of tautology and that evolutionary theory is not testable are easily refuted. This separation, it is suggested, can only be achieved by avoiding recourse to misleading catchphrases such as ‘survival of the fittest’ and resisting the temptation to reduce complicated evolutionary details to tautological statements, propounded by Sober (Ch.2) - *Trait X is fitter than trait Y if and only if X has a higher probability of survival and/or a greater expectation of reproductive success than Y.* The tautological nature of this ‘principle of natural selection’ was discussed (Ch.2) but now one can hopefully see a resolution to the problem. It is that the principle as outlined above has nothing to contribute to the explanans for the first-stage explanandum of evolutionary theory.

### *Levels of selection*

Structuralists such as Reid and Lima-de-Faria are not generally concerned with the problem of ‘which is the level or unit of selection?’ This problem is seen to be a consequence of incoherence within neo-Darwinism.

‘Selection’, strictly by its definition, is only causal in the sense of confirming or disconfirming. The real work, which is of explanatory interest, focuses upon the generation or emergence of *de novo* features that constitute the enormous diversity of life. With appreciation of this point, it is suggested that the ‘levels or units of selection’ debate need not apply to evolutionary pluralism. The debate over which level natural selection is said to apply or ‘act’ upon is voluminous and something of a philosophical quagmire that sucks one in. Once one enters or commits to it, it is extremely difficult to get out. Part of the problem is that the term ‘selection’ as it stands at the moment is anomalous; there are many ways of perceiving its attributes and application. It has never received a formal scientific definition. Natural selection could be construed as causal, non-causal, preserving, eliminative, descriptive, a universal law of nature, a filter or filtering process, a process, a mindless algorithm, a universal acid, honing or sculpting and so forth. Before entertaining participation in the ‘levels of selection’ debate, one should really be clear about what sense of natural selection is the appropriate sense. Unfortunately, this task is extremely difficult and, even if some clarity were achieved here, there is no guarantee it would meet with consensus. One would never be sure that one’s interlocutors were of the same mind and the validity of any argument could soon be lost. Philosophers and theoretical biologists have entered the discussion assuming that natural selection needs tweaking (Ch.2), but unfortunately this is not enough.

Evolutionary pluralism has an advantage here, for it can bypass the quagmire without any loss of explanatory power. For instance, selection, by definition, must occur only when there are already in place pluralities of things that can then be selected. Selection therefore cannot apply to singularities; it requires differentials. Variation precedes selection. Therefore the first phase of evolutionary change identified earlier can be considered independent of natural selection. To illustrate this take, an uncomplicated example. The classic study of finches on the Galapagos has been pursued admirably by the Grants (2008). They have been fortunate to discover a speciation event, a new species of finch never in existence before. Closer examination morphologically and genetically has shown that the new species of finch is a hybrid of two other species. This speciation event by hybridisation is a clear example of a causal first-stage process that has no recourse to natural selection. In other words, identifying and verifying the hybridisation event explains the speciation. The situation with the second stage is somewhat different. For instance, it is not known how the newly arrived hybrid finches may fare. They may only survive for a few generations before becoming extinct. On the other hand, they may have some attribute of hybrid vigour that enables them to extend their numbers. Alternatively again, they might just exist alongside the other finches without significantly increasing or decreasing the strength of their population. They may even introgress with the parent population and slowly lose their identity. Who knows? No one can predict with certainty; a long period of drought or some other natural disaster might sweep them away forever. Where is it during the second stage that natural selection might act? Moreover, would it make sense to consider the issue of ‘which level’ selection is acting upon during the second stage? Natural selection, similar to any other theory, has no power to predict the fate of the finches. It seems therefore that natural selection can only look retrospectively, describing the events once they have happened. The problem here, though, is that natural selection does not seem to carry much explanatory power if all it is thought to be doing is mapping events. It seems a little superfluous to declare that if the finches increase their numbers then they are ‘selected for’, or if the numbers decline and they go extinct then the finches are ‘selected against’, or if the numbers barely move then the finches are subject to ‘stabilising selection’. One is not much wiser, for if the finches were to increase or decrease numbers, what one is really seeking is an explication of the causes. Once again, recognising plurality here, there could be a variety of reasons as to what determines the finches' fate. One could argue that all the different reasons that determine the fate of the finch collectively constitute natural selection. However, the problem is that as the term 'natural selection' is so ambiguous and poorly defined then it is recommended that one refers directly to the cause or causal process.

If one also observes that evolutionary events do not necessitate selective advantages and adopts the more sufficing account, then there is little requirement to pose the 'at which level?' question. Whatever the process of the emergent property is, it is not necessary to assume eventual advantage or disadvantage in all situations. To be of evolutionary interest, the change must entail that the affected population meets the conditions of existence.

*Evolutionary pluralism and heredity*

The importance of descent with modification in principle is uncontroversial; however, the details of the matter are not. Following the concerns of 'which level of selection?', there is another issue, which links and touches on too narrow a perspective. As observed, the early population geneticists sought explanation by examining changes in gene frequencies and then extrapolated to explain changes to the phenotype. This methodology was seen by some later neo-Darwinists to suggest that evolutionary problems could be resolved if the level of selection was fixed at that of the gene (Williams 1966, Dawkins 1976). The merits of adopting a gene-centric approach have already been discussed. What is important here is that, if one were to look solely at any changes to genomes during heredity, then this would preclude other areas of research that also have evolutionary implications. Arguably, organisms do not only inherit genetic material; they also inherit the cell and all its qualities and the bacteria that eventually occupy many parts of the body. The significance of the 'maternal effect' on future generations, which recognises the importance of the yolk during early development, has already been noted. There are also at least two other factors of significance but these have received little attention. The first is the qualitative nature of the cell and particularly the membrane one inherits. Crawford and Marsh have researched this perspective and argue:

> From the evidence we have presented, it is difficult to regard substrate-driven change or plastic heredity as a trivial force as it seems to have been behind many of the great evolutionary thrusts, including the origin of life, the nature of the first living forms, the emergence of oxygen breathing animals and the shaping of our own species. (Crawford and Marsh 1989 p247)

In 'substrate-driven', the authors include all the conditions of the environment that impinge upon the organism that may directly affect how genetic material is expressed. Particular consideration is given to the importance of nutrition in shaping morphology.[82] For instance, the evolution of vertebrates from soft-bodied ancestors included a mineralisation process that can only be fully understood if one examines the nature of the chemicals ingested or absorbed. Crawford and Marsh consider many similar examples and conclude that much of what is thought to be unpredictable by neo-Darwinism is actually determined directly by the environment and availability of resources and therefore offers the possibility of some predictive capability. There can be no evaluation here of whether the empirical observations are correct, but Crawford and Marsh

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[82] See also Blumberg (2009 pp182–187) for a modern endorsement of the 'more than simply genes' approach.

present a plausible and clear example of evolutionary pluralism that coheres with the main proposals of structuralism.

The second factor that has been given little attention concerns recognition of molecular accretion in the evolution of complexity. Thims (2005) has drawn up a ‘Molecular Evolution Table’ (see Appendix 5), which illustrates a novel perspective of the earliest stages of cosmological evolution through to the evolution of humans. The table shows when new combinations of molecules have accrued and produced the complexities and diversities in nature. The lesson is that phenotypes are more than reflections of genotypes; molecular qualities are also acquired. The arguments presented by Thims and by Crawford and Marsh illustrate well the first stage of evolutionary processes that explains the major transitions and emergence of new forms. There is opportunity here for research programmes that could have great explanatory value for evolutionary theory.

### *Drift versus natural selection*

There is a temptation to view and try to explain evolution in just two ways: either it is natural selection at work or it is some form of drift. Unfortunately, this narrowness precludes other interpretations and seems to focus solely upon the role of micro evolution.[83] As witnessed, there are many other viable processes that can be considered; it is not necessary to recite these again. One does have to be careful, though, when talking of drift. Naegeli and Darwin[84] were discussing the neutral traits of the phenotype, whereas the debate since Kimura’s *Neutral Theory of Molecular Evolution* has addressed the importance of intrinsic changes to proteins and amino-acid sequences etc., which may not necessarily be observed in phenotypes. Both drift and selection recognise that the causal element in explanation is random small mutational changes, but they see the effects differently. It is said that drift describes the changes that arise from the mutations that do not alter fitness whereas selectionism describes the advantageous or disadvantageous changes to fitness. Advantageous changes could lead to adaptation but disadvantageous changes could lead to extinction. It can be appreciated that drift is a sufficing account of evolutionary change but selectionism demands more. For example, one could argue that if there is continuous drift within a population that has separated from its ancestral population, then the accumulation of changes to a phenotype could lead to creatures that no longer share similarity with the ancestral population. In other words, a sufficing account of allopatric drift could explain speciation without recourse to natural selection.

### *Gradualism and natural selection*

Evolutionary theory that resides in gradualism has often been criticised on the grounds that there are gaps in the fossil record or a lack of evidence of intermediate stages between species. (Carroll.R 2000 p27, Eldredge & Tattersal 1984 p45-46, Gould 1982 p189) However, this criticism cannot be directed at evolutionary pluralism. It is only a problem for those neo-Darwinists who insist that evolutionary changes exclusively culminate gradually from a series of small mutations, shepherded by natural selection. This incompatibility with palaeontology requires a further hypothesis that argues that the fossil record is incomplete because fossils are rare and difficult to preserve and that otherwise gradualism would be demonstrated. The problem

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[83] See Amundson (2007) for a discussion of the importance of development in evolutionary explanation.

