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**An Examination of the Role of Symbiosis
and Symbiotic Systems in Evolutionary Theory**

by

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Abstract

This thesis intends to address one type of approach to evolutionary theory that seeks to criticise the neo-Darwinist account of evolution and individuation, that of symbiosis. This thesis will begin by examining current evolutionary theory through Darwin to neo-Darwinism, with a view to discerning which types of mechanisms neo-Darwinism rules out, and which it allows. This will be achieved by using a methodology which treats groups of related scientific theories or practices as research programmes. This methodological approach will allow comparison between competing research programmes, and it will be possible to determine whether or not a competing research programme is really a challenge to neo-Darwinism, or simply a sub-programme which shares some of the same metaphysical commitments and mechanisms as neo-Darwinism. The second half of the thesis will assess the 'symbiosis' challenge to neo-Darwinism on these terms. This section will conclude that symbiosis as it is usually formulated by its proponents is not a separate research programme that rejects neo-Darwinism in any significant way, but rather it is a sub-programme of neo-Darwinism. But I will also argue that there are aspects of this programme, if they were to be made more prominent, would in fact constitute an alternative research programme which could not only be treated as a separate research programme, but a research programme that is incompatible with neo-Darwinism. Bacteria in particular are organisms which function through symbiosis and their functioning problematises neo-Darwinism's account of individuation on a fundamental level. It will be concluded that neo-Darwinism is either a theory of very limited scope, or one which can be made into a general theory, but this can only be achieved through fundamental changes to neo-Darwinism itself.

Chapter 1

Introduction: An explanation of the approach this thesis will take to problems in the philosophy of biology

1.1 Context: The difficulties in assessing challenges to a theory which has many interpretations

Darwin's powerful explanation of the adaptedness of living things has given rise to one of the most pervasive conceptual changes science has encountered in modern times. Odd, then, that the proper interpretation of Darwin's theory of evolution by natural selection has been the subject of intense debate almost since its inception. Seldom has such an important scientific theory been so variously understood.

At the time of the publication of *The Origin of Species* in 1859 there was not only the notoriously hysterical reaction from the Church of England, and all of its concomitant argument against Darwin's theory on theological grounds, but also many other reactions, coming from the much more receptive scientific community itself. French biologists (as well as many English ones) saw traces of vitalism in Darwin's theory of evolution by natural selection, and heartily agreed. German biologists saw Darwin as the ultimate weapon against vitalism. British biologists influenced by empiricism saw Darwin as the scion of empiricism at work (general laws discovered through particulars). On the other hand, rationalist philosophers of science were quite happy to claim Darwin as one of their own as well, as an anti-metaphysician *par excellence*.

What can one make of a theory that has so many antagonistic interpretations? In fact, given this multitude of interpretations, is it proper to call this a theory at all? Even if we ignore the higher-level philosophical interpretations of Darwin's theory, it is not at all clear that biologists themselves have ever agreed on the proper interpretation of Darwin's theory. Of course, there is nothing surprising in the fact that a theory may mean different things to different people, or even have entirely different consequences depending upon its application. However, what is remarkable about evolutionary theory is that, since Darwin's initial formulation, evolutionary theory's theoretical and methodological refinement has been carried out by research groups with widely varying interests and viewpoints. It was often the case that their views of biology and

the nature of life were so at odds with each other that it is hard to see how they were even talking about the same 'theory' at all. Add to this the fact that operational terms introduced into evolutionary theory were often treated in totally different ways depending on the research interests involved, and the picture becomes even more complicated. For instance, in the area of genetics, followers of Mendel were interested in the mechanism of heredity, but used a methodology that was allied with the statistical methods used in mathematics to deal with variation in an otherwise uniform population.¹ At the same time, plant biologists in Germany were looking at the same problem through techniques in botany and biochemistry to see how variation was transmitted in a population. And the discoverers of the physical basis of heredity used a different methodology entirely. All were refining the mechanisms of heredity, but it seems unlikely that they were all seeking the same type of refinement of Darwin's initial description of the role of heredity. The same phenomenon, that of the disparate approaches to operational terms integral to evolutionary theory, has also occurred with reference to other important fundamental terms in evolution: for instance, phenotype, adaptation, fitness, species, and others.

The fact that evolutionary theory and Darwinism itself are so variously understood has important ramifications for any philosophical treatment of biology as a discipline. Evolutionary theory seems such a remarkably concise and simple explanatory framework with which to describe the living world, yet from the point of view of philosophy of science its precise theoretical structure and mechanisms seem elusive. However, the problem is not that evolutionary theory is so widely contested. This may in fact be a positive aspect of evolutionary theory. That it is an explanatory theory which is so flexible as to allow such divergent interpretations and still enjoy progress, although in a peculiar manner, is perhaps the reason why even today evolutionary theory enjoys such controversy and redescription. Rather the difficulty lies in deciding how to differentiate between the different interpretations of neo-Darwinism as the theory which currently dominates evolutionary theory and biology.

¹ Depew and Weber provide a useful and complete account of Mendelianism in Chapter 9 of *Darwinism Evolving*. Depew, David J. and Weber, Bruce H. *Darwinism Evolving: Systems Dynamics and the Genealogy of Natural Selection* (Cambridge MA: MIT Press 1995)

Debates over the proper interpretation of evolutionary theory have led to the rise of what has been called the "Darwin industry."² Although, as has been described above, there has always been controversy in the scientific community about how evolution actually functions (and the nature of this 'scientific community' has been fragmentary due to the wide variety of disciplines which have come to constitute modern biology), these debates have tended to have a somewhat limited audience outside academic science itself. The popularisation of Darwin has led to a seemingly endless supply of popular science books that seek to explain Darwin and his theory, as well as the science by which the theory is used, to a more general readership.³ Nevertheless, the growth of this industry, rather than simplifying the interpretation and mechanisms of evolution, has instead exposed the presence of different camps not only in the scientific community, but also within Darwin scholarship. This has made for an interesting and sometimes confusing mishmash of approaches and agendas, involving biologists, geneticists, biographers, philosophers of biology, cognitive scientists, microbiologists, and mathematicians. In such an environment, it is difficult to decide where popularisation begins and scholarship ends, and even more difficult to identify the areas of real debate and difficulty in evolutionary theory itself and distinguish them from debates of a more ideological or methodological nature.

This thesis intends to identify some of these areas of difficulty. Much has been made in both academic and popular scholarship of various 'alternative' approaches to Darwinism, or more specifically neo-Darwinism. There are attacks on neo-Darwinism, defined as the combination of Darwin's macro-evolutionary framework with modern genetics and molecular biology, from many sides. The scope of this thesis will only address some of these. It will not address creationist anti-neo-Darwinist attacks, and will not address 'vitalist' attacks where vitalism is conceived of as the mere postulation of a 'life force' with no more sophistication than this. It is outside the scope of this thesis to discuss 'dialectic' approaches to Darwin in the vein of Hegelianism and Marxism, and the critiques of Darwinism in the philosophies of Bergson and Nietzsche. In short, an analysis of neo-Darwinism and its purported alternatives at this level of

² See Brown, A. *The Darwin Wars: How Stupid Genes became Selfish Gods* (London, Simon and Schuster 1999).

³ For example, Dawkins, Richard. *The Selfish Gene* (Oxford: Oxford University Press 1976) and Dennett, Daniel. *Darwin's Dangerous Idea* (New York: Penguin Books 1995)

generality will not be adopted. An approach at this level of philosophical analysis would obscure the 'scientific' or at least methodological issues involved in the debates I wish to address.

1.2 Methodological Approach: The relative advantages and disadvantages of other approaches

This thesis intends to address one type of approach to evolutionary theory that seeks to criticise the neo-Darwinist account of evolution and individuation. It is thus a challenge of a different nature than challenges to neo-Darwinism which merely seek adjustments to its theoretical apparatus. This approach will be treated under the heading of a 'symbiosis-based research programme'. Symbiosis is a term which has been used to characterise the evolution of early life on earth, namely bacterial evolution, by proposing that early collective cells were symbiotic unions of various bacteria, and that these symbiotic unions formed the basis of later complex organisms. Thus, symbiosis is not merely a perspective on evolution, but also a scientific research programme with important results. In order to look at the specific issues I wish to address, those of symbiosis and bacterial evolution, it is necessary to adopt a methodology that will allow structural as well as historical aspects of the theory of evolution captured by neo-Darwinism to become clear.

X A methodology which might focus only on the larger metaphysically oriented criticisms of Darwinism and neo-Darwinism, such as a Bergsonian or a Dialectical one,⁴ would simply obscure the scientific practices and changes in theory that neo-Darwinism represents. This type of approach would be too broad for my purposes. However, neither can this thesis adopt a methodology which would treat neo-Darwinism merely as a collection of theories in a certain structural relationship to each other, for this approach would be too narrow. The exclusive adoption of any one approach from the philosophy of science, which might treat the issues in this thesis on the level of 'theory' only, would obscure the differences between various alternatives to neo-Darwinism, although it may make possible a description of neo-Darwinism itself. A characterisation of neo-Darwinism, although essential in this thesis as a

⁴ See Levins, Richard and Lewontin, Richard. *The Dialectical Biologist* (Cambridge MA: Harvard University Press, 1984)

starting point from which to view its alternatives, is not the final purpose of this overview. It is plain that issues in the philosophy of biology are important to this thesis and will be discussed, but a methodology adopted exclusively from this discipline would eventually prove too cumbersome. This is again because the status of evolutionary theory as 'theory' is an issue that is already very complex, and any such endeavour would involve a precise commitment to a view of issues of causality, probability, classes, and theories. A simple theory-oriented approach might eventually allow a characterisation of neo-Darwinism as theory, but would not allow a meaningful comparison with other alternative challenges to neo-Darwinism. Another approach that would be too narrow would be one that focused on the actual practice of science at the cost of theory. Although this thesis will depend on the results of actual scientific practice in reaching its conclusions, it does not seek to conclude from this any 'logic of discovery' in evolution or an exhaustive description of the theoretical-experimental apparatus of evolutionary theory.⁵ Nor does this thesis intend to tell a history of the various challenges to neo-Darwinism by investigating 'what scientists do' in the manner of sociology of science. What is needed in order to adequately address the 'symbiosis-based research programme' is a methodology which is not too exclusively oriented toward metaphysics, theories, or practice, but one that is able to deal with each of these without cost to the others.

In this thesis, I will focus on those alternatives to neo-Darwinism which claim to challenge it through a change of emphasis. These alternatives, though they often claim to be at odds with neo-Darwinism, are really attempts to refine neo-Darwinism, or at least to re-interpret its basic tenets in such a way that they can better reflect the actual processes of evolution. These alternatives do not want to do away with the whole theoretical apparatus of evolutionary theory, but they do disagree with some of the theoretical tenets of neo-Darwinism. For instance, symbiosis as an approach to evolution does not seek to deny that natural selection is important in evolution, but it does deny that its usual characterisation in neo-Darwinism (as a competitive process) is correct.

Because the alternative approaches I wish to consider in this thesis do not seek to undermine completely orthodox evolutionary theory but only to challenge it, they

⁵ For 'logic of discovery' see Popper, Karl. *Logic of Scientific Discovery* (London: Hutchinson, 1959)

can only be discussed with reference to the actual theoretical tenets of neo-Darwinism. And since they purport to challenge neo-Darwinism, we must examine neo-Darwinism itself to determine whether or not they can be regarded as challenges of note. Therefore, the methodology required for the purposes of this thesis is one that can accurately describe the actual theoretical apparatus of neo-Darwinism in such a way that both the fundamental tenets of neo-Darwinism and the challenges to these can be compared.

Furthermore, this methodology must also be able to track the changes that evolutionary theory has undergone in its past and present interpretations. Since it is the case that theoretical aspects of evolutionary theory are both theoretical idealisations as well as interpretations that affect the progress of actual research, it is necessary that the methodology we adopt in this thesis be able to meet these demands. This approach will allow an analysis that is aware of both the philosophically oriented debates within evolutionary theory together with the actual orientation of scientific research in evolution.

In order to outline a methodology which succeeds in meeting these demands, we must first examine some alternative methodologies which deal with biology and evolutionary theory. I will show that these approaches do in fact delineate a conceptual structure for evolutionary theory which I will also adopt and expand upon in the course of this thesis. Yet they are not sufficient if our aim is to deal adequately with the dynamic controversy both inside and outside neo-Darwinism. I will adopt a structure for discussing neo-Darwinism in which neo-Darwinism is seen as consisting of three elements: natural selection, variation, and heredity. I wish to exploit this structure in such a way that useful comparisons can be made between alternative approaches. For this purpose I propose to use a neo-Lakatosian framework for evaluating the changing dynamics of research programmes.

1.3 The Structure of Neo-Darwinism: the three interdefined components of natural selection, variation, and heredity

Let us first look at some ways in which philosophers of science, and philosophers of biology in particular, have characterised the structure of Darwin's theory of evolution

as descent with modification.⁶ The ways in which various aspects of the theory of evolution by natural selection are related to each other, either inferentially or deductively, have been treated at length by many writers of the history of biology.⁷ In this thesis, I will characterise Darwin's theory with reference to what I see as the three main elements of a theory of evolution: variation, natural selection, and heredity. It would appear that any theory of evolving entities must contain these three features. In fact, these elements seem to be the base-line necessity for any naturalistic theory of evolving entities, as opposed to an argument by design or a creationist account of adaptedness. No naturalistic theories of evolution have been produced which do not include these three elements of variation, natural selection, and heredity. Darwin's insight was to propose the interaction of these elements as an alternative explanation for the adaptedness of living things. It is often stated that evolution needs only natural selection and variation (in the sense of differential selection of variants) in order for evolution to occur. However, if this were true, evolution could never be cumulative or progressive. Without a hereditary mechanism of some kind, evolution would lead to constantly shifting and disorganised change. Therefore it is correct to characterise evolutionary theory in these terms.

⁶ Interestingly, the word "evolution" now means exactly the opposite of what it used to mean, as pointed out by S.J. Gould in *Ontogeny and Phylogeny* (Cambridge MA: Harvard University Press, 1977). The proper way to describe Darwin's theory would be "descent with modification", while "evolution" would (and used to) describe the unfolding of previously existing characteristics. However, in this thesis I will use the more common term "evolution" to describe Darwin's theory and the contemporary neo-Darwinist theoretical apparatus. I think it would be foolish to ignore common usage to make a philosophical distinction that is, after all, somewhat outside the scope of my thesis.

⁷ By "writers of the history of biology" I mean in particular those writers who have described Darwin's theory by reference to ideas of evolution contemporary to Darwin, for instance, Ernst Mayr's *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought* (New York: Penguin Books, 1991); David L. Hull's *Darwin and His Critics: The Reception of Darwin's Theory of Evolution* (Cambridge MA: Harvard University Press, 1973); Michael Ruse's *The Darwinian Paradigm: Essays on its History, Philosophy and Religious Inspiration* (London: Routledge, 1989). These writers focus on the differences between Darwin's ideas and contemporary accounts of evolution, especially on the Church of England's antagonism toward the idea of evolution. However, they do not focus precisely on the structure of the theory itself, and thus are of limited use in an endeavour which seeks to clarify the way in which the theory functions today. Therefore, use of this material will be left until the second chapter of this thesis, where it will be of more relevance.

Elliott Sober points out that "evolution" is difficult to define precisely as it "denotes the subject matter of an extremely variegated discipline ... [whose] subfields differ from each other in their aims, methods and results."⁸ But he concedes that, at base, evolution is change in gene frequency in a population.⁹ Now this minimal definition of evolution, though clear, does not really describe the processes that are involved in such change in gene frequency. Robert Brandon is a bit more explicit and uses a definition adopted from Lewontin:

The following three statements are crucial components of the Darwinian (or neo-Darwinian) theory of evolution.

(1) Variation: there is (significant) variation in morphological, physiological, and behavioral traits among members of a species.

(2) Heredity: Some traits are heritable so that individuals resemble their relations more than they resemble unrelated individuals, and, in particular offspring resemble their parents.

(3) Differential Fitness: Different variants (or different types of organisms) leave different numbers of offspring in immediate or remote generations.¹⁰

Whilst I agree with Brandon and Lewontin's characterisation for the most part, I do have some problems with it. My own characterisation includes both variation and heredity, as does theirs, but my third element is natural selection, while theirs is differential fitness. Although 'differential fitness' is perhaps closer to the minimal definition posed by Sober above, I think it is perhaps not the best way of characterising an important *process* in evolution, that of natural selection. I will leave until chapters 2 and 3 my own analysis of natural selection, but for the moment I would like to point out that the way in which 'change' occurs in an evolutionary process is through a 'selecting mechanism' of some type (for want of a better term) and this mechanism is at least structurally separate from the variants it 'selects' even if this 'selection' is

⁸ Sober, Elliott. *Philosophy of Biology* (Oxford: Oxford University Press, 1993) p. 5

⁹ Sober, Ibid.

¹⁰ Brandon, Robert "Adaptations and Evolutionary Theory" in *Concepts and Methods in Evolutionary Biology* (Cambridge: Cambridge University Press, 1996) pp. 5-6. Lewontin's own formulation can be found in Lewontin, Richard C. "Adaptation" in *The Encyclopedia Einaudi* (Milan: Einaudi, 1980)

conceived of as 'culling' variants. It is for this reason that "differential fitness" does not really express the third element of evolutionary theory well, for it makes this third element a 'result' of evolution and not a separable process or mechanism. In fact, Brandon and Lewontin's 'components' have more the look of 'facts which must be dealt with' than 'processes' in evolution. Even if there were general consensus about the correctness of these facts, there might still be no consensus about the mechanisms which explained these facts. For instance, their definition of differential fitness displays a curious interest in the *number* of offspring produced. In contrast, Sober points out that evolution is not itself interested in the actual number of organisms in a population (this would have ecological and not evolutionary significance) but rather it is interested in the gene frequencies of statistical proportions of these populations.¹¹ The actual "different numbers of offspring" discussed by Brandon following Lewontin have little place in evolutionary analysis. For these reasons I designate the third element as natural selection.¹² I would characterise the three crucial components in such a way as to draw attention to the mechanisms that these elements either presuppose or are linked to, rather than to merely focus on the 'results' of evolutionary processes.

Such characterisations as those of Brandon and Lewontin clearly have their place in terms of looking at Darwin himself and his own development of the theory of evolution. However, these characterisations are somewhat limiting in terms of looking at the structure of neo-Darwinism as a scientific theory and its corresponding mechanisms. Although I agree for the most part with the characterisation of neo-Darwinism in terms of this three-part structure, it is clear that more is needed. In order for useful comparisons to be made in terms of challenges to neo-Darwinism, it is necessary that we have a more refined approach to neo-Darwinism's theories and what they reflect. This can be done by using the idea of a research programme which can show that what is ruled out by a theory is at least as important as the explanatory structure of the theory itself. This brings into focus the difficulties that one encounters with giving a definition of neo-Darwinism which only notes its theoretical structure, as do Sober and Brandon's above. First, such characterisations do not give enough

¹¹ Sober, Elliott. *Philosophy of Biology* p. 6

¹² I also have some difficulties with Brandon's expression of the second component of heredity, though I will accept that it is a necessary component. To me, heritability must have much more to do with the actual mechanism of "copying", or at least with the mode of transmission, than with mere "resemblance".

weight to the actual mechanisms that play an important role in evolutionary theory. Second, whilst they do point to some of the 'metaphysical' considerations that are at the heart of neo-Darwinism as a naturalistic theory of evolution, they do not succeed in locating the precise role that metaphysics plays in the theory.

1.4 Metaphysics versus mechanisms: merits and disadvantages of different approaches to research programmes

The role of metaphysics and mechanism must be more precisely characterised in order for challenges to a theory to be evaluated.¹³ This can be done by using the concept of a 'research programme' to show the various roles that these two aspects play in scientific theory.

Karl Popper introduced the idea of a "metaphysical research programme" to describe how untestable metaphysical considerations could be seen as 'guiding' or 'steering' a line of scientific inquiry.¹⁴ Although these metaphysical commitments were not testable parts of the scientific theories, they did play an important role in at least delineating the general trends of two competing metaphysical research programmes. However, for Popper the way in which one of these competing programmes won out in the end was through the success of its own theories considered as *hypotheses*. The test was whether these hypotheses provided better predictions and explanations. Thus, for Popper's metaphysical research programmes there was no *internal* means of ruling out any scientific theory; anything is fair game and the proof is in the pudding, so to speak.

Now there are many reasons why this picture may intuitively seem incomplete, since one might point out that there do seem to be constraints on what types of theories are acceptable or unacceptable in any given scientific community, practical and ideological reasons at least. After all, not every testable theory that is proposed is taken seriously. But I do not want to consider this intuitive objection too seriously.

¹³ A point of clarification: I do not mean to use "mechanism" in the sense of the philosophical doctrine that is the subject of "mechanism versus vitalism" debate in philosophy of biology. Rather, my use of this term reflects a methodological principle: to show how the metaphysical principles of a research programme are instantiated in certain physical models of functions or processes at the empirical level.

¹⁴ See Popper, Karl *Conjectures and Refutations*, (New York: Basic Books, 1962)

Rather, I intend to focus on the role of 'mechanism' in a scientific theory. For Popper, a theory's content lies entirely in the collection of its true statements and thus there is no need for internal constraints on what a theory rules out. Consequently there is no need to look at the actual practice of the scientific community which wields the theory nor to look closely at any mechanism which might embody these theories. 'Metaphysics' for Popper is uncoupled from the actual scientific theories which make up a research programme and merely records the untestable commitments which, while driving the research programme, cannot constrain the content of science. Popper's view of science is similarly not concerned with how 'mechanisms' figure in scientific theories since in his view scientific theories are only collections of true statements.