[84] See Chapter 7 of the sixth edition of the *Origin*. Darwin clarifies and admits to the existence of neutral traits.

with this reasoning is how can one be sure that gradualism would be demonstrated? Is it because the gradualist theory demands it? This would be circularity and one would be open to the accusation that the facts are being tailored to fit the theory. Fortunately, the situation for evolutionary pluralism is not problematic; under its auspices, one would expect a discontinuous or episodic fossil record. Evolutionary pluralism recognises that gradualism is not a universal phenomenon and that there are many evolutionary routes, some of which may be rapid and others slow. (Russell et al 2008, Janzen & Etienne 2012) Lateral gene transfer (Shapiro 2011), symbiogenesis (Margulis 2001) and hybridisation (Arnold 2006, Soltis et al 2010) are examples of rapid evolution and may explain why the fossil record appears to be discontinuous.[85] Evolutionary pluralism does not deny that changes can also occur slowly through mutations, but it should recognise that, because of the extremely long time scales involved, empirical verification of causal chains is much more difficult to establish than the causal chain of, say, a polyploidy or hybridisation event. If one takes a strictly monist view of evolutionary change, then is not one likely to preclude other avenues of research that may resolve the criticisms directed at evolutionary theory?

### *Non-synonymity of evolutionary pluralism and evolution*

In attempting to extend the explanatory powers of natural selection, one unwittingly creates anomalous selection, which has become difficult to distinguish from ‘evolution’. Without a null hypothesis, selection and evolution can become synonymous and, of course negate any explanatory influence. One reads on occasions that evolution ‘selects’ or has a ‘strategy’ or ‘favours’, which are terms normally applied to natural selection (Nichols 2011). Evolutionary pluralism, on the other hand, avoids this conflation. The objective is to identify the particular causal process that resulted in the evolutionary change. The process explains the evolutionary event. The principle of the matter is simple to comprehend; the details and the research will often not be.

### *Evolutionary pluralism and the reification fallacy*

With evolutionary pluralism, there is no danger of some ‘thing’ – such as an indefinable material force, pressure or filter – appearing in any explanation. If the research is based upon the *CM* model of explanation, then one identifies the causal physical processes thought to be involved. Of course, one must be clear what the explanandum is that one is trying to explain. For example, is it a question of emergence or is it a question of demographic distribution once the character has emerged?

### *Evolutionary pluralism and abiogenesis*

One important reason for incorporating the structuralist perspective within an evolutionary pluralistic account is that it provides continuity between abiogenesis and evolutionary theory which is currently missing. There is a persistent attack from outside the parameters of science to suggest that evolutionary theory fails to account for the origins of life in the primordial soup. However, this can be refuted by recognising that biological evolution is not divorced from general or cosmological evolution but is subsumed within it. The

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[85] See also Venditti, C., Meade, A. & Pagel, M. (2009.Nature advance online publication doi:10.1038/nature08630) whose research undermines the ‘Red Queen Hypothesis’.

order, regularities and symmetries observed in the physical and chemical evolution of the universe do not disappear when it comes to biological evolution on earth. To understand the structure of the basic molecules or building blocks of life, such as the cell, the proteins and DNA etc., one has to examine the topology in relation to tensegrity and chirality (Ch.8). Elucidation of these points can demonstrate the continuity that natural selection fails to provide. As Kauffman (1995) says, 'order is for free'.

> Biologists have not entirely ignored the spontaneous emergence of order, the occurrence of self-organization. We all know that oil droplets in water manage to be spherical without the benefit of natural selection and that snowflakes assume their evanescent sixfold symmetry for spare physiochemical reasons. But the sheer imponderable complexity of organisms overwhelms us as surely as it did Darwin in his time. We customarily turn to natural selection to render sensible the order we see, but I think the answer to our questions about the origins or [*sic*] order is broader. We already have some inkling of the kinds of spontaneous order which may bear on biological evolution, and I believe we must make the most profound assessment of such self-organization. We must look in any direction that seems profitable because whatever spontaneous may abound is available for evolution's continuing uses. (Kauffman 2006)

### *Evolutionary pluralism and teleology*

Evolutionary pluralism recognises that there are many documented pathways that illustrate evolution's occurrence for both explananda, the emergent phase and the 'sustainable or not' stage. These are empirical observations that do not assume that biological characters or attributes are necessarily the product of advantage. The neo-teleologist seemingly assumes that natural selection is causal not only for the second-stage explanandum but also for the first-stage explanandum. However, as argued earlier, the first stage of evolution, which provides an explanation of the variation or diversity, is independent of selection. Evolutionary pluralism, on the other hand, takes a more modest perspective, appreciating that characters, emerging or existing, need only meet the conditions of existence. There is therefore no requirement to open a philosophical can of worms that invites the type of teleological considerations already discussed.

### Conclusions

Evolutionary theory can be more transparent and avoid many of the philosophical and empirical problems that have afflicted natural selection. Darwin divorced natural selection from other evolutionary processes, but this separation was not pursued by his followers. The trend is to subsume independent evolutionary processes under natural selection. This has overburdened the explanatory power of natural selection, stretching it to such a state that there is now anomalous selection with the word 'selection' now meaningless. Resulting from this, there are the problems of tautology and untestability, the confusion over where natural selection is said to act, the conflation of natural selection with evolution, and so forth. To avoid these problems, the adoption of a more pluralistic approach and less demanding terminology was suggested. This would recognise documented evolutionary processes in their own right but address the relevant evolutionary explanandum.

For example, one must be clear whether issues of emergence or transformation on the one hand, or issues of sustainability on the other, are being addressed. To put it simply, explanation is where natural processes meet the prevailing conditions for existence. These considerations should open up areas of research that have to date been excluded and thus strengthen evolutionary theory.

# Chapter 14: Conclusions

How does one explain evolution and all that it entails in a coherent manner? The conclusion to this question demonstrates that there are two solutions available. The first is that if one is to continue with natural selection as an explanation then it must be reformed with a formal definition that is not given to ambiguity. The second solution is a more radical one where the term 'natural selection' is replaced with the term 'natural processes'. Guidelines are provided below in respect to reforming natural selection. However, given the historical legacy, it is unlikely that a clear characterisation or definition of natural selection that commands a consensus will be achieved. It is recommended therefore that serious consideration and philosophical scrutiny is given to the radical alternative.

The ambition has been to strengthen evolutionary theory and present a coherent account where the parameters of explanation are more easily recognised and the argumentation respects validity. Here the unwritten premise to date has been that evolutionary theory can resolve many of the controversies with some fairly simple revisions. To begin, this work sought to identify what natural selection is and, following this ontological question, determine its appropriate explanandum. The historical analysis here has demonstrated that the early explanandum that natural selection sought to explain was unclear at its origins and moreover the explanandum gradually evolved arbitrarily, with an increasing explananda. The most serious problem identified is one of ambiguity. Without a clear definition and agreed parameters there arise from natural selection miscellaneous philosophical problems, which after 150 years or so are still unresolved. The current philosophical discussion has failed to appreciate the anomalous nature of natural selection and it's associative terminology, seeking to tweak a more accurate characterisation of natural selection. This work concludes that the tweaking should stop and a more radical solution is required.

(a) A clear definition of natural selection is drawn that commands universal respect and that clearly demarcates it from other evolutionary processes. Guide lines are provided below.
Or
(b) The term 'natural processes' replaces the term 'natural selection', as outlined in Chapter 13.

### *The Disambiguation of Natural Selection*

Alternative recommendation (a)

At the heart of evolutionary theory is the concept of natural selection, which has survived a chequered history, declining after Darwin's death in the period now known as the 'eclipse of Darwinism' and being revived and prospering from the 1930s. Today, there is again a polarisation of opinion (Ch.s 2; 3; 4) Natural selection is seen by some as such a valuable explanatory model that it can be employed far beyond the biological fields into areas such as cosmology, mineralogy etc. (Ch.5). At the other end of the spectrum, there are those who wish not only to limit the extension of natural selection but also to restrict its application within evolutionary theory (Ch.11). Indeed, it is a curious state of affairs that what is considered by many to be the central premise of evolutionary biology has never received a formal scientific definition that has achieved consensus. Without such, individuals maintain their own perceptions of what natural selection is deemed to be. Overall, this often results in contrary and even contradictory attributes. Furthermore, it was witnessed that the explanandum that natural selection is said to address can shift ground and gradually expand. Darwin and Wallace both saw natural selection as explaining speciation primarily (Ch.1), whereas their followers in the mid-twentieth century placed the main focus of natural selection on explaining adaptation (Ch.2). Historically, many of the alternatives to natural selection actually became subsumed under natural selection, inducing a new ontology for natural selection (Ch.s3; 13). Taking all these issues into consideration, the situation urgently requires address, if not, the charge of a new biological phlogiston looms ever more serious.