Thomas Kuhn's picture of scientific theories took the objection from the actual practice of science very seriously indeed.¹⁵ Kuhn's recommendation that 'research programmes' ought rather to be treated as "paradigms" at least was more concerned with the actual history of science itself. Additionally, Kuhn was concerned to make it clear that science, as a progressive discipline, ought to be described as a dynamic and changing activity, whereas Popper's view of science had little to say about where any given theory or research programme was heading. For Popper, there was no way to look at a given hypothesis and say whether it was going to be fruitful in future scientific research; this could only be said *after* a hypothesis made correct predictions. Kuhn proposed that science was, in the main, a "puzzle-solving" activity.¹⁶ When things were going well with a theory, scientists were generally agreed on the fundamental points and simply tied up the loose ends. But when major problems began to be noticeable, in the form of anomalies that could not be explained away easily, this marked the beginning of an incipient "paradigm shift". In this situation theories were in a chaotic state, amenable to complete transformation, and could be turned on their head, as with the famous "Copernican Revolution". But even Kuhn was not explicit about the reasons for these transformations. That is, he did not claim that there was anything about the way the paradigms were constructed that could give any hints about why they might come to fail eventually. Furthermore, he did not give any special priority to the role of metaphysical considerations, or the content of theories themselves.

¹⁵ Kuhn, Thomas. S. *The Structure of Scientific Revolutions* (Chicago: Chicago University Press, 1962; 2nd edn 1970)

¹⁶ See Kuhn, *Ibid.*

Imre Lakatos used Popper's basic terminology to deal with these very issues.¹⁷ For Lakatos, in this sense very much like Kuhn, research programmes could be seen to be either "progressing" or "degenerating" and the reasons for this could be seen in the way in which the research programmes themselves functioned. But Lakatos, while using the terminology of Popper, turned the entire role of metaphysics on its head. Whilst for Popper, the metaphysical untestable considerations were in a way 'outside' the research programme itself, for Lakatos metaphysics was the core of the research programme itself. Metaphysics were considered to constitute the core of the research programme in the form of a 'protective belt' of hypotheses which ruled out certain types of competing hypotheses in a controlled way. Thus, metaphysics could serve both roles, namely as a 'steering' ideal, and as a practical internal brake on challenges to the theory. Thus, Lakatos thought he had responded to the claim made against Popper earlier, namely that in order for science to proceed as an activity at all, there must be some constraints on what is to be taken seriously as a challenge. For if each theory was falsified every time a new one came to light (as Lakatos believed Popper's philosophy of science entailed) nothing could ever get done. Furthermore, Lakatos believed that he had responded to and improved upon Kuhn's picture. Whereas Kuhn had provided no means of gauging the progress of any scientific paradigm except *ex post facto*, Lakatos claimed that the means of deciding whether a research programme was progressing or degenerating was to look at the 'protective belt' of the research programme. Since the protective belt of hypotheses served to rule out challenges to the theory in the form of 'anomalous phenomena' that could not be easily explained away, these hypotheses took the form of allowable exceptions. If the protective belt had too many exception statements in it, this meant the theory was in trouble, and was degenerating. If challenges, or anomalies, could be absorbed by the research programme, then the research programme was progressing and explaining more and more.

Thus for Lakatos, metaphysics served two roles; it *guided* the research programme as well as *constituting* it. The "hard core" of the research programme was

¹⁷ Lakatos, Imre. "Falsification and the methodology of scientific research programmes" in *Criticism and the Growth of Knowledge*; Lakatos, I and Musgrave, A., eds. (Cambridge, Cambridge University Press, 1970); Lakatos, Imre. *The Methodology of Scientific Research Programs* (Cambridge, Cambridge University Press, 1978)

composed of the untestable metaphysical theoretical statements of the theory. Yet there were some problems with Lakatos' story, which were highlighted by Watkins' treatment of the research programme.¹⁸ Watkins recognised that the 'untestable' nature of the hard core presented problems for any positivist conception of truth since this hard core, if thought to consist of metaphysics, was technically meaningless. The difficulty was how to deal with these untestable metaphysical statements, for if they were central to any scientific theory, yet strictly metaphysical, then they were untestable and meaningless. One might ask that if this were the case, then how could one ever evaluate the theoretical core of any scientific theory?¹⁹ Watkins' response was to conjoin metaphysical theoretical statements or hypotheses with other parts of the theory, that is, with those parts of the theory that made reference to testable or observable consequences of the theory; in effect with mechanisms. For instance:

Now a metaphysical hypothesis, as I conceive them, though neither entailed by, nor compatible with, any finite observation report whatever, may very well be entailed by some, and incompatible with other, *unverifiable* scientific *hypotheses*. It is this which ensure that such metaphysical hypotheses have truth values and helps to explain their significance for science.²⁰

This response resolved part of the difficulty. The "metaphysical core" or "theoretical ontology," as Watkins called it, was still the distinctive part of any scientific theory. However, it was testable by its conjunction with other aspects of the theory, namely the observables or mechanism which the theory used. Phrased in terms of corroboration, the above allows metaphysical statements to be at least falsifiable, even if not verifiable. Phrased in terms of the structure of scientific theory, it also makes clear the interdependence of metaphysics and mechanism for the delineation of research programmes.

¹⁸ Watkins, J.W.N. "Metaphysics and the Advancement of Science" *British Journal for the Philosophy of Science* 26 (1975) pp. 91-121

¹⁹ Watkins, J.W.N. *Science and Scepticism* (London: Hutchinson and Co., 1984) p. 193

²⁰ Watkins, J.W.N. "Confirmation, the Paradoxes and Positivism" in *The Critical Approach to Science and Philosophy* ed. Mario Bunge (New York: Free Press of Glencoe, 1964) pp. 92-115

Furthermore, in Watkins' earlier paper in *Mind*, he pointed out that metaphysics can be said to have regulative role in science even if metaphysical statements *are* untestable in themselves:

Although [metaphysical statements] are unempirical in the sense that they are compatible with every conceivable finite set of observation statements, they are not analytic or vacuous, but synthetic and factual, because there are empirical *theories* with which they will *not* be compatible.²¹

Thus, metaphysics can play a regulative role by clashing with certain empirical hypotheses which they rule out.

In a later paper of 1975 Watkins claimed that he, like Lakatos, did seek to provide "an internalist account of the influence of metaphysical ideas on scientific developments."²² That is to say, he attempted a method of finding the metaphysical statements which were internal to scientific theories themselves, as opposed to Popper's method of treating metaphysics as having merely an external steering role. Watkins believed it was incorrect to suppose that science only needed metaphysics in its infancy, and suggested that this conclusion about the role of metaphysics in science was what Popper's externalist view of the influence of metaphysics on science led to.²³

We might summarise this discussion as follows. Metaphysics imposes internal constraints on a research programme by ruling out certain types of theories, namely those that contradict the internal metaphysics of the programme. The conjunction (or collision) described here leads to the formation of what Lakatos called a "protective belt of auxiliary hypotheses", where certain challenges to a research programme are ruled out.²⁴ But these auxiliary hypotheses might better be called 'mechanisms' in the sense of empirical claims. The metaphysics must be expressed as a mechanism in terms of empirical research. Watkins, in his 1958 paper, also used this term to show how untestable metaphysics could clash with related empirical theories. For instance, he

²¹ Watkins, J.W.N. "Confirmable and Influential Metaphysics" *Mind* (67) 1958 pp. 344-365

²² Watkins, J.W.N. "Metaphysics and the Advancement of Science" pp. 91-121

²³ Watkins, J.W.N. "Metaphysics and the Advancement of Science", p. 106

²⁴ Lakatos, Imre. "Falsification and the methodology of scientific research programmes"

argues that the metaphysical doctrine of Atomism, which can be expressed as the belief that all that exists is particles moving in a void, might be expressed as mechanism in the corpuscular theory of light, and this mechanism would clash with a theory which said light is transmitted instantaneously. Thus the metaphysics is replaced by a mechanism, namely the corpuscular theory of light, which is at odds with any other mechanism which does not share the same metaphysical assumptions.

We have now established a framework for discussing the issues I wish to deal with in the course of this thesis and the methodology I adopt might be termed a 'neo-Lakatosian' approach to appraising scientific theories. It should be clear that it is very different to Lakatos' view in many respects. For instance, it is not particularly concerned with evaluating the 'progressive' or 'degenerating' aspects of scientific research programmes. However, it can still disclose the dynamism of historical changes in science. It is concerned with theory, but is also intended to make plain the way that theories are instantiated in certain physical models of functions or processes at the empirical level.

1.5 A 'neo-Lakatosian' methodology for dealing with evolutionary theory

The methodological considerations above allow us to show that both metaphysics and mechanism play a role in defining a research programme. I will argue in this thesis that neo-Darwinism can be largely defined by its anti-Lamarckist constraints as instantiated in its mechanisms. The apparatus described above can now be applied to neo-Darwinism.

This thesis will examine a challenge to Darwinism embodied by a set of approaches to biology which can loosely be grouped under the heading 'symbiosis'. The purpose of setting up neo-Darwinist evolutionary theory in the way described (as composed of three mutually dependent components, each recording both the metaphysical claims behind the theory as a whole as well as defining the hard core of the research programme through the elucidation of an appropriate mechanism) is to allow us to evaluate whether or not challenges to neo-Darwinism should best be characterised as separate research programmes or mere sub-programmes. That is, by defining the 'protective belt' as constitutive of any given research programme in terms

of both metaphysics and mechanism, a more sophisticated analysis of exactly what falls inside and outside the scope of neo-Darwinism is available.

In this thesis I will provide a characterisation of neo-Darwinism as a research programme in terms of the methodology outlined above. I will conclude that the allowable mechanisms (the ways in which the three elements of neo-Darwinism function in relation to each other) instantiate metaphysical commitments that are anti-teleological and anti-Lamarckist. Then we will be in a position to assess the symbiosis challenge to neo-Darwinism on these terms. I will conclude that symbiosis as it is usually formulated by its proponents is not a separate research programme that rejects neo-Darwinism in any significant way, but that, at best, it is a sub-programme of neo-Darwinism. But I will also argue that there are aspects of this programme which, if they were to be made more prominent, would in fact be an alternate research programme which could not only be treated as a separate research programme but a research programme that is incompatible with neo-Darwinism. This will be shown by example of bacterial evolution, which shows exactly which aspects of the symbiosis-oriented research programme might be taken more seriously for this incompatibility to be manifested.