One difficulty demonstrated here is that metaphors are not precise scientific tools and are open to many different interpretations. If one is to continue with the usage of natural selection then a clear definition must be sought avoiding the present incoherence. The historical study illustrated this ambiguity, demonstrating how natural selection itself has evolved and diversified into many concepts. Many of the controversies over the explanatory power were inherent in the earliest writings and have persisted, becoming more complex and unclear overtime. These can now be identified and evaluated, recognising the strengths and weaknesses. In doing so, one must be clear about what aspects of evolutionary theory one is addressing. For example, is the explanandum speciation, adaptation, stasis, demographic changes or extinction? With these qualifications in mind, the variants of natural selection can be observed and evaluated. The disambiguation falls into the six main groupings listed below. One must be cautious, however, as there are many variants or 'sub-species'; one can only try to capture the principal themes as they occur in the literature. Namely-

1. Proto or pre-Darwinian natural selection
2. Malthusian natural selection
3. Survival of the fittest – fitness
4. Natural selection as a process
5. Natural selection as a filter
6. Anomalous selection

## Proto or Pre-Darwinian Natural Selection

Proto or pre-Darwinian natural selection was conceived by such thinkers as Hutton, Wells, Matthew and Blyth, but without them coining the term (Ch.1). To Darwin's credit, such antecedence was recognised. This early naturalistic perspective sought to explain the diversity of form one might observe within a species. Moreover, it recognised that favourable traits could spread through a population in a gradual manner and, in some instances, might lead to a species becoming better adapted. The factors behind such changes were perceived as ecological, and one can witness this expression of natural selection in the more contemporary accounts of Endler (1986) and Peter and Rosemary Grant (2008), all concerned with fieldwork. The serious limitations to this early perspective are that there is no account or consideration of speciation and little consideration of extinction. The studies by the Grants on the famous Galapagos Islands observed acts of hybridisation as the *only* cause of speciation amongst the finches.

## Malthusian Natural Selection

Malthusian natural selection was simultaneously conceived by Charles Darwin and Alfred Russell Wallace, arguing that the competition for resources between individuals would result in the preservation of favourable traits on the one hand and elimination of unfavourable traits on the other hand. Thus natural selection and extinction go together 'hand in hand'. This account, following the earlier account above, accepted that favourable traits would be naturally preserved, spread through a population gradually and result, in some instances, in adaptation. The boldness of this account was the postulation that, after many generations of slight variation and 'advancement', the present population would comprise characters so different from those of its ancestors that a new species had evolved. The great advantage of this account is that, being essentially an empirical claim, it escapes the charge of tautology. Further, the fierce competition between individuals is argued to result in physical attributes, thus providing a naturalistic explanation of adaptations. It was maintained that, without the struggle for existence, it is difficult to see how physical adaptations are explained. The weakness of this perspective, however, is that too much reliance is placed upon Malthusian competition, the Malthusian argument being itself fallacious (Fisher. A, 1988). The 'struggle for existence' is not a universal phenomenon necessary for evolution to occur; some latter-day Darwinists argue that rapid evolution occurs under relaxed or lifted selection (Ch.11). Kropotkin reasoned that organisms may also struggle directly against the environment. Individuals that collaborated and forged mutuality were more likely to survive than those going it alone; group selection took its embryonic form. Moreover, Kropotkin suggested that continuous strife and struggle degraded a population rather than enhancing all its qualities (Ch.1).

One further conclusion recognised some limitation on vertical lines of heredity. The emphasis on modification through descent overlooks important issues of genetic exchange / lateral gene transfer. The account also lacks an explanation of the initial 'unity of type' and the initial variation that precedes and is prerequisite to natural selection. William Bateson, perhaps anticipating evolutionary developmental biology, argued that an understanding of the causes of variation was the key that unlocked evolutionary theory and not the struggle for existence (Ch.1).

## Survival of the Fittest – Fitness

Many of the concerns about Malthusian natural selection led to a reformulation of natural selection in terms of 'fitness', but this was not without a cost. 'Survival of the fittest' was the phrase coined by Herbert Spencer to encapsulate the ideas of Darwin and Wallace. However, this was thought too crude by the architects of the modern synthesis. As Gould (1982) commented later, 'survival of the fittest' is too demanding; 'survival of the fit enough' is more appropriate. If only the fittest survive, there would be few organisms remaining. Moreover, it was deemed that survival of the fittest, if taken literally, is a deeply conservative concept with no inkling to suggest how evolution might occur (Ch.2). The fitness concept was intended as a sophisticated replacement for 'survival of the fittest', recognising that an organism need not require physical attributes of strength in order to survive. All that was necessary for continuity was the ability to reproduce effectively. However, the drawbacks to such modifications of Malthusian natural selection include the charges of circularity and untestability (Ch.2). Further, fitness becomes essentially conservative and lacks any causal explanation for the origin of both adaptation and speciation. Philosophers have attempted to provide some coherence, but little consensus has been achieved (Ch.2). Dawkins recognised some serious problems and urged that the term ‘fitness’ should be avoided wherever possible. His attempt to resolve the issues concerned with fitness rested heavily on a gene-centric foundation to ‘inclusive fitness’. This reliance, however, cannot be substantiated in the light of new discoveries. A new assessment appreciates that ‘genes’ are less particulate, much more pleiotropic and context-sensitive, than originally perceived. Could it not be argued that Biology has moved toward a more holistic account that includes recognition of factors espoused within Systems Biology? Appreciation of the cell, its contents and structure, together with its interface with the environment, is nowadays considered essential (Ch.2). ‘Genes’ can also be seen as intermediaries within a causal chain and not as causal ‘agents’ or as ‘mediators’. Moreover, it is recommended that one avoids anthropomorphic language in such circumstances.

### Natural Selection as a Process

Natural selection perceived as a process is really an explanation that identifies a series of chronological steps that, after many generations, comes to fruition in adaptation or speciation or extinction (Ch.4). For speciation or adaptation, the causal element is a series of favourable point mutations that eventually affect gene frequencies; this constitutes the *de novo* aspect of evolution. The favourable changes are preserved and accumulate over generations and the unfavourable changes are quickly eliminated. The strength of this perspective is that there is good evidence for the variety of form observed within a population. Furthermore, the process identified is not essentially tautological and is not subject to the criticism levelled at the principle of fitness. The weakness of the theory is a lack of empirical evidence for speciation, which is very difficult to test. Further, the gradualist approach is difficult to reconcile with the episodic evidence of the fossil record. There are many examples of fairly rapid evolution, as considered earlier in the sections on lateral gene transfer, symbiogenesis and hybridisation. The idea that the accumulation of point mutations can explain all of evolution is overburdened and leaves many things unexplained. It should therefore be seen as only one explanatory process amongst many. Another challenge is to distinguish clearly the process from evolutionary drift. Drift, in the modern sense of the term, shares with this sense of natural selection that evolution is the result of small changes to gene sequences. One would therefore need a clear account of why the process of natural selection but not drift leads to adaptation, without looking arbitrary.

### Natural Selection as a Filter

Natural selection as a filter or filtering process has largely emerged in recognition of the pluralism inherent in modern interpretations of evolutionary explanation. Natural selection under this construal can be seen as an arbiter or filter that acts not only upon changes induced by point mutation but upon *any* changes, however they originate. Under this formulation, natural selection can be seen to act upon changes such as symbiogenesis, hybridisation, macro-mutation, endogenous inheritance, sexual selection, and developmental plasticity. Moreover, there seems no logical reason why the filter analogy cannot be applied indiscriminately to other sciences, such as cosmology and mineralogy (Ch.5). The advantages of this perspective are difficult to discern, other than it endorses fitness as essentially conservative. If natural selection is purely a filter then, by definition, it lacks any causal account for the emergence of novel features. Further, it was demonstrated that the filter concept of natural selection would never allow evolutionary change to begin at the ancestral beginnings, preventing argogenesis and the great diversity of biological life (Ch.4). If natural selection is purely a filter, then 'what's making the coffee?' seems to be the more important evolutionary question to be addressed. This issue has resurfaced within evo-devo and the importance of development, but the issue is not a new one. This same pertinent problem was raised by Mivart, Butler,  De Vries and Bateson (Ch.1) and led to the 'eclipse of Darwinism'.  (A more accurate phrase was suggested: the *eclipse of natural selection*). It is not easy to see how the filter concept escapes the charge of superficiality, as the understanding of the sources of variation and orthogenesis is arguably the main challenge.

There is equivocation over what it is that constitutes 'variation', that which natural selection is said to filter. The original concept saw natural selection sifting through variation of small genetic changes, where harmful changes are eliminated and beneficial changes accumulate gradually and eventually new species may result (Ch.4. Rosenberg & McShea). However, natural selection is also seen to act on larger biological entities such the products of symbiogenesis and hybridisation (Ch.7. Margulis, Arnold). Should one conclude therefore that the products of symbiogenesis and hybridisation also constitute variation? The original formulation of the relationship between variation and natural selection is seen to explain speciation, in the second formulation natural selection is seen to act upon speciation. Again, there is no formal definition of variation and it looks that natural selection not only acts on variation but also acts on diversity. Furthermore, if there is no formal definition of variation, then variation can be constituted by anything that has a plurality, such as variation in universes or minerals or elements. One could even extend the filtering concept of variation to 'explain' why there is more matter in the earth than there is antimatter, obviously antimatter has been selected against and matter has been selected for. Without rules or defined parameters one could argue that the earth's environment has filtered out all the helium and selected nitrogen.