Neo-Darwinism can be seen to be a theory which rules out several metaphysically oriented explanations. For instance, it is a naturalistic theory of evolving entities and thus might be said to rule out explanations which appeal to a God or Creator. Similarly, neo-Darwinism is an anti-teleological theory and thus it rules out explanations or theoretical claims which postulate final causes for life on earth or which account for modification in terms of intentional explanations. Neo-Darwinism might similarly be conceived of as an anti-vitalist theory, and would then rule out any explanations that resorted to a 'life force' as an explanation of the evolution of living forms. Similarly, it might rule out any in principle distinction between the living and the non-living. I am aware that these characterisations themselves merit further examination, but I use them here only to show that the various metaphysical 'anti-'s that neo-Darwinism is defined by are not present in any one of the elements of the theory of evolution that neo-Darwinism provides, but rather in the interaction between different elements in the theory as they are expressed in the form of *mechanisms*.

For instance, one of the anti-Lamarckist constraints of neo-Darwinism which will be discussed at length in this thesis is the Weismann Barrier.²⁵ The Barrier excludes the possibility of the environment actively influencing the organism toward hereditary change during its lifetime. It effectively claims that the organism cannot actively change itself to suit the environmental constraints it lives in, for such an option would be teleological, or perhaps even vitalist. The Weismann Barrier posits a physical barrier which prevents the environment from changing the hereditary component of an organism, and prevents the 'inheritance of acquired characteristics'. It might be thought that this constraint is simply part and parcel of the hereditary component of neo-Darwinism's theoretical apparatus. But if we look closer, we see that the constraint is born of the interaction between natural selection and heredity, and is expressed as a *physical mechanism*. That is, natural selection is conceived of as a force that 'weeds out' unfit organisms, and heredity is the means by which organisms make copies of themselves. Natural selection can only reject unfit organisms but it cannot influence organisms to change in any directed or *adaptive* way. An organism's hereditary material is sequestered from the action of natural selection by the Weismann Barrier, and thus cannot be influenced by natural selection in any adaptive way. Thus the way in which both natural selection and heredity are conceived are expressed in the mechanism of the Weismann Barrier.

Another example of the way in which the elements of neo-Darwinism are mutually dependent and expressed as a constraint in the form of a mechanism is in the idea of variation as 'random'. This is usually expressed by the phrase 'evolution proceeds through the accumulation of random mutations' or the like. To avoid the possibility that the organism could generate variation toward a pre-defined 'plan of nature', variation is conceived of as stochastic or random. This might seem to be a mere theoretical definition of variation as one of the components of neo-Darwinism, but again, it is really an effect of the interaction of several of the components, and again, it takes its form as a mechanism. It is not so much that variation is random, but that variation *must be* random, in order for natural selection to function as an undirected, goal-less process. Heredity too is implicated, since if evolution needs faithful copying in order to be a stable, progressive, and conservative process, then heredity must be constrained as a process which admits of only small 'random

²⁵ See Glossary

mutations'. So the stochastic metaphysical guiding ideal of neo-Darwinism as an undirected, non-teleological process is expressed in the mechanism of random mutation.

Therefore the methodology outlined allows an investigation into the way in which the theory of evolution functions, and also a means of assessing challenges to it from both inside and outside neo-Darwinism. Discussions concerning the ways the three elements are to be properly interpreted can be addressed, for instance, in terms of the adaptationist programme, the role of random drift, and the unit of selection. Additionally, challenges such as the symbiotic challenge, which focus on questioning the entities or individuals which neo-Darwinism delineates (the organism, the environment, the role of the gene), can also be addressed.

1.6 General outline of the thesis

This thesis is comprised of two parts. The first part, comprised of chapters 2 and 3, will discuss Darwinism and neo-Darwinism, and the various tensions within this conception of evolutionary processes, with a view to discovering just how metaphysical considerations behind it are instantiated into mechanisms which both define the theory and rule out certain other processes in evolution. The second part, comprised of chapters 4 and 5, will assess challenges to neo-Darwinism and see whether they can be said to be true challenges to the fundamental assumptions behind neo-Darwinism. The conclusion will address what the implications of the results of these chapters are for neo-Darwinism, and ultimately, for the philosophy of biology.

It is important first to characterise Darwinism and neo-Darwinism as a body of theory and mechanism, even if not a wholly complete or homogeneous one. This thesis will begin by undertaking such a characterisation through an examination of the history of Darwinism, tracing its refinements, additions, and unifications with other areas of biological theory. This account will culminate in a characterisation of contemporary neo-Darwinism. Along the way, some of the tensions within the theory will become clear, as they must if we are to consider that what neo-Darwinism rules out determines in a real sense its central tenets.

After a characterisation of neo-Darwinism is in place, we will turn to an approach to biology that is, in an important sense, outside the scope of neo-

Darwinism. Symbiosis is a general category, but 'symbiotic approaches to evolution' have been touted as true alternatives to neo-Darwinism in recent years.²⁶ The category of 'symbiosis' is useful since it can incorporate discussion of many different alternative approaches to neo-Darwinism, such as self-organisation, coevolution, Gaia theory, and the like. The analysis of symbiosis as several symbiosis-based approaches will show how it conflicts with neo-Darwinism. It will also be discussed to what extent symbiosis can be incorporated into neo-Darwinism. During the course of this discussion, the importance of bacteria in symbiosis will become apparent. Bacteria are in fundamental ways different to the types of entities envisioned as explainable in neo-Darwinism. The results of this analysis will then be applied to some debates in the philosophy of biology, and these results may help to discern exactly what is at issue in these debates.

In Part I, chapter 2 I will argue that, within the context of Darwin's theory of evolution as he delineated it, there is more than one way to interpret the three components of natural selection, variation, and heredity. The limitations placed on the interpretations of these elements by the work of August Weismann and Gregor Mendel were incorporated into evolutionary theory as it developed into neo-Darwinism. In the case of natural selection, it is possible to read this component as either an active creative force or as a passive mechanism which simply conserves existing adaptations. The possibility that natural selection may be treated as an active force allowed a teleological interpretation of Darwin's theory to become prominent, at least for a short time. But this type of metaphysics was eventually ruled out, as changes in the interpretation of the theory of evolution by natural selection led to an anti-Lamarckist, anti-teleological metaphysical interpretation. Both of the two other components, variation and heredity, similarly could be treated in such a way that their functioning was consistent with a teleological metaphysical principle. The work of Weismann and Mendel, as it was incorporated into neo-Darwinism, led to a denial of this type of interpretation. The mechanisms which Weismann and Mendel helped to create were anti-Lamarckist, and anti-teleological. However, there was still room for much disagreement even with these explicit mechanisms in place. For even though certain mechanisms which would violate the anti-Lamarckist character of Darwinism and neo-Darwinism had been ruled out, there was little agreement about the way each

²⁶ For instance, Lynn Margulis, Kevin Kelly, Stanley Shostak, Humberto Maturana, Francisco Varela.

component should be defined. Moreover, there was no general agreement on the question of what role each played in evolution and how powerful this role might be.

Chapter 3 continues to address the fact that it is still possible for evolutionary theory as a discipline to have varying interpretations of each of the three components of evolution. Although the question of whether natural selection was an active teleological force was answered in the negative by neo-Darwinists, this result causes problems for any theory which purports to be explanatory or predictive. The question of how natural selection can be an empirical law if it is a passive conserver of adaptations becomes paramount for philosophers of biology. It is necessary to deal with this problem before one can address the question of whether natural selection has a powerful role in evolution or merely a subordinate role to other sources of evolutionary change. The question of the role of chance in evolution is similarly difficult to address unless one has a view on the relative roles of natural selection and variation. In the case of heredity, which depends upon a concept of information in order to fulfil its role as the 'copying process' in evolution, one cannot investigate the role of heredity without examining closely this concept of information. The question of whether heredity is an important source of evolutionary innovation requires an investigation into its functioning. I shall argue that questions such as these can only be answered by looking at the way in which the three elements of evolution are mutually dependent. This entails looking at the mechanisms which instantiate the metaphysical principles that underlie neo-Darwinism. What these mechanism rule out are at least as worthy of discussion as what they rule in.

Part II of the thesis, beginning with chapter 4, attempts to use the results of the analysis in Part I to address some challenges to neo-Darwinism. Chapter 4 will explicitly discuss symbiosis-based challenges to neo-Darwinism. A short history of the 'symbiosis research programme' will be provided, which will serve to make clear the various differing claims behind the symbiosis challenge. It will be argued that some aspects of the challenge, particularly those which criticise natural selection and randomness as parts of neo-Darwinism, do not succeed in fundamentally challenging neo-Darwinism. However, it will be noted that in the case of one challenge (that neo-Darwinism fails to deal with cooperation as an evolutionary strategy), neo-Darwinism may in fact be guilty as charged. This does not, however, constitute a fundamental contravention of neo-Darwinist tenets, and at best, this criticism entails some small

adjustments to neo-Darwinism, changes which it can easily accommodate. There is one aspect to the symbiotic challenge to neo-Darwinism which does contravene neo-Darwinism's basic metaphysical assumptions, and this concerns the proposal of a Lamarckist mechanism of heredity.

Chapter 5 will explain the importance of this Lamarckist mechanism through the example of bacterial evolutionary processes and explain that this type of hereditary mechanism is not only highly important in evolution, but also inadequately addressed by neo-Darwinism's metaphysics and mechanisms. This leads to several important results. It will be shown that these Lamarckist bacterial processes cause such a fundamental shift in the way that the organism (or individual) is to be conceived, that they are incompatible with neo-Darwinism. This leads to the further result that neo-Darwinism is a very narrow theory, which only applies to a small proportion of life on this planet. And this in turn means that neo-Darwinism, if it wants to be able to apply to *all* evolutionary systems, must fundamentally change some of its metaphysics and mechanisms. The conclusion of the thesis will provide a sketch of what might be involved in such a change, and what this might mean both for science and for philosophy of biology.

Part I

Darwinism and Neo-Darwinism: Characterisation and Controversy

"I assure the reader that I find the task of forming a clear, well-defined conception of Mr. Darwin's meaning comparable only to that of one who has to act upon the advice of a lawyer who has obscured the main issue as far as he can, and whose chief aim is to make as many loopholes as possible for himself..."

—Samuel Butler, *Evolution, Old and New* (1882)

Introduction to Part I

The first part of this thesis will outline the development of Darwin's theory of evolution and describe some of the tensions within it. These tensions, as well as various limitations on the mechanisms of Darwinism which form the basis of the neo-Darwinist interpretation of evolution, will be shown to have significant effects upon various debates within the neo-Darwinist research programme. Thus, a historical discussion of Darwin, and the work of Weismann and Mendel in the wake of the *Origin of Species* will be essential in setting the stage for some of the debates over the proper interpretation of natural selection, variation, and heredity that were to become prominent in neo-Darwinism itself. These different interpretations will then be discussed in the context of neo-Darwinism itself and also as they appear in philosophy of biology. The central questions in both the history of Darwinism and neo-Darwinism are: what role does natural selection have in evolution? Is it the cause of evolution, or a description of the result of the interaction between organism and environment? Does natural selection produce variation, or select variation? How is variation passed on between generations of organisms? Does heredity produce variation or simply conserve it? These questions will be discussed in Part I.

Chapter 2

The History of Darwinism and Neo-Darwinism

This chapter will serve as both an historical introduction and a theoretical exposition of the fundamental aspects of the theory of evolution by natural selection. It will first describe the fundamental elements that are present in Darwin's theory of evolution by natural selection. The first section will deal with these elements of variation, natural selection, and heredity in terms of Darwin's own ideas. The second section will show how limitations on the mechanisms of Darwinism were completed by neo-Darwinism. The limits on heredity and variation as introduced by August Weismann and Gregor Mendel will be explained, as well as what is at stake in this limitation. In the third section the move from Darwinism to neo-Darwinism, known as the "Modern Synthesis" will be discussed.

Section 2.1 will look at the three elements of Darwinism through Darwin's own exposition of how these elements were to function in relation to each other. In each case, I will show that the element under scrutiny has more than one metaphysical interpretation and that often these metaphysical aspects are not yet grounded or instantiated in a specific mechanism. This is often a result of the way in which Darwin himself presented his ideas in the *Origin of Species*. Rather than positing specific mechanisms, Darwin instead makes use of comparisons and metaphors to draw attention to the ideas that he wanted to convey. Additionally, the structure of the *Origin* moves through examples to generalisations or principles. It is for this reason that I have considered variation, natural selection, and heredity in that order, since this mirrors more closely the order in which Darwin's argument is presented. I will show that variation and natural selection are tightly knit together, insofar as natural selection needs variation to work upon and, unchecked, variation cannot lead to evolutionary change without the selecting influence of natural selection.

However, there is still a difficulty in determining whether or not natural selection is an *active* or *passive* principle, for this distinction cannot be made unless we consider the way in which natural selection works *with* variation as a mechanism. If we assign an anti-teleological character to Darwinism as a theory we must find a mechanism for the generation of variation apart from the action of natural selection itself. For if natural selection is an active producer of evolutionarily valuable change,

then this might violate the anti-teleological character of Darwinism in its metaphysical aspect. This need for, and characterisation of, heredity as a means of transmitting traits between generations of organisms will also be addressed in section 2.1.3. This will be approached through Darwin's theory of Pangenesis. It will be argued that Darwin's characterisation of the element of heredity still leaves unanswered many questions about mechanism. That is to say, Pangenesis left open the possibility of a teleological interpretation of the functioning of natural selection and variation since it still allowed variation to come from use and disuse or through the inheritance of acquired characteristics. These notions of heredity are now thought of as Lamarckist ideas.

Section 2.2 will examine the limitations on Darwinism which resolved some of the issues concerning its metaphysically anti-teleological character through the introduction of certain mechanisms which embodied these metaphysical prohibitions. These took the form of the Weismann Barrier and of Mendel's laws of heredity. These mechanisms forced a change in the way in which natural selection and variation were envisaged. Ultimately these changes were incorporated into the Modern Synthesis of neo-Darwinism which will be outlined in section 2.3. However, whilst it will be noted that these proposed mechanisms still did not completely solve the question of whether natural selection was an active or passive force, they did at least shift the question from one of how structure was passed on from parent to offspring, to that of development and growth. This interest in development rather than heredity as a mechanism eventually came to be established as a separate research programme within biology. The interest in how an organism grew *after* it received its hereditary material meant that this separate research programme could still make use of a teleological or 'vitalist' life force to explain how the organisation of living beings emerged in the process of embryogenesis.²⁷ But this teleological principle was on a different explanatory level from that of natural selection and variation, mediated by heredity. For after Weismann and Mendel, the flow of information was curtailed in such a way that the organism could never produce adaptive variations by itself, to be transmitted to its offspring. This was the anti-Lamarckist and anti-teleological result of the limitations on Darwinism.

²⁷ For an example of this tendency within biological research, see Hans Driesch's *The Problem of Individuality* (London: Macmillan, 1914)

Yet the Modern Synthesis, while retaining and strengthening these limiting mechanisms, still faced issues connected with the relative importance of these mechanisms in evolution. As we shall see, defining heredity as particulate and discrete, or variation as random, did not lead to any necessary consensus about which of them were important agents of evolutionary change. Disputes concerning these questions form the basis of controversy in neo-Darwinism today, which will be discussed in Chapter 3.

2.1 Darwinism: the history of Darwinism and Darwin's own conception of his theory

The contemporary opinions in Darwin's time concerning the natural world were ideologically conservative.²⁸ The strongest themes were creationist and teleological in character. Paley's *Natural Theology* focused on the evident perfect adaptedness of living things to their environment, which was considered to be empirical evidence of God's perfect divine plan. All species were thought to have been separately created. Bishop Ussher's widely accepted calculation of the age of the world made it less plausible that change in species could occur in such a short time.

The discipline of geology was one area where change was studied seriously, it became clear that the earth was subject to change and catastrophe, and massive extinctions of flora and fauna. Those who studied change in species due to extinction, such as Lamarck, believed that species did not become extinct, they rather transformed completely into other forms. This transformation has been characterised as one of teleological progression toward perfection.²⁹ Charles Lyell, on the other hand, believed

²⁸ There is a large body of research into the history of Darwin's path to his theory of evolution by natural selection. Much of it concentrates on the Voyage of *The Beagle*, and on the intellectual reaction to the publication of *On the Origin of Species* in 1859. The intellectual and socioeconomic background in which Darwin worked is covered well in Michael Ruse's *The Darwinian Revolution: Science Red in Tooth and Claw* (Chicago: University of Chicago Press, 1979). Another discussion of the history of Darwinism is in Ernst Mayr's *One Long Argument*. A discussion of Paley can be found in Depew and Weber, and Gigerenzer, Gerd et al. *The Empire of Chance: How Probability Changed Science and Everyday Life* (Cambridge: Cambridge University Press, 1989).

²⁹ This characterisation has been disputed, and indeed it seems that Lamarck's *Philosophie Zoologique* (English trans. H. Elliott *The Zoological Philosophy* (London: Macmillan, 1914)) does not contain many explicit claims about tendency toward

that species did become extinct, but were replaced with other new species that filled the gaps, presumably through Divine creation. Lyell was therefore able to accept the notions of extinction and geological change while also appeasing creationists. It was Lyell who most influenced Darwin, but for Darwin the most important matter was the one Lyell had left somewhat unresolved; how do species originate, if not by Divine creation? Darwin's first break with the thought of his contemporaries was to recognise that species did in fact change, and this in turn led to the postulation of a mechanism by which species could do so.

At this stage it is worth introducing an issue concerning the character and rate of change in evolution that will become important later in the thesis; that of 'gradualism' versus 'saltationalism'. Lyell, in claiming that species could and did change over time, also thought that this change must be sustained by a uniform process, thus gradually and not subject to sudden changes. This was in opposition to Lyell's 'catastrophist' opponents who held that evolutionary change was caused in the main through geological events, like volcanic eruptions. As will be argued later in this thesis, this opposition is difficult to maintain unless a single privileged time scale is agreed upon. For as Depew and Weber note, even in geological time, events seem to happen 'gradually' if you look back far enough.³⁰ Although this gradualism has more to do with the timescale of the earth than it does with the process of evolutionary change, it appears that Darwin accepted that change happened gradually in species and that this was mirrored in the internal laws of life insofar as natural selection worked gradually as well. In opposition to this meaning of gradualism, there was 'saltationalism' (based on Huxley's phrase *natura non facit saltum*, nature does not make leaps). Saltationalists, such as Francis Galton (Darwin's cousin) believed that evolution could happen quickly, in 'jumps' by the evolutionary phenomenon of 'sports' or in Richard Goldschmidt's phrase, "hopeful monsters". These strange variations, freaks of nature, if you will, were the means by which evolution speeded up.³¹ Again,

perfection, rather, it implies a mere tendency toward *progression* or complexity. The descriptor 'teleological' for Lamarck's theory of evolution, is, however, uncontroversial in this context, in my opinion. It could be said that for Lamarck, no evolutionary change is merely accidental or random, all changes are directed in some way. Samuel Butler claims that Lamarck's treatment of causality (as well as Darwin's!) is *teleological*, but not *theological*. See Butler, *Evolution, Old and New* (London: Fiffeld, 1911)

³⁰ Depew and Weber, p. 98

³¹ Depew and Weber, p. 200

here it is difficult to differentiate between these two claims about the rate of evolution since there is no baseline timescale available with which to compare them. The dispute should rather be seen as an indication of the various ways in which natural selection and variation can be interpreted as acting.

2.1.1 Variation: Can be seen as the material upon which natural selection acts, and as that which is created by natural selection

We can see Darwin as having several 'insights' all of which contributed to elements of his approach to the problem of change in the natural world. First, on his *Beagle* voyage, Darwin noticed that species, which were previously thought to be essential types and thus sharply delineated from one another, showed a great deal of *variation*. Darwin was always bothered by the arguments between naturalists in taxonomy. Some thought that variants from the normal range of organisms in a species were varieties, some saw them as subspecies, and others saw them as separate species. It was difficult to judge whether a given variation was significant enough to distinguish a variety as a separate species, given the contemporary dependence on what Mayr has called the typological species concept (adhered to by the taxonomist Linnaeus).³² This typological species concept depended upon each species having an 'essence' of some kind which gave that species its 'species-ness'. Given the intangible nature of this supposed essence (since a horse was a member of the species horse depending upon its similarity to, or participation in, 'horse-ness') it was difficult to even distinguish variants sufficiently, much less be able to classify them in a meaningful way. More importantly, this intangible species essence was unobservable, and had to be inferred in some way, thus making it impossible to have any criteria at all for distinguishing types. The problem of distinguishing species from variants seemed to engage Darwin for much of his life and eventually, in the final chapter of *On the Origin of Species*, he claimed that his theory solved this problem once and for all.

The endless disputes whether or not some fifty species of British brambles are true species will cease... Hereafter we shall be compelled to acknowledge that the only distinction between species and well-

³² Mayr, *One Long Argument*, pp. 40-42

marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected...This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species³³

This insight is immensely important. It marks a major shift in the way in which species were conceived ontologically. Rather than treating species as natural kinds or ideal types, as had been done previously, species were henceforth to be treated as spatiotemporally contingent entities. In addition, Darwin here makes it clear that the intangible 'essence' of species in the typological species concept is an obstacle to proper taxonomy. Variation should be constitutive of species and speciation, in Darwin's view. Yet when Darwin was on the *Beagle* voyage the problem of taxonomising varieties suggested itself only because he saw such endless variety within a species. He consequently concluded that species could not be sharply delineated. A population of individuals showed sufficient variety such that a species could be seen as consisting of gradations along a continuum. Mayr suggests that shortly after returning from the *Beagle* voyage, Darwin had given up the typological species concept and was already using a definition of species that had much more to do with breeding habits. In particular he suggests that Darwin was concerned with the propensity of species to interbreed with each other.³⁴

Darwin had noticed the great variability amongst organisms, and this observation led to a confusion in his thinking which seems to have persisted throughout the development of his theory of natural selection. On the one hand, Darwin's observations of variation in nature made him realise that the existence of such variation had to be explained by his theory. On the other hand, he also thought of variation as a major mechanism or component to his theory of evolution, in the sense that variation was the material upon which natural selection acted. Thus variation is both the already extant variability within species in the natural world and also the mechanism by which such variability is produced. The ambiguity in the term 'variation' will be examined in more detail later. However, for the moment let us note that

³³ Darwin, Charles *On the Origin of Species* (Oxford: Oxford University Press, 1996) pp. 391-2

³⁴ Mayr, *One Long Argument* p. 29

variation and natural selection are closely tied to each other in terms of their functioning within evolution. Natural selection needs variation to work upon, yet the action of natural selection also produces variability by differential selection of varying traits.