Is there still yet another modal sense of variation that includes hypothetical entities? In early Darwinian terms an actual physical trait could be contrasted or compared with another actual physical trait and research could then be conducted to discover if either trait actually produced reproduction advantage. However, there is another sense of variation when, for instance, a novel biological entity emerges and pertains no physical comparative. Instead, a hypothetical comparative is introduced to fulfil the selective necessity of variation. If this seems a little obscure then let's consider an example, take the eukaryote: For the sake of argument it will be said that the first eukaryote came into existence by symbiogenesis. This first eukaryote is unique, having no comparative and therefore lacks the variation necessary for natural selection. However, although there is no physical comparative to this original in existence as yet, one might still want to say it was selected. The problem is however, what was the eukaryote selected in favour of? One might find a solution here, to the lack of actual variation for filtering, by positing hypothetical scenarios. One could argue for instance that there may have been many aborted acts of symbiogenesis but only the one sustained, and was therefore selected. Unfortunately, there is a problem here with the employment of hypothetical entities. One cannot conclude that selection has taken place, indeed it would be a logical fallacy to do so. The reason is simply that the symbiogenesis event that produced the first eukaryote may have been the only event, there may not have been other aborted acts of symbiogenesis.

There is a real problem here that concerns philosophers and logicians, 'variation' requires a definition that prevents the filter analogy being extended *reductio ad absurdum.* However, even if a suitable definition is forthcoming, the filter analogy seems consigned to explaining demographics and reductions in biological diversity and has nothing to say concerning the emergence of biological novelties or the major evolutionary transitions. In Chapter 3 it was also observed how the filter concept of natural selection is subject to the reification fallacy.

### Anomalous Selection

As there has never been an accepted singular formal scientific definition of natural selection, anomalous selection has emerged. Anomalous selection is a description of the situation we find ourselves in today, with several definitions or concepts of natural selection in hand and a massive proliferation of selective terminology. For obvious reasons, this is not a desirable situation. The first concern is the underlying ambiguity. The danger is that, if there is not a single and precise definition of natural selection, one might unwittingly slide from one sense of natural selection to another. If natural selection is attacked for being circular, then the Malthusian brand of natural selection is brought forward to refute the attack. If Malthusian natural selection is attacked for its reliance upon competition, then the concept of fitness, which embraces any mechanism of reproductive success, is produced to defend the integrity of natural selection. If the filter concept of natural selection is attacked for being non-causal, then the attack can be countered by appeal to natural selection 'as a process' and by saying that genetic mutations are a source of evolutionary novelty. Then again, if one argues that natural selection as a process of mutational changes is insufficient to explain all of evolution, one is told that natural selection can act upon all manner of biological emergences. Of course, it is not only proponents who could slide from one meaning of natural selection to another; opponents could cherry-pick and attack the version of natural selection they find weakest but, if this tack is unsuccessful, they can switch attack to another meaning of natural selection. The ambiguity of the situation is the problem here, but it is not the only one.

Unfortunately, selective terminology covers nowadays such a vast range of biological phenomena that it is difficult to find anything that has not been covered with a selective whitewash (Appendix 2). The charge here is that the term 'selection' has been stretched to such an extent that its explanatory currency is completely devalued. It is not simply the case that the term 'natural selection' is ambiguous; it is also the case that natural selection is anomalous. If one considers, for instance, relaxed or lifted selection, evolution is no longer here explained by natural selection but is explained by the absence of natural selection.

Another concern, is 'selection' shorthand for the term 'natural selection' or does it hold its own separate identity? If it has its own identity then what distinguishes it from the term 'natural selection'? If 'selection' is solely shorthand for the term 'natural selection' then does 'natural selection' also hold all the attributes that the word 'selection' holds, as identified in Appendix 4? When one says 'there is selection of trait X' or 'selection for trait X', what sense of selection is one alluding to? Is it to 'natural selection' or is one alluding to one (or more) of the vast miscellaneous selective terminology available? Or does one hold some other definition of 'selection' in ones own mind? The conclusion is that under present circumstances the word 'selection' is meaningless. This undesirable situation is compounded further by the evolution of 'natural selection' to 'survival of the fittest' to one of 'fitness' (Ch.2). The continuous debate since Victorian times, concerning any causal qualities (nowadays 'negative selection' versus 'positive selection') has not clarified the matter and there is no sign of any resolution. It is a messy affair.

Natural selection, then, has itself evolved into several 'species' but none has become extinct; all are in play and supplemented by an enormous vocabulary of selective terminology. This ambiguity is undesirable and undermines any explanatory power natural selection may hold. As it stands, there seem to be five possible remedies (1–5 from above), but unfortunately each comes with some cost. If one were to accept the prevailing proliferation and generalise the principle of natural selection so widely, then one would have to accept that the generalised principle could equally apply to other domains, such as cosmology, mineralogy and evolutionary psychology. This in turn would invite the charges of vacuity, circularity and a new phlogiston. Moreover, natural selection under these circumstances looks suspiciously synonymous with evolution. Theories that claim to explain all, selectionist or non-selectionist, are often theories that explain nothing worthwhile. The explanation may even be true but becomes so generalised that nothing informative is gleaned.

One hopefully can appreciate why it is not advisable to extend this messy affair to other sciences and disciplines (Ch.5). The idea that natural selection is some form of substrate that can be applied to all manner of studies cannot have any explanatory value until that substrate is clearly defined or characterised, with all the current ambiguities exorcised. As demonstrated, the anomalous nature of 'selection' makes it undesirable for export.

Alternative conclusion (b)

It was argued that rather than seek a single explanation for all of the diverse forms of evolution, it would be better to recognise that there are many natural processes that lead to evolutionary change. For the sake of explanatory clarity these mostly fall into two chronological stages. The first stage addresses emergent or *de novo* factors; for example, natural processes such as hybridisation or symbiogenesis *explain* the emergence of new forms of life. Once these new forms have emerged their sustainability is tested over time by factors in the environment: resource availability, the presence of predators, climatic conditions etc. It's the ecological processes that *explain* any sustainability. Of course the details behind these causal changes could be extremely complex and no doubt open to debate, but then that is the role for the biologist to elucidate the empirical evidence. The role of the philosopher in this instance is to provide a structural framework for scientific theories that is not besieged with ambiguity, confusion and controversy. The advantage of the two stage structural framework recommended here is that it is simple to apprehend in principle, it is parsimonious and not contaminated by the historical legacy that afflicts natural selection. Moreover, it is clearer to see which explanandum is being alluded to and reduces the risk of applying an inappropriate explanation to the explanandum in question. As an example, sexual selection *may* explain why the unusual peacock train has been *preserved* over time but sexual selection cannot explain the *origin* or *emergence* of this novel feature. Again, predation *may* explain the numbers of melanic moths within an environment but predation does not explain the origin of moth melanism. Moreover, Kropotkin in Ch 1, anticipating 'group selectionism', gives not an example of emergent causes but an example of preserving causes. Mutualism, *may* protect individuals and explain why they reproduce effectively but that is all.

Indeed, one may wish to think of all this in shorthand and as a question of causes. For instance, the first-stage processes are the initial or originating cause and the second-stage processes are the preserving or eliminating cause. This may also be a clearer ascription than the conventional ascription of proximate and ultimate causes. The term 'ultimate cause' has something of an emotive grandiosity, as if it were analogous to a trump card, and there is some confusion over what ultimate causes should explain. Attributes considered advantageous were employed not only as preserving causes but also as emerging causes. This was deemed fallacious (Ch.11).

To establish these reforms fully, it is necessary to embrace an outlook of evolutionary pluralism that is not subsumed under natural selection. In other words it is strongly advised that one does not introduce extra vocabulary based on 'selection', and consigning these two recommended chronological stages as 'first stage selection' and 'second stage selection'. As argued above, the reason for this preclusion is that it is very difficult to know exactly what the word 'selection' means.

The question then arises: does one actually require selective terminology to explain evolution? Is it not a necessary condition? This answer is seemingly no, or at least the alternatives to natural selection are worthy of further philosophical investigation and scrutiny. To date the philosophical community has not addressed these possibilities. This work calls for a change in direction and has presented an unprecedented and concise outline of the 'structuralist' thinkers [86] (Ch.8 & 9). D'Arcy Thompson and Lima-de-Faria are identified as the torch bearers for a wider multi-disciplinary approach toward evolutionary explanation that extends beyond a genetic/natural selection perspective. One can read the works of either thinker and observe they are free of selective terminology and the arguments presented are not lacking in coherence. One may not agree with the authors interpretations of the details but it does not follow that the arguments themselves are invalid. More recently Conway Morris has produced a comprehensive study of 'convergence' devoid of explanation in selectionist terminology and instead physical law provides most of the explanatory factors. Again, there seems to be no lack of coherence and the work is explanatory plausible. The challenges to neo-Darwinism are there for the uptake, they should not be dismissed out of hand without proper examination. Nevertheless, there are differences. Unlike Thompson, Lima-de-Faria and Conway Morris both recognise that genes play an important role within evolutionary explanation. Nevertheless, Lima-de-Faria maintains also the limitations of genetic reductionism, advocating the requirement of recourse to cosmological evolution and the physical principles that underpin it.

The view that evolutionary explanation requires much more input from other disciplines, such as physics, chemistry, geometry, topology and tensegrity has also been embraced by such academics as Ball, Crawford, Ingber, Gardner, Marsh, Scarr and Stewart (Ch.8). This pluralistic approach is endorsed here in principle but under the banner of natural processes. The conclusion is that evolutionary theory requires a much stronger

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[86] These thinkers share a more eclectic interpretation of evolutionary than anything suggested by reformers, such as Jablonka and Lamb, Gilbert, Gould, Lewontin and Pigliucci or even 'revolutionaries' such as Carroll, B.S and Carroll, R.L.

measure of these disciplines than has been previously recognised and in contraposition to the view that physics et al requires a measure of natural selection.