Darwin's second 'insight' was in relation to the selection processes instituted by man in domestication and breeding. Darwin saw that man himself selected organisms that were beneficial to him and 'perfected' these organisms through breeding techniques. Darwin eventually decided that since breeders 'picked' the best individuals to be bred later on, this was the ideal way in which to characterise the action of selection in nature as a whole; natural selection picked those organisms that were better suited to their environments. Darwin clearly realised the power of this metaphor in explaining his theory.

Both of his early essays before the long-delayed publication of the *Origin*, (the 1842 Sketch and the 1844 Essay)³⁵, show that Darwin saw human selection processes as analogous to what actually occurred in nature as a whole. However, in these early works it seems that Darwin thought that although *human* selection in breeding tended to increase the amount of variety in species (in that breeders tended to choose variants that had unusual characteristics and develop these by crossing them with other unusual organisms to obtain an ever-widening variety of traits), he also seemed to think that *natural* selection might actually tend to decrease variability. It might decrease variation, in Darwin's view, because in a natural environment organisms would breed randomly with each other, and crosses between organisms with varying traits would be unlikely to produce novel variants, since Darwin believed in blending inheritance, where a cross between a tall and short organism would generally produce a medium height organism, so natural interbreeding would tend to diminish the strength of unusual variations.

Thus, his earlier works appear to suggest that Darwin was unsure as to where variation came from in nature and, since he thought that variation would tend to decrease through natural selection, he needed some external means of generating variation. Thus natural selection in this earlier form is quite weak as a speciating force. Since by this time he was unsure of his metaphor which equated human selection with

³⁵ Reproduced in *On Evolution* ed. Thomas F. Glick and David Kohn (Indianapolis: Hackett, 1996). pp. 87-115

natural selection, Darwin had difficulty explaining both where variation came from, and how it was acted upon in a context of selection. Later, after his work with barnacles³⁶, Darwin began to accept what he had initially suspected on the *Beagle*, that variation was rampant in the natural world, and he then decided that natural selection already had the raw materials to work upon for the process of speciation. Again, Darwin was struggling with two aspects of variation. On the one hand, variation was seen by Darwin as the raw material already extant in nature and upon which natural selection acted. On the other hand, since he was trying to explain change and speciation in nature, he needed to explain by what means variation is produced.

So at first Darwin seemed to have been unclear about the extent to which variation was available or produced in nature. His reliance on the phenomena of human selection and breeding processes may have contributed to this. Darwin was struck by the way in which human cross-breeding techniques often caused sterile offspring and clearly considered this as a problem for his theory. If natural selection really was like human breeding techniques, he thought, then it may tend toward producing sterile offspring which would obviously not contribute toward evolution and change in the long run. Also, Darwin noticed that breeders tended to pick varieties that would breed 'true', that is, these true breeds would have little variation. This fact, when placed in the context of natural selection, would also lead to less variation, which would again be counter what he saw his theory as trying to explain. In Darwin's 1838 Notebook C he tried to explain away these problems:

If varieties produced by slow causes, without picking become more and more impressed in blood with time, the generation will only produce an offspring capable of producing such as itself,--therefore two different varieties will produce hybrids but not varieties, which are not impressed on blood. will cross and produce fertile offspring.³⁷

³⁶ Darwin studied barnacles and concluded that male and female sexes evolved into each other, passing through an intermediate hermaphroditic form. He wrote extensively on this in *A Monograph of the Sub-class Cirripedia* (1851) reproduced in *On Evolution* ed. Glick and Kohn. See also Glick and Kohn, p. 130

³⁷ Darwin, *On Evolution* ed. by Glick and Kohn, Notebook C, [34] p.68

An elliptical remark to be sure, but here is one way in which we can reconstruct it. Darwin is worried that any variety produced "without picking" (that is to say, through *natural* and not *artificial* selection) will tend toward limited variation and will "become impressed in blood" and 'breed true'. If these true breeds cross, they will only produce hybrids and Darwin knows that hybrids from distant breeds are often sterile. He hopes that these varieties, "not impressed on blood" will be able to cross with each other to produce viable non-sterile offspring. The remark at least shows that he is unsure as to whether or not natural selection is really the same as human selection with respect to how variation is managed.

The problem for Darwin of whether variation is produced by natural selection, or already extant in nature was probably made more pressing for him because Darwin did not think that 'mere chance' had a very great role in producing variants. Darwin greatly depended on the effects of use and disuse for the generation of variation, as will be examined in the remarks to come about heredity. Later, 'random' as a characterisation of variation came to be adopted by neo-Darwinism, so it is worth noting that there are very few references to the role of chance in Darwin's writings, he did not appear to think it important to the generation of variation. Mayr himself concludes that the role Darwin assigned to chance has never been properly analysed, but suggests that Darwin did have a basic understanding that chance may operate on some level in evolution, although Darwin appeared to be satisfied with use and disuse as a mechanism of change.³⁸

We can see that at this stage in Darwin's thinking variation, already abundant in nature, has a very strong role in evolution as the raw material upon which natural selection acts. We can also see that variation does not at this stage have the character later assigned to it by neo-Darwinism: as random in nature. But what is clear at this stage is that variation and natural selection are closely tied together as an evolutionary process: there must be variation for selection to occur, but selection itself serves in turn to cause yet more variation. We may now turn to Darwin's characterisation of natural selection, to see more about this relationship between variation and natural selection.

³⁸ Mayr, *One Long Argument*, p. 49

2.1.2 Natural selection

The concept of natural selection was famously inspired by Darwin's reading of Malthus. His notebook entry on 28 September, 1838, after reading Malthus, is now regarded by many as the most important moment in Darwin's thinking in terms of the concept of natural selection.³⁹ It is at this point that Darwin appears to rely less on his metaphor of human selection and turn more toward competition as a characterisation of natural selection. What impressed Darwin most was Malthus' insight that the population of human beings, left unchecked, would increase at an exponential rate.⁴⁰ Darwin realised that limited resources were the key to the fact that species, with minor fluctuations, maintained the same number of individuals. Since any population, no matter how high or low its output of offspring, would increase exponentially, the stability of any population was governed by limited resources. Competition for limited resources meant there was a struggle for existence. A further insight to note was Darwin's realisation that this struggle could be construed as a cause of adaptive change in organisms. This of course is the source of the characterisation of natural selection, and evolution in general, as essentially competitive; 'Nature red in tooth and claw'. This issue is related to many ideological disputes concerning Darwinism and this therefore outside the scope of the methodology of this thesis. However, the interpretation of natural selection as 'competitive' forms the basis of some challenges to neo-Darwinism which will be discussed in part II of this thesis. Therefore the characterisation of natural selection as 'competitive' as opposed to 'cooperative' will be addressed on the level of function and mechanism later in the thesis, not on the level of ideology.

Darwin's reading of Malthus led him to suppose that natural selection, in a context of a struggle for existence, actually *produced* variation in the sense of different modifications. In the section "Natural Selection" in the *Origin*, Darwin clearly states that chance could not support such variation. Rather, speciation is the result of a struggle for existence: "Mere chance, as we may call it, might cause one variety to differ in some character from its parents...but this alone would never account for so

³⁹ Darwin, *On Evolution* ed. by Glick and Kohn, Notebook D [134] p. 73

⁴⁰ *Ibid.*, p. 75

habitual and large an amount of difference as that between varieties of the same species and species of the same genus"⁴¹ Since more offspring are born than can possibly survive in a struggle for existence, any checks on survival will serve to cause speciation, and in effect produce variation. But this raises the question of whether natural selection *causes* variation or merely selects variations. The two descriptions are clearly different.

We have seen that Darwin used at least two different metaphors to illustrate natural selection, that of artificial human selection, and that of the "struggle for existence" via Malthus. From the use of these metaphors alone it is difficult to reconstruct how *exactly* natural selection should be characterised. The issue of what Darwin meant by his term 'natural selection' in terms of how it was supposed to function in evolution, is made more difficult since Darwin was not always consistent in his discussion of this term. Above it was noted that Darwin did occasionally use natural selection in an active sense, since he used it in conjunction with the metaphor of human breeding processes. Let us look at a few selections from the *Origin* to make this point. To begin with, keep in mind that this discussion is concerned with whether natural selection has a positive active role in producing variation.

This *preservation of favourable variations* and the rejection of injurious variations, I call Natural Selection. ⁴² (*italics added*)

We have reason to believe...that a change in the conditions of life, by specially acting on the reproductive system, causes or increases variability; and in the foregoing case the conditions of life are supposed to have undergone a change, and *this would manifestly be favourable to natural selection*, by giving a better chance of profitable variations occurring, and unless profitable variations do occur, natural selection can do nothing. Not that, as I believe, any extreme amount of variability is necessary...to *produce* new and unoccupied places for natural selection to *fill up by modifying and improving* some of the varying inhabitants. ⁴³ (*italics added*)

⁴¹ Darwin in Glick and Kohn, p. 195

⁴² Darwin, *On the Origin of Species*, p. 68

⁴³ Darwin, *On the Origin of Species*, p. 69

I have added the italics to show the difference in what Darwin is saying about natural selection in both remarks: first, "preservation of favourable variations" is all that natural selection consists in, it is a mere culling mechanism. Second, Darwin is saying that variability would be "favourable to the action of natural selection", and natural selection can do nothing without variation to work upon. But in the same remark, natural selection is characterised as "producing" and "filling up" niches, "modifying and improving" inhabitants, seemingly a more active role in promoting variation. Darwin's remark after reading Malthus, though still a bit obscure, seems to treat natural selection in an active sense: "one may say there is a force like a hundred thousand wedges trying force into every kind of adapted structure into the gaps of in [sic] the œconomy of Nature, or rather forming gaps by thrusting out weaker ones."⁴⁴

Yet in later editions of the *Origin*, Darwin claimed that natural selection was not a force that induced variability. In these later works it seems that Darwin thought that natural selection acted only when there was available variability. Furthermore, in this passage Darwin seems to claim that the misconstrual of natural selection as an active force is simply a result of his use of an expression that indicates a natural law, just like the law of gravity.

Several writers have misapprehended or objected to the term Natural Selection. Some have even imagined that natural selection induces variability, whereas it implies only the preservation of such variations as occur and are beneficial to the being under its conditions of life...In the literal sense of the word, no doubt, natural selection is a misnomer; but whoever objected to chemists speaking of the elective affinities of the various elements?...but whoever objects to an author speaking of the attraction of gravity as ruling the movements of the planets? Every one knows what is meant and is implied by such metaphorical expressions; and they are almost necessary for brevity.⁴⁵

⁴⁴ Charles Darwin, Notebook D [134] in Glick and Kohn, p. 74

⁴⁵ Quoted in *Keywords in Evolutionary Biology* ed. Evelyn Fox Keller and Elisabeth A. Lloyd (Cambridge MA: Harvard University Press, 1992), p. 216

Darwin's remark here seems at first to solve the argument about what natural selection is once and for all, for here he seems to reject any active use of the concept. However, the interpretation of natural selection in the years after Darwin shows that Darwin's final proviso was not taken as seriously as he would have liked, and varying interpretations of variation and natural selection became important aspects of different research programmes that dealt with evolutionary theory. Both versions make sense given what Darwin himself claimed about evolution, and we will see later in the thesis that neo-Darwinism's resolution of this difference caused more complex issues surrounding a characterisation of natural selection to be raised.

The two possible interpretations of natural selection, as either an active force which generates variation, or as a passive force which simply works with existing variation, show two possible metaphysical interpretations of natural selection. Moreover, this distinction shows very clearly the tight relationship between variation and natural selection. Natural selection needs variation to work upon, but this variation must come from somewhere, and it is not wholly clear whether natural selection generates it, or if there is some other source for variation.

At this stage in characterising Darwinism as opposed to neo-Darwinism as a research programme, it is difficult to tease apart these two quite distinct interpretations. Although the metaphysics behind each interpretation are different, these are not yet instantiated in a mechanism which would allow us to rule out anything as non-Darwinist in this case. Again, we might characterise the difference as follows: if natural selection generates variation, then metaphysically it is tantamount to a cause or force, then natural selection itself causes change. But this might lead to a teleological view of natural selection, it might even lead to a teleological characterisation of life in general. German biologists immediately after Darwin certainly tended toward this view, as we shall see shortly. However, if we decide that natural selection must act on variation that already exists, *after* such variation is generated (by whatever means) we can see that the metaphysical thought behind this interpretation is *anti-teleological*. For here, selection is not correlated with adaptive variation.

On this second interpretation the variation must come from somewhere else, since it is not created by natural selection, but merely culled by natural selection. Perhaps it comes from the function of heredity itself? That is, there may be something

in the way that organisms pass on their characteristics to their progeny that itself generates variants, as the raw material for natural selection to act upon. At any rate, we could say that Darwin on this interpretation needed a mechanism for the generation of variation that was different from natural selection. It is hence not surprising that he began to depend on heredity to solve his problem. And the history of heredity after Darwin shows how the changing conceptualisations of heredity hinged to a large degree on the tension I have outlined between interpretations in the term 'natural selection'.

2.1.3 Heredity: Darwin's Pangenesis and the Spectre of Lamarck

It has often been remarked that Darwin treated the mechanism of heredity as a "black box"⁴⁶, in the sense that he did not have a theory to explain it at his disposal, and simply glossed it. However, this assertion is not fully accurate. Darwin knew that in order for cumulative evolution to work, there must be heredity, since there must be some kind of faithful copying process involved. In order to accumulate variations over time, successive generations must by and large resemble their progenitors, and then minute changes in their morphology can be cumulatively conserved. He did not gloss the problem of heredity, he even came up with a theory to explain it. Darwin's theory of heredity, called Pangenesis, is clearly a theory that proposes a mechanism for heredity. Furthermore, this hereditary mechanism had to explain not only how offspring resembled their parents, but also how the offspring were slightly different to their parents. So Darwin treated heredity as a "black box" only in the sense that he did not need a sophisticated mechanism of genetics for the theory of natural selection to get off the ground. He did, however, realise that heredity was necessary for cumulative natural selection.

Darwin's own theory of heredity attempted to explain how heredity worked by appealing to the existence of what he called "gemmules". These gemmules were like tiny replicas of cells that were "thrown off"⁴⁷ during cell division and accumulated in the reproductive organs of sexually reproducing species. Alternatively, they could accumulate in asexually reproducing organisms and lead to budding and the growth of

⁴⁶ Mayr, *One Long Argument* p. 82

⁴⁷ Glick and Kohn, p. 219ff

new individuals. Darwin's Pangenesis thus attempted to cut across both sexual and asexual organisms and was intended as a unifying theory. Darwin thought Pangenesis could unify many different phenomena, but all these need an explanation of both how offspring resemble their parents, and how they can be different from their parents, and in turn how asexual reproduction is related to these:

Everyone would wish to explain to himself, even in an imperfect manner, how it is possible for a character possessed by some remote ancestor suddenly to appear in the offspring; how the effects of increased or decreased use of a limb can be transmitted to the child; how the male sexual elements can act not solely on the ovules, but on the mother-form; how a hybrid can be produced by the union of the cellular tissue of two plants independently of the organs of generation; how a limb can be reproduced on the exact line of amputation, with neither too much or too little added; how the same organism may be produced by such widely different processes, as budding and true seminal generation...⁴⁸

Pangenesis could explain observed 'examples' of the inheritance of acquired characteristics since the gemmules were thrown off during the whole of the organism's development, and any changes that occurred would then be transmitted to the offspring of that individual. Darwin's theory importantly recognised that what was needed was a theory that could explain how offspring were generally similar to their parents, but nevertheless dissimilar in some respects. Fidelity in heredity is needed, but not perfect fidelity, since some variation is necessary for natural selection to work. Pangenesis is Lamarckist in that it relies, in some part, on the inheritance of acquired characteristics. As was noted above, Darwin needed variation as the raw material for natural selection to work upon, and the inheritance of acquired characters was one possible source for such variation. The reasons why this source was later ruled out by August Weismann, as an important influence on the neo-Darwinist Synthesis, will now be discussed.

⁴⁸ Darwin, Charles. *The Variation of Animals and Plants under Domestication* ed. by Francis Darwin (London: John Murray, 1905) p. 433

Before we examine Weismann's work, it will be useful to discuss the importance of Lamarck and his ideas concerning heredity.⁴⁹

Lamarck, as has already been discussed, saw species as evolving or progressing in a teleological manner. By this I mean that Lamarck thought that this change in organisms was largely due to an active response in the organism to the conditions of its environment. As the standard (and somewhat unfortunate) example of Lamarck goes, the long necks of giraffes could be explained by way of the conditions they lived in; through the effects of use and disuse while trying to eat leaves off tall trees. These changes in the organism would be transmitted to their progeny, and long-term environmental conditions became impressed upon the species over time. In effect, what Lamarck proposed was that organisms came up with responses to suit the changes in their environments.

There is considerable debate as to the extent to which Darwin agreed with the ideas of Lamarck, and of course the debate is somewhat ideological in nature.⁵⁰ But it is important to differentiate between Lamarckism as first, a reliance on the inheritance of acquired characteristics, and second, an account of evolution where change or variation in the organism is directly influenced by the environment in the sense that an organism actively seeks solutions in response to a given environmental condition.⁵¹ The first is a statement of the actual mechanism of heredity, the second is a characterisation of the generation of variation as teleological with respect to the interaction between the organism and its environment. Earlier it was shown that Darwin's theory of Pangenesis relied in some part on the inheritance of acquired characteristics, but it is not wholly clear that Darwin believed that variation was directed by the environment in quite the same way Lamarck did. Lamarckism taken as the permissibility of the inheritance of acquired characteristics as a source for variation was prevalent for many years until the work of August Weismann.

To conclude what we have learned through our discussion of Darwin's own ideas concerning his theory, we may say that there were several possible interpretations of natural selection, variation, and heredity. To begin with, variation could be thought

⁴⁹ Depew and Weber provide an excellent discussion of the history of Lamarckism in America and Germany in chapter 7 of *Darwinism Evolving*:

⁵⁰ See for instance chapter 3 of *On Evolution* ed. Thomas F. Glick and David Kohn

⁵¹ It is in this second sense of Lamarckism that Lamarck's position has been called *teleological*.

of as either the extant raw material for selection to work upon, already abundant in nature, or alternatively as that which is created by natural selection. This in turn allows two possible definitions of natural selection. Natural selection can be thought of as a passive law or force which simply culls existing variation, or alternatively, as an active force which creates variation, if it is the case that variation is not particularly abundant in nature. The availability of these two opposite interpretations leads to the further result that heredity can be conceived of in two different ways. First, if it is the case that natural selection itself is not sufficient to create variation and relies upon existing variation in nature, there might be a way for variation to be created through heredity itself, and these changes at the hereditary level may come about through use and disuse, or the inheritance of acquired characters. But if it is the case that natural selection creates variation through its own action, then this extra source of variation is not necessary.

This may go some way to explain why it is unclear to what extent Darwin was Lamarckist, since it is clear that two interpretations are possible. Given the different and opposite ways all three components of Darwin's theory can be interpreted, it can be said that Darwin either needed Lamarckist mechanisms as a further source for variation, or it can be claimed that he did not need such a source for variation. Of course, it is clear that Darwin did not respect some of Lamarck's ideas,⁵² but this in itself does not preclude the possibility that Darwinism as a theory needed use and disuse, or the inheritance of acquired characteristics. It all depends upon one's interpretation of the three components as to whether or not one assigns a teleological interpretation to Darwinism, at least at this stage. Later, in the change from Darwinism to neo-Darwinism, one interpretation was settled upon and it was this interpretation that defined neo-Darwinism as essentially anti-Lamarckist. This was achieved through the establishment of certain limitations on Darwinism, to which we now turn.