To recognise such evolutionary pluralism may prove difficult, as the case could be made that natural selection has been seen as 'the only game in town' and to give criticism is to supply the 'opposition' unnecessarily with ammunition. However, it could be said that the defensive attributes and desire for conformity have stifled alternative conjectures or missed opportunities for new research programmes. It is not the case that alternatives have not been developed. The brief historical survey demonstrated that evolutionary processes that seemed to run contrary to natural selection were resisted at first but then later subsumed under natural selection (Ch.2). Sometimes, new selective terminology was added. In other instances, alternative hypotheses were edited and rendered ineffectual (D'Arcy Thompson) or completely missed or passed over (Antonio Lima-de-Faria), (Ch.13). Despite its early origins going back to figures such as Mivart, structuralism is in its infancy and requires further articulation and development. Elucidation here could be exciting and prove to be a valuable research. Seeking to explain biological phenomena purely in terms of 'advantage' or 'disadvantage' overlooks the possibility that many phenomena are caused directly without the need to postulate selection pressures. This issue was widely debated during the 'eclipse of Darwinism' but then lost attraction. Recently, however, there has been an increasing interest in the interface of organism and environment. Mary Jane West-Eberhard (2003) has reflected that, "contrary to the notion that mutated novelties have superior evolutionary potential, there are strong arguments for the greater evolutionary potential of environmentally induced novelties". The direct impact of such factors as gravity, temperature and nutrition, without recourse to selection pressures, has indeed been largely neglected (Ch.10).

Another instance of missed opportunity – the importance of hybridisation within *Animalia* – has been for the most part underestimated, with too few researchers appreciating its full potential, it was concluded. (Ch.7). Hybridisation does not sit easily with gradualist neo-Darwinism and the traditional phylogenic tree of life. Nevertheless, hybridisation has excellent direct empirical evidence for speciation. The full impact and historical value of hybridisation events is far from known; it deserves its own field of enquiry and provides another excellent opportunity for a vibrant research programme.

The controversy concerning neo-teleology was seen as deeply related to the advocacy of natural selection. The desire to explain the issues of design and adaptation led some to postulate a degree of purposefulness to some biological attributes, such as hearts not simply pumping blood but hearts being *for* the pumping of blood. It was argued that this further claim of teleology was difficult to substantiate but, moreover, that it was an unnecessary excursion. The problem of neo-teleology is pressing only if one insists on evolutionary explanation in terms of advantageous traits. One can avoid the problems here with a few simple alterations in terminology and expectation. Butler and Reiss have recommended that the term 'meeting the conditions for existence' is clearer to apprehend, less ambitious and preferable to the term 'natural selection'. It seems to be forgotten that Darwin correctly appreciated the 'conditions for existence' as the 'higher law' (p261 6th edition of the *Origin*). In modern terms this means that both natural selection and neutral evolution are covered by the term 'meeting the conditions for existence'. It is not the case that natural selection is synonymous with 'meeting the conditions for existence'. Indeed, if one adopts a more modest and sufficing terminology to explain evolutionary events, together with the perspective of natural processes suggested here, then many of the issues that have afflicted evolutionary theory are bypassed without any explanatory loss. (Ch.13).

## A Brief Summary of the Conclusions

To achieve a more coherent evolutionary theory free of many of the persistent criticisms, problems and so-called paradoxes that lack resolution to date, it was recommended that one examine and clarify natural selection. The challenge to neo-Darwinists and philosophers who support neo-Darwinism is to provide an unambiguous scientific definition of natural selection with the explanandum clearly identified. This would enable the establishment of criteria that provide boundaries to the explanatory power of natural selection. However, this could be a futile task, as the best minds have failed over a very long period to provide a clear uncontroversial characterisation of natural selection and fitness. Natural selection is now so anomalous and the word 'selection' is employed in so many contrary ways it has become meaningless. The difficulty of formal definition is that if the definition is very general and wide-ranging, then the term invites criticism of vacuity, tautology and untestability, with natural selection looking synonymous with its intended explanandum, evolution. On the other hand, if the definition is very tight, then many evolutionary events remain outside its explanatory powers. To resolve this dilemma, it was suggested that there are indeed evolutionary processes present that should be recognised as independent natural processes and not subsumed under natural selection. The term 'conditions of existence' was deemed more appropriate when addressing evolutionary theory in general terms (Ch.13). Evolution by means of natural processes conforms well to the *CM* model of explanation. If the term is adopted, then many of the criticisms of tautology and untestability are diffused. Moreover, its adoption opens up the opportunity of new research programmes and consideration of those that have been passed over or ignored. It has been demonstrated that the study of form and structure is essential to a comprehensive evolutionary explanation, which in turn requires at least recourse to physics, chemistry, mathematics, tensegrity and topology. In chapter 10 it was discovered that gravity and thermodynamics were fundamental to understanding form, and from this understanding biological scaling laws can be derived. For the sake of parsimony it is recommended that these explanatory powers are not perceived to be a product of some form of contrastive selection process. The explanatory models by West et al (Ch.10) are the explanatory icing on the cake, but there is little point or value in icing the cake twice with a further layer of selective terminology. This perspective of evolutionary pluralism in turn recognises that not all evolutionary change needs to be addressed in terms of accumulated *advantage*. Accretion of genetic and molecular substances explains the physical diversity of life but it is not necessary to assume that complexity is the result of a selective process. It is sufficient that these chemical properties combine together with some persistence. These novel chemical combinations do not necessarily have to be 'better' than those that already exist, but they do have to meet the prevailing conditions of existence. Thus a more sufficing account than at present is less demanding and desirable. Moreover this sufficing account allows the employment of terminology that is less ambiguous, clearer to apprehend and potentially not inclined toward neo-teleology (Ch.12). One might argue that these natural processes, hybridisation, symbiogenesis, accumulative beneficial mutation, the direct effects of gravity and temperature, predator/ prey relationships, niche construction and so forth, can all be said to constitute natural selection. The reply to this argument is no, it is the actual natural processes that constitute (and explain) evolution, they do not constitute natural selection. Natural processes constitute natural selection only if natural selection is synonymous with evolution and that is not desirable.

Natural selection is characterised in many ways and is without a formal definition. Resulting from this is an array of philosophical problems that have to date proved seemingly irresolvable. There is however a way to avoid such problems with simple revision of terminology and our conceptive framework. Darwin’s groundbreaking book is thus re-titled: *On the Origin of Species by means of Natural Processes………*.

## Appendix 1

## Natural Selection before Darwin

### Hutton

> (1)If an organised body is not in the situation and circumstances best adapted to its sustenance and propagation, then, in conceiving an indefinite variety among the individuals of that species, we must be assured, that, on the one hand, those which depart most from the best adapted constitution, will be most liable to perish, while, on the other hand, those organised bodies, which most approach to the best constitution for the present circumstances, will be best adapted to continue, in preserving themselves and multiplying the individuals of their race. (Hutton 1794)

### Wells

> (2)[What was done for animals artificially] seems to be done with equal efficiency, though more slowly, by nature, in the formation of varieties of mankind, fitted for the country which they inhabit. Of the accidental varieties of man, which would occur among the first scattered inhabitants, some one would be better fitted than the others to bear the diseases of the country. This race would multiply while the others would decrease, and as the darkest would be the best fitted for the [African] climate, at length [they would] become the most prevalent, if not the only race. (Wells 1818 appendix)

### Matthew

> (3)There is a law universal in nature, tending to render every reproductive being the best possible suited to its condition that its kind, or organized matter, is susceptible of, which appears intended to model the physical and mental or instinctive powers to their highest perfection and to continue them so. This law sustains the lion in his strength, the hare in her swiftness, and the fox in his wiles. As nature, in all her modifications of life, has a power of increase far beyond what is needed to supply the place of what falls by Time's decay, those individuals who possess not the requisite strength, swiftness, hardihood, or cunning, fall prematurely without reproducing—either a prey to their natural devourers, or sinking under disease, generally induced by want of nourishment, their place being occupied by the more perfect of their own kind, who are pressing on the means of subsistence …
>
> There is more beauty and unity of design in this continual balancing of life to circumstance, and greater conformity to those dispositions of nature which are manifest to us, than in total destruction and new creation … [The] progeny of the same parents, under great differences of circumstance, might, in several generations, even become distinct species, incapable of co-reproduction. (Matthew 1831 appendix p364)

### Blyth

> (4)How beautifully do we thus perceive, as in a thousand other instances, the balance of nature preserved: and even here we see another reason why sickly or degenerate animals (those, I mean, which are less able to maintain the necessary vigilance) must soon disappear; and why the slightest deviation from the natural hue must generally prove fatal to the animal. (Blyth 1835 p53)
>
> *Breeds* are my third class of varieties; and though these may possibly be sometimes formed by accidental isolation in a state of nature, yet they are, for the most part, artificially brought about by the *direct* agency of *man*. It is a general law of nature for all creatures to propagate the like of themselves: and this extends even to the most trivial minutiæ, to the slightest individual peculiarities; and thus, among ourselves, we see a family likeness transmitted from generation to generation. When two animals are matched together, each remarkable for a certain given peculiarity, no matter how trivial, there is also a decided tendency in nature for that peculiarity to *increase*; and if the produce of these animals be set apart, and only those in which the same peculiarity is most apparent, be selected to breed from, the next generation will possess it in a still *more* remarkable degree; and so on, till at length the variety I designate a *breed*, is formed, which may be very unlike the original type. (Blyth 1835 p46)

### Darwin

> (5)If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organisation, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and

> this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection. (Darwin 1859 p154)

## Appendix 2

## Darwin and pluralism: Factors that shape evolution other than natural selection

### Use and disuse

> (1)It is well known that several animals, belonging to the most different classes, which inhabit the caves of Styria and of Kentucky, are blind. In some of the crabs the foot-stalk for the eye remains, though the eye is gone; the stand for the telescope is there, though the telescope with its glasses has been lost. As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, I attribute their loss wholly to disuse.
>
> In the same manner as in Madeira the wings of some of the insects have been enlarged, and the wings of others have been reduced by natural selection aided by use and disuse, so in the case of the cave-rat natural selection seems to have struggled with the loss of light and to have increased the size of the eyes; whereas with all the other inhabitants of the caves, disuse by itself seems to have done its work. (Darwin 1859 p155)

### Habit

> (2)How much of the acclimatisation of species to any peculiar climate is due to mere habit, and how much to the natural selection of varieties having different innate constitutions, and how much to means combined, is a very obscure question. That habit or custom has some influence I must believe, both from analogy, and from the incessant advice given in agricultural works, even in the ancient Encyclopaedias of China, to be very cautious in transposing animals from one district to another; for it is not likely that man should have succeeded in selecting so many breeds and sub-breeds with constitutions specially fitted for their own districts: the result must, I think, be due to habit. On the other hand, I can see no reason to doubt that natural selection will continually tend to preserve those individuals which are born with constitutions best adapted to their native countries. (Darwin 1859 p159)

### Correlation of Growth

> (3)*Correlation of Growth.*—By this term I mean that the whole organisation is so connected, that when one part varies, other parts vary; but which of two correlated variations ought to be looked at as the cause and which as the effect, or whether both result from some common cause, we can seldom or never tell. The point of interest for us is that, when fanciers, by the continued selection of slight variations, have largely modified one part, they often unintentionally produce other modifications. (Darwin 1868 p182)
>
> Correlation is an important subject; for with species, and in a lesser degree with domestic races, we continually find that certain parts have been greatly modified to serve some useful purpose; but we almost invariably find that other parts have likewise been more or less modified, without our being able to discover any advantage in the change. No doubt great caution is necessary with respect to this latter point, for it is difficult to overrate our ignorance on the use of various parts of the organisation; but from what we have seen, we may believe that many modifications are of no direct service, having arisen in correlation with other and useful changes. (Darwin 1868 p365)

### Diet

> (4)With respect to the causes of the modifications which horses have undergone, the conditions of life seem to produce a considerable direct effect. Mr. D. Forbes, who has had excellent opportunities of comparing the horses of Spain with those of South America, informs me that the horses of Chile, which have lived under nearly the same conditions as their progenitors in Andalusia, remain unaltered, whilst the Pampas horses and the Puno horses are considerably modified. There can be no doubt that horses become greatly reduced in size and altered in appearance by living on mountains and islands; and this apparently is due to want of nutritious or varied food. (Darwin 1868 p67)

Direct impact of the climate

> (5)Dr. Falconer informs me that bulldogs, which have been known, when first brought into the country, to pin down even an elephant by its trunk, not only fall off after two or three generations in pluck and ferocity, but lose the under-hung character of their lower jaws; their muzzles become finer and their bodies lighter. English dogs imported into India are so valuable that probably due care has been taken to prevent their crossing with native dogs; so that the deterioration cannot be thus accounted for. The Rev. R. Everest informs me that he obtained a pair of setters, born in India, which perfectly resembled their Scotch parents: he raised several litters from them in Delhi, taking the most stringent precautions to prevent a cross, but he never succeeded, though this was only the second generation in India, in obtaining a single young dog like its parents in size or make; their nostrils were more contracted, their noses more pointed, their size inferior, and their limbs more slender. (Darwin 1868 p53)

The 'laws of variation or growth'

> (6)In many cases we are far too ignorant to be enabled to assert that a part or organ is so unimportant for the welfare of a species, that modifications in its structure could not have been slowly accumulated by means of natural selection. In many cases, modifications are the probably direct result of the laws of variation or growth, independently of any good having thus gained. But even such structures have often, as we feel assured, been subsequently taken advantage of, and still further modified, for the good of the species under new conditions of life. (Darwin 1900 p259)

Darwin confirms his pluralism

> (7(Thus a large yet undefined extension may safely be given to the direct and indirect results of natural selection; but I now admit, after reading the essay by Nageli on plants, and the remarks by various authors with respect to animals, more especially those recently made by Professor Broca, that in the earlier editions of my 'Origin of Species' I perhaps attributed too much to the action of natural selection or the survival of the fittest. I have altered the fifth edition of the 'Origin' so as to confine my remarks to adaptive changes of structure; but I am convinced, from the light gained during even the last few years, that very many structures which now appear to us useless, will hereafter be proved to be useful, and will therefore come within the range of natural selection. Nevertheless, I did not formerly consider sufficiently the existence of structures, which, as far as we can at present judge, are neither beneficial nor injurious; and this I believe to be one of the greatest oversights as yet detected in my work. I may be permitted to say, as some excuse, that I had two distinct objects in view; firstly, to shew that species had not been separately created, and secondly, that natural selection had been the chief agent of change, though largely aided by the inherited effects of habit, and slightly by the direct action of the surrounding conditions. (Darwin 1871 p152)

## Appendix 3

## Quotations critical of Natural Selection

### Mivart

(1)Convergence:

Thus it is here contended that the similar and complex structures of both the highest organs of sense, as developed in the vertebrates on the one hand, and in the mollusks on the other, present us with residuary phenomena for which 'Natural Selection' alone is quite incompetent to account : and that these same phenomena must therefore be considered as conclusive evidence for the action of some other natural law or laws conditioning the simultaneous and independent evolution of these harmonious and concordant adaptations. (Mivart 1871 p88)

(2)Incipient organs

'Natural Selection', simply and by itself, is potent to explain the maintenance or the further extension and development of favourable variations, which are at once sufficiently considerable to be useful from the first to the individual possessing them. But Natural Selection utterly fails to account for the conservation and development of the minute and rudimentary beginnings, the slight and infinitesimal commencements of structures, however useful those structures may afterwards become. (ibid. p35)

(3)The Incomplete Fossil Record

The mass of palaeontological evidence is indeed overwhelmingly against minute and gradual modification. It is true that when once an animal has obtained powers of flight its means of diffusion are indefinitely increased, and we might expect to find many relics of an aerial form and few of its antecedent state with nascent wings just commencing their suspensory power. Yet had such a slow mode of origin, as Darwinians contend for, operated exclusively in all cases, it is absolutely incredible that birds, bats, and *pterodactyles* should have left the remains they have, and yet not a single relic be preserved in any one instance of any of these different forms of wing in their incipient and relatively imperfect functional condition! Whenever the remains of bats have been found they have presented the exact type of existing forms, and there is as yet no indication of the conditions of an incipient elevation from the ground. (Mivart 1871 p143)

### Kropotkin

(4)Animal struggle

I failed to find – although I was eagerly looking for it – that bitter struggle for the means of existence, among animals belonging to the same species, which was considered by most Darwinists (though not always by Darwin himself) as the dominant characteristic of struggle for life, and the main factor of evolution. (Kropotkin 1902 p1)

(5)Narrow sense of struggle

It may be that at the outset, Darwin himself was not fully aware of the generality of the factor which he first invoked for explaining one series only of facts relative to the accumulation of individual variations in incipient species. But he foresaw that the term which he was introducing into science would lose its philosophical and its only true meaning if it were to be used in its narrow sense only – that of a struggle between separate individuals for the sheer means of existence. (ibid. p10)

(6)Wider sense of struggle

He (Darwin) pointed out how, in numberless animal societies, the struggle between separate individuals for the means of existence disappears, how struggle is replaced by co-operation and how that substitution results in the development of intellectual and moral faculties which secure to the species the best conditions for survival. (ibid. p11)

(7)Mutual aid is a strong factor of evolution

Sociability is as much a law of nature as mutual struggle. Of course it would be extremely difficult to estimate, however roughly, the relative numerical importance of both these series of facts. But if we resort to an indirect test, and ask nature: 'who are the fittest: those who are continually at war with each other, or those who support one another?' we at once see that those animals which acquire habits of mutual aid are undoubtedly the fittest. They have more chances to survive, and they attain, in their respective classes, the highest development of intelligence and bodily organisation. (ibid. p13)

(8)Lack of evidence

We were both under the fresh impression of the Origin of Species, but we vainly looked for the keen competition between animals of the same species which the reading of Darwin's work had prepared us to expect, even after taking into account the remarks of the third chapter (p.54). We saw plenty of adaptations for struggling, very often common, against the adverse circumstances of climate, or against various enemies, and Polyakoff wrote many a good page upon the mutual dependency of carnivores, ruminants, and rodents in their geographical distribution; we witnessed numbers of facts of mutual support, especially during the migration of birds and ruminants, but even in the Amur and Usuri regions, where animal life swarms in abundance, facts of real competition and struggle between higher animals of the same species came very seldom under my notice, though I eagerly searched for them. (ibid. p16)

Butler

(9)Causality

It is plain that natural selection cannot be considered a cause of variation, for the variations must make their appearance before they can be selected. (Butler 1882 p346)

Suppose that it is an advantage to a horse to have an especially hard and broad hoof, then a horse born with such a hoof will indeed probably survive in the struggle for existence, but he was not born with the larger and harder hoof because of his subsequent surviving. He survived because he was born fit, not he was born fit because he survived. The variation must arise first and be preserved afterwards. (ibid. p346)

(10) Conditions of existence

I think I can show moreover that Mr Darwin himself holds natural selection and the conditions of existence to be one and the same thing. For he writes 'in one sense' and it is hard to see any sense but one in what follows, 'the conditions of life may be said not only to cause variability' – so that here Mr Darwin appears to support Lamarck's main thesis – 'either directly or indirectly, but likewise, to include natural selection; for the conditions determine whether this or that variety shall survive.' But later on we find that 'the expression of conditions of existence, so often insisted upon by the illustrious Cuvier' (and surely also by the illustrious Lamarck, though he calls them circumstances) 'is fully embraced by the principle of natural selection.' So we see that the conditions of life include natural selection and yet the conditions of existence are fully embraced by natural selection, which I take it is an enigmatic way of saying they are one and the same thing. (ibid. p20)

## Appendix 4
## Collecting Selection Terminology *(in reverse alphabetical order)*

| | |
|---|---|
| Weak selection | Nearly neutral evolution. (Lawson and Jensen 2009) www3.imperial.ac.uk/portal/page?_pageid=61 |
| Unnatural selection | The effects of human activity upon evolution. (http://people.ucsc.edu/~cwilmers/publications/Stenseth2009%20human%20predators.pdf) |
| Sweeping selection | Reduction or elimination of variation among the nucleotides in neighbouring DNA of a mutation as the result of recent and strong natural selection. (www.nature.com/scitable/topicpage/Negative-Selection) |
| Strong natural selection | Speciation. www.ithaca.edu/biology/pres_bssmr03.pdf |
| Stabilising selection<br>*Also called:*<br>Normalising or Purifying selection | This type of selection acts to prevent divergence of form and function. (Bell 2008) |
| Stabilising frequency-dependent selection | Selection will favour rare genotypes and result in the maintenance of genetic variability. (Bell 2008) |
| Species selection and multi-species selection | In ecology, species under environmental threat. (www.cell.com/trends/ecology.../S0169-5347(09)00232-8. 2008) |
| Social selection | Social competition can drive convergence or parallelism. (Tobias and Seddon http://www.zoo.ox.ac.uk/egi/Tobias&SeddonEvol_2009.pdf) |
| Sexually antagonistic selection | Solves the Darwinian puzzle of homosexuality. (Cox, 2013 www.dartmouth.edu/.../Cox%20%26%20Calsbeek%202009%20Am%20) |
| Sexual selection | The frequency of traits can increase or decrease depending on the attractiveness of the bearer. (Darwin. E 1792) |
| Selective pressure | Unknown definition. |
| Runaway sexual selection | Sexual selection that leads to the rapid evolution of exaggerated traits. (Bell 2008) |
| Reversed sexual selection | The male selects the female for reproduction. See Darwin's reply to Mivart; (Darwin 1900 6th edition) |
| Reverse selection | Characters or traits unaffected by 'selection processes'. (J. S. Allan 2009 journals.cambridge.org/production/action/cjo) |
| Relaxed selection<br>*Also called:*<br>Lifted selection | Traits that were advantageous in one time and place become obsolete in another. Traits that aren't actively maintained by natural selection tend to become smaller or less functional over time. (D. C. Lahti, N. A. Johnson et al. 2012). www.ncbi.nlm.nih.gov/pubmed/19500875 |
| Purifying selection | Removes deleterious mutations from a population; in other words, it is directional selection in favour of the advantageous heterozygote. (Bell 2008) |
| Progressive selection | *See:* Directional selection |

| | |
|---|---|
| Positive selection | Opposite to negative selection. Example – where a duplicated gene is under pressure to evolve new functions. Pevsner, 2012. faculty.clayton.edu/Portals/367/Content/Biol4900/Biol-4900-Ch-07.ppt |
| Positive frequency-dependent selection | The fitness of a phenotype increases as it becomes more common.( 2009.www.dorak.info/evolution/fselect) |
| Paradoxical intrathymic positive selection | Cells are not subjected to negative selection but, paradoxically, undergo positive selection *in vivo*. (Viret, He and Janeway.2001.www.ncbi.nlm.nih.gov/pubmed/11470911) |
| Overdominant selection | *See:* Balancing selection |
| Oscillating directional selection | Selection can favour one phenotype at one time and another phenotype at another time. (2009) www.nature.com/nature/journal/v327/n6122/abs/327511a0 |
| Orthoselection | Chromosomes show a very ordered organisation and evolution. An oxymoron? (White 1973) |
| Normalising selection | *See:* Stabilising selection |
| Neutral selection | Maximum fitness attained during the adaptive walk of a population evolving on such a fitness landscape increases with an increasing degree of neutrality. (Newman 2009, http://ideas.repec.org/p/wop/safiwp/98-01-001.html) |
| Negative selection | The selective removal of rare alleles that are deleterious. See also purifying and background selection. 2009. (www.nature.com/scitable/topicpage/Negative-Selection) |
| Negative frequency dependent selection | The fitness of a phenotype increases as it becomes less common. (2009.www.dorak.info/evolution/fselect.) |
| Mineral selection | Some minerals are more likely to survive than other minerals through ‘competition’. Hazen (2010) The evolution of minerals. Scientific American 303, #3, 58-65 |
| Linear selection | *See:* Directional selection |
| Lineage selection | A process by which traits that are not directly assessed by the fitness function can evolve. G. W. Braught (2005) http://www.researchgate.net/publication/4140633 |
| Lifted selection | *See:* Relaxed selection |
| Koinophilia selection | When sexual creatures seek a mate, they prefer that mate not to have any unusual or deviant features Koeslag (1994). www.sciencedirect.com/science/article/pii/S0022519384710496 |
| Kin selection | Evolution of characters that favour the survival of close relatives of the affected individual, by processes that do not require any discontinuities in the population breeding structure. (Haldane 1932). |
| Intrasexual selection | Members of the less limited sex (typically males) compete aggressively among themselves for access to the limiting sex. T. H. Clutton-Brock, S. J. Hodge, G. Spong, A. F. Russell and N. R. Jordan. (2007). www.zoo.cam.ac.uk/zoostaff/larg/pages/tim.htm |

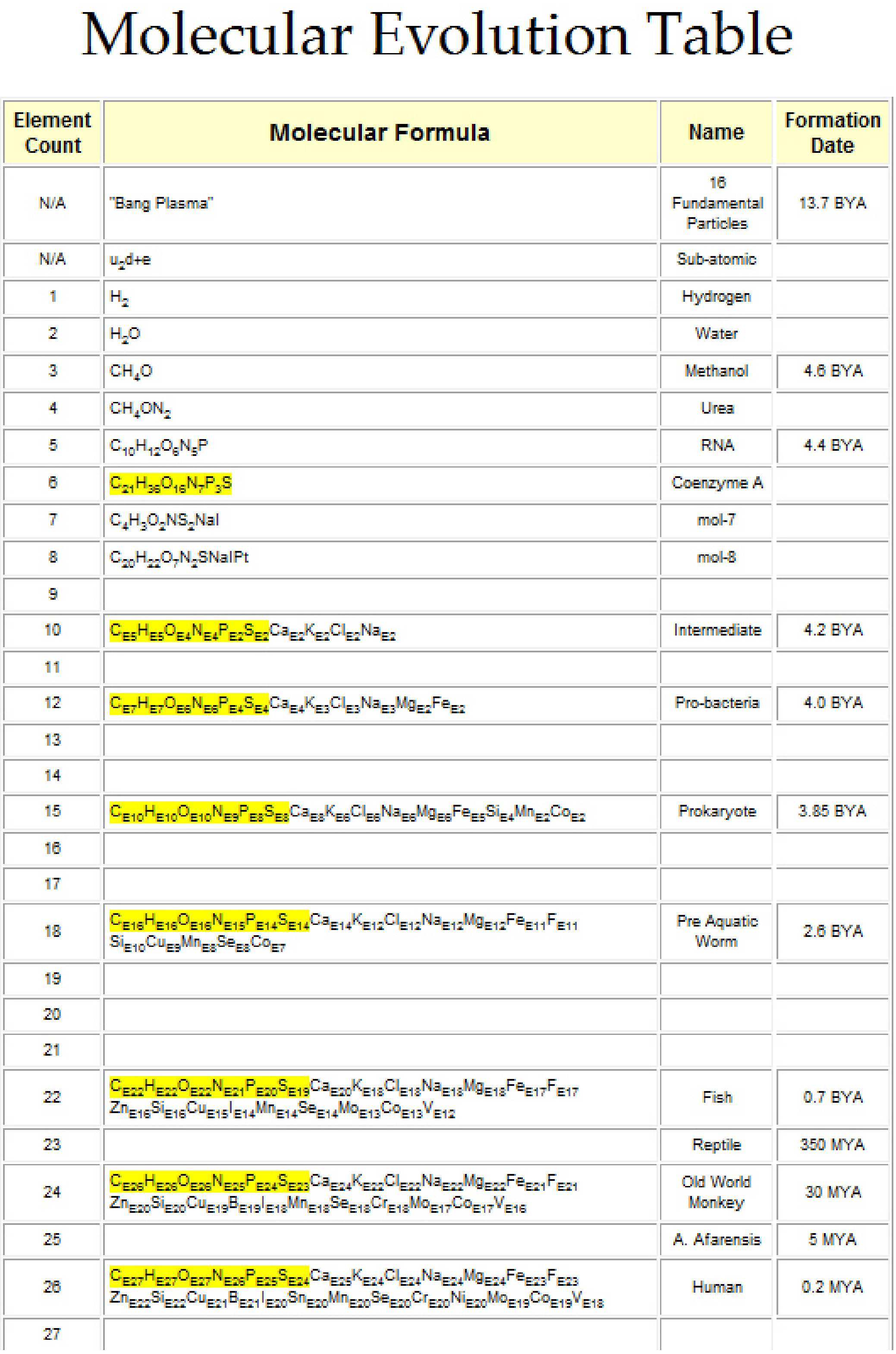
| | |
|---|---|
| Intersexual selection | In which males compete with each other to be chosen by females. (2009).www.associatedcontent.com/article/42665/ |
| Group selection | Alleles can become fixed or spread in a population because of the benefits they bestow on groups, regardless of the alleles' effect on the fitness of individuals within that group. (Wynne –Edwards 1962) |
| Frequency-dependent selection | The term given to an evolutionary process where the fitness of a phenotype is dependent on its frequency relative to other phenotypes in a given population. (Bell 2008) |
| Fluctuating directional selection | *See:* Directional selection |
| Fierce selection | Natural selection with fierce competition when the climate is harsh and the food is sparse. Under these conditions only the best, well-adapted individuals survive. (2009).www.mail-archive.com/friam@redfish.com |
| Environmental selection | Ambiguous artificial-plus-ecological factors. (2009. www.natur.cuni.cz/flegr/pdf/FL12-environmental.pdf |
| Ecological selection | Where inheritance of specific traits is determined by ecology alone without direct sexual competition (2009). www.pnas.org/content/97/23/12398.full |
| Dynamic selection | *See:* Directional selection |
| Disruptive selection | A descriptive term used to describe changes in population genetics that simultaneously favour individuals at both extremes of the distribution. (Bell 2008) |
| Disruptive frequency-dependent selection | Rare types cannot invade and genetic variability will not be maintained. (Bell 2008) |
| Disassortative sexual selection | Sexual selection in which one sex chooses the other, in such a way that the offspring benefits from the diversity of the parental genotypes. (Penn. 1996) stormy.biology.utah.edu/publications/X_fostering.pdf |
| Directional selection<br>*Also called:*<br>Dynamic selection<br>Fluctuating directional selection<br>Linear selection<br>Progressive selection | When natural selection favours a single phenotype and therefore allele frequency continuously shifts in one direction. Under directional selection, the advantageous allele will increase in frequency independently of its dominance relative to other alleles (i.e. even if the advantageous allele is recessive, it will eventually become fixed). (Bell 2008). |
| Cosmological natural selection | Universes selected with the highest number of black holes. (Smolin 1998) |
| Correlational sexual selection frequency | May be an important mechanism for maintaining the honesty of sexual signals. (Sinerco 2002). behav.zoology.unibe.ch/sysuif/uploads/Sinervo_Heredity.pdf |
| Correlated selection | May lead to the integration of functionally related traits. (Sinerco 2002). behav.zoology.unibe.ch/sysuif/uploads/Sinervo_Heredity.pdf |
| Contradictory selection | Different selection pressures at work. (Spieth 1979) www.jstor.org/stable/2460203 |
| Conflicting selection | Selection may be different at different stages of an organism's life. (Schluter 1991) adsabs.harvard.edu/abs/1991RSPSB.246...11S |

| | |
|---|---|
| Canalising selection | Reduces phenotypic variation. (Waddington 1942) |
| Balancing selection<br>*Also called:*<br>Overdominant selection | Balancing selection within a population is able to maintain stable frequencies of phenotypic forms. (Bell 2008) |
| Background selection | Opposite of a selective sweep. If a specific site experiences strong and persistent purifying selection, linked variation will tend to be weeded out along with it, producing a region in the genome of low overall variability. (2008).<br>www.nature.com/scitable/topicpage/Negative-Selection |
| Asexual selection | 'Selective' forces working against nuclear types in a population of *N. crassa*. (Davis 1959) www.ncbi.nlm.nih.gov › Journal List › Genetics › v.44(6) |
| Artificial selection | Intentional breeding of certain traits, or combinations of traits, over others. (Darwin 1859) |
| Anomalous selection | Any biological event, evolutionary or non-evolutionary (but can also apply to other sciences). Colin Beckley 2008 |

See also: Graham Bell *Selection: The Mechanism of Evolution* OUP 2008

Autoselection
Death selection
Leapfrog selection
Marker-assisted selection
Mass selection
Part-record selection
Periodic selection
Phototaxis selection
Pollen selection
r-K selection
Roundabout selection
Speed limit selection
Synclinal selection
Threshold selection
Truncation selection
Visual selection

**Appendix 5 Molecular Evolution Table**



# Molecular Evolution Table

| Element Count | Molecular Formula | Name | Formation Date |
|---|---|---|---|
| N/A | "Bang Plasma" | 16 Fundamental Particles | 13.7 BYA |
| N/A | $u_2d+e$ | Sub-atomic | |
| 1 | $H_2$ | Hydrogen | |
| 2 | $H_2O$ | Water | |
| 3 | $CH_4O$ | Methanol | 4.6 BYA |
| 4 | $CH_4ON_2$ | Urea | |
| 5 | $C_{10}H_{12}O_6N_5P$ | RNA | 4.4 BYA |
| 6 | $C_{21}H_{36}O_{16}N_7P_3S$ | Coenzyme A | |
| 7 | $C_4H_3O_2NS_2NaI$ | mol-7 | |
| 8 | $C_{20}H_{22}O_7N_2SNaIPt$ | mol-8 | |
| 9 | | | |
| 10 | $C_{E5}H_{E5}O_{E4}N_{E4}P_{E2}S_{E2}Ca_{E2}K_{E2}Cl_{E2}Na_{E2}$ | Intermediate | 4.2 BYA |
| 11 | | | |
| 12 | $C_{E7}H_{E7}O_{E6}N_{E6}P_{E4}S_{E4}Ca_{E4}K_{E3}Cl_{E3}Na_{E3}Mg_{E2}Fe_{E2}$ | Pro-bacteria | 4.0 BYA |
| 13 | | | |
| 14 | | | |
| 15 | $C_{E10}H_{E10}O_{E10}N_{E9}P_{E8}S_{E8}Ca_{E8}K_{E6}Cl_{E6}Na_{E6}Mg_{E6}Fe_{E5}Si_{E4}Mn_{E2}Co_{E2}$ | Prokaryote | 3.85 BYA |
| 16 | | | |
| 17 | | | |
| 18 | $C_{E16}H_{E16}O_{E16}N_{E15}P_{E14}S_{E14}Ca_{E14}K_{E12}Cl_{E12}Na_{E12}Mg_{E12}Fe_{E11}F_{E11}$ $Si_{E10}Cu_{E9}Mn_{E8}Se_{E8}Co_{E7}$ | Pre Aquatic Worm | 2.6 BYA |
| 19 | | | |
| 20 | | | |
| 21 | | | |
| 22 | $C_{E22}H_{E22}O_{E22}N_{E21}P_{E20}S_{E19}Ca_{E20}K_{E18}Cl_{E18}Na_{E18}Mg_{E18}Fe_{E17}F_{E17}$ $Zn_{E16}Si_{E16}Cu_{E15}I_{E14}Mn_{E14}Se_{E14}Mo_{E13}Co_{E13}V_{E12}$ | Fish | 0.7 BYA |
| 23 | | Reptile | 350 MYA |
| 24 | $C_{E26}H_{E26}O_{E26}N_{E25}P_{E24}S_{E23}Ca_{E24}K_{E22}Cl_{E22}Na_{E22}Mg_{E22}Fe_{E21}F_{E21}$ $Zn_{E20}Si_{E20}Cu_{E19}B_{E19}I_{E18}Mn_{E18}Se_{E18}Cr_{E18}Mo_{E17}Co_{E17}V_{E16}$ | Old World Monkey | 30 MYA |
| 25 | | A. Afarensis | 5 MYA |
| 26 | $C_{E27}H_{E27}O_{E27}N_{E26}P_{E25}S_{E24}Ca_{E25}K_{E24}Cl_{E24}Na_{E24}Mg_{E24}Fe_{E23}F_{E23}$ $Zn_{E22}Si_{E22}Cu_{E21}B_{E21}I_{E20}Sn_{E20}Mn_{E20}Se_{E20}Cr_{E20}Ni_{E20}Mo_{E19}Co_{E19}V_{E18}$ | Human | 0.2 MYA |
| 27 | | | |

Source: http://www.humanthermodynamics.com/evolution-table.html

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