⁵² Glick and Kohn provide a discussion of the annotations Darwin made to Lamarck's *Philosophie Zoologique*, one of which reads "Very poor & useless Book". See Glick and Kohn pp. 82-86

2.2 Limitations on Darwinism: Weismann and Mendel

2.2.1 Weismann and the Weismann Barrier: the anti-Lamarckist reinterpretation of Darwinism

As was noted before, Darwinism allowed two possible interpretations of natural selection and the relative importance of its role in evolution. It could be regarded not only as an active or passive force, and one's view on this question often determined whether or not it was the most important force in evolution, or whether it was a weak force. Ernst Haeckel, probably the most influential contemporary reader of Darwin in Germany, had a rather unDarwinian interpretation of Darwin, and it was this interpretation that had a strong influence in Germany for many years.⁵³ Haeckel emphasised Darwin's story about the common descent of all living things, but tended to downplay the role of natural selection in speciation. Haeckel's "recapitulationist"⁵⁴ doctrine reflects the way in which he took Darwin to be telling a story more about progressive development than natural selection. Natural selection, for Haeckel, had a limited role in evolution, as an occasional 'tweaker' of life forms toward perfection. Haeckel believed strongly in the role of inheritance of acquired characteristics as a source of variation, he relegated natural selection to the subordinate role of culling novel forms that did not contribute to developmental perfection.⁵⁵ The actual mechanics of heredity as the generation of variation, for Haeckel and his followers, was part and parcel of the progressive direction of evolution. This is the interpretation

⁵³ Haeckel was not bothered by teleology, but he was bothered by vitalism. He was also a reductionist, since he was anti-Idealist. His reductionist materialism did not include a belief in Newtonian physics, interestingly enough. This distrust of Newton allowed Haeckel to concede that life was reducible to fundamental laws of nature, but these laws were intrinsic to life itself, and were more 'laws of life' than 'laws of nature', yet these laws of life were somehow to be carefully distinguished from a vitalistic 'life force'. A more thorough discussion of the strange bedfellows found in German philosophy of biology at this time can be found in Depew and Weber, *Darwinism Evolving*, chapter 7.

⁵⁴ Also known by the slogan "Ontogeny recapitulates Phylogeny", it claims that each individual organism's development reflects the stages that the life form itself took in historical speciation and development. S. J. Gould relates the details of recapitulationism in *Ontogeny and Phylogeny*, pp. 76-85

⁵⁵ Depew and Weber, *Darwinism Evolving*, p. 179

of Darwin's natural selection that August Weismann was working within, as one of Haeckel's students.

Weismann as a young man still believed in the inheritance of acquired characteristics, as did most biologists of the time. What impressed Weismann the most about Darwin's theory was its assault on teleology.⁵⁶ He was happy to explain selection as an adjunct to the inheritance of acquired characteristics, or use and disuse, until 1883, when he wrote his essay "On Heredity" where suddenly he utterly repudiated all Lamarckist ideas.⁵⁷ The reasons for his sudden shift are fairly obscure, since even in 1881, Weismann still used Lamarckist explanations. One possible reason for his shift is his work on the separation of germ cells and somatic cells in embryogenesis, where he claimed that the differentiation between these types of cells must happen very early on in development, and this separation persists throughout the life of the organism. Weismann's experiments showed that rats with their tails cut off did not breed tail-less baby rats, he interpreted this result in the light of cytological discoveries of the time regarding the separation of germ and soma. Weismann's 'Theory of the Continuity of the Germ Plasm' reflects this.⁵⁸ This led him to postulate a theoretical barrier, known as the Weismann Barrier, which separated the germ from the soma. Changes in the environment could affect the soma, or body of the organism, but these changes were prevented from affecting the hereditary material of the organism by the Weismann Barrier. The Weismann Barrier, although it was a theoretical entity, did have a physical counterpart, the nucleus of the cell, which sequestered the genetic material from the rest of the cell.

As we shall discuss in more detail later in chapter 3, Weismann's work was interpreted as delineating the flow of information in living systems by denying the possibility inheritance of acquired characters, although Weismann himself did not think in these terms. Information⁵⁹ flows only in one direction, in the sense that the organism cannot gain information from the environment and change itself accordingly. This

⁵⁶ Mayr, *One Long Argument* p. 113

⁵⁷ Cited in Mayr, *One Long Argument* p. 110

⁵⁸ The Theory of the Continuity of the Germ Plasm states that the germ line and somatic line are separate, but the germ line is continuous between generations, whereas the somatic line dies with each organism. The germ plasm line, in effect, is continuous through all generations.

⁵⁹ Admittedly, the use of the term "information" needs more discussion in the context of evolutionary theory, the use of this term will be more thoroughly investigated in section 3.3.

requirement of one-way information flow was eventually reflected in the Central Dogma of Biology after Watson and Crick's discovery of the structure of DNA.⁶⁰ The Central Dogma states that information flows from the DNA to protein via the mediation of RNA, but never from protein back to DNA, thus the Central Dogma of neo-Darwinism claims that information flows from the genome to the phenotype of the cell. In effect, it is a restatement of the same limitations that the Weismann Barrier also defined. This means that the organism only has its own genomic instructions that are made manifest in the morphology of the organism, and it is on the organism as its phenotype that natural selection acts. Any organism unable to cope with its environment is culled, and those left over are able to carry on reproducing, and hence their genomes survive. At no time is an organism able to selectively reprogram its own genome to cope with an unfriendly environment. Hence the organism cannot reprogram itself since information about the environment can never be retranscribed on the genome of the organism.

Weismann had now thoroughly reinterpreted German biology's view of Darwin, and insisted that phenomena observed in nature could be explained through selection without any reference to the inheritance of acquired characteristics. So Weismann's work was a limitation on how variation can be generated, by way of the way heredity functioned. The nature of heredity, in terms of the Continuity of the Germ Plasm, was in fact the reason that certain types of variation were ruled out. Weismann went some way to establishing the neo-Darwinism view of natural selection as the only source (or creator) of variation, and gave it a very prominent role in evolution.

By disallowing the inheritance of acquired characteristics, Weismannism effectively made the flow of information one-way. This move meant that a more detailed level of explanation for the generation of variation and heredity is necessary. Weismannism shifted the problem of heredity from one of how structure is passed on (Darwin's Pangenesis treated the problem on these terms) to one of development and differentiation.⁶¹ Since the germ plasm or germ line is 'immortal', the problem of heredity is really one of how organisms develop from this separate germ plasm. This

⁶⁰ Watson, James D., and Crick, Francis. "Genetical Implications of the structure of Deoxyribonucleic Acid" *Nature* 171 (1953) 964-967

⁶¹ Kauffman, Stuart. *Origins of Order: Self-organization and Selection in Evolution* (Oxford: Oxford University Press, 1993) p. 8

divorcing of the mechanics of heredity from the development of the organism meant that heredity was suddenly a separate level of explanation in evolutionary terms. This meant that heredity itself had to be looked at to find out how variation was generated, especially since now natural selection could only act upon variation *after* it was generated.

This allowed Weismann to provide his own alternative account of a mechanism of heredity, the theory of germinal selection, which was largely concerned with explaining the existence of maladaptive traits. Anticipating the 'unit of selection' debate, it allowed for different levels of competition and selection by proposing that germinal cells might compete with one another, and the result may be maladaptive for the organism at large. Though Weismann's work put a much stronger emphasis on natural selection as the agent of evolutionary change, it also caused hereditary mechanisms to become much more prominent in research programmes dealing with evolutionary theory. Many writers have commented on this effect, and Weismann's work is seen as the most important move in the shift in emphasis toward genes in the Modern Synthesis, which has elsewhere been called the "gene program" by Kauffman, and the "nucleocentric" research program by Sapp.⁶² However, Weismann's research was eclipsed by another conception of heredity which led to the development of the science of genetics, and this conception was due to the work of Gregor Mendel.

So Weismann, even though he had given natural selection a strong role in evolution, was also claiming that natural selection culled existing variation. It was thus a passive force which merely culled variation and did not create variation in an active sense. So there was still room for another source of variation in nature, but Weismann claimed that this source could not be the inheritance of acquired characteristics, or use and disuse. It could, however, be the case that heredity itself had another means of generating variation. Perhaps it was the case that hereditary material itself contained latent traits which might be brought out through the action of natural selection. This idea was taken up by the followers of Mendel, as we shall see.

⁶² Sapp, Jan. *Evolution by Association: A History of Symbiosis* (Oxford: Oxford University Press, 1994), Kauffman, *Origins of Order*

2.2.2 Mendel and particulate inheritance: the introduction of statistics into evolutionary theory

Gregor Mendel, the pea-counting monk, was devoted to discovering the laws of variation that were observed in hybrids. He and others had noticed, as Darwin had, that certain traits in hybrids tended to dominate others. Mendel sought an explanation for this in the form of a law. But importantly, Mendel proposed a statistical law, not a causal law that referred to what actually happened in the organism in terms of the generation of variation; Mendel's laws merely describe the expected statistical distribution of traits.⁶³ Mendel's studies led him to believe that blending of traits did not occur in the way that plant and animal breeders (including Darwin) had believed. That is, the union of a tall and a short plant did not yield a medium-height plant, as it would if 'blending inheritance' did occur. As we saw above, this was a source of worry for Darwin, who believed that natural selection may tend to decrease variation if blending occurred. Mendel's work showed that sexual recombination, though it always involved two traits in the zygote, led to the expression of one dominant trait in the organism. However the recessive trait was preserved, it could be expressed in the progeny of that organism. A fuller explanation of Mendel's work is provided in appendix 1. Although Mendel's work focused on the discovery of a statistical law governing heredity, its results did give a hint as to the physical basis of heredity, it meant that heredity had to be particulate in nature. It must be particulate since the discrete 'factors' joined up with each other in pairs, there was no blending of factors, and hence the mechanism in its physical basis called for discrete particles that could pair off in this way. Watson and Crick's discovery of the structure of DNA supported the particulate nature of heredity.

More importantly, Mendel's work showed that variation could be *latent* in organisms, due to the dominant-recessive relationship for some traits. This could be interpreted in such a way as to downplay the role of natural selection, however. First, the 'statistical' interpretation of Mendel allowed the possibility of downplaying the role of natural selection in generating variation by appealing to random, chance factors in 'mixing' sexual reproduction, given the particulate nature of heredity. This aspect of

⁶³ An excellent treatment of this point is present in Gigerenzer et.al. pp. 145-152

Mendelism was taken up by the geneticists in the Modern Synthesis by R.A. Fisher and Sewall Wright, as we shall see. Second, it was also possible to downplay the role of natural selection by appealing to the possibility of latent traits hidden in the recessive traits of organisms, and thereby still seek a more active role for the organism itself in evolution.

So again we see two possible interpretations of the three components of natural selection, variation and heredity. What was conserved from Weismann was the separation between the germ and the soma, where he disallowed the inheritance of acquired characteristics. And this gave a strong role to natural selection. Furthermore, it influenced researchers to look more closely into the way heredity functioned as a mechanism. Paradoxically, due to the influence of Mendel's work, this led to a view of heredity where it was possible to *downplay* the role of natural selection by claiming that random mixing and latent traits hidden in the actual physical mechanism of heredity were important factors in the generation of variation. What was conserved from Mendel was, in the words of Depew and Weber: "The key concept of the Mendelian revolution is that heredity comes in discrete units that are combinable and dissociable in mathematically predictable ways."⁶⁴

So these limitations on Darwin still allowed various metaphysical interpretations of the way in which the three components of natural selection, variation and heredity were thought to operate. These limitations served only to establish neo-Darwinism as an essentially anti-Lamarckist theory, but they did not succeed in giving a strict definition of any of the three components. For instance, Weismann's prohibition of the inheritance of acquired characters, by postulating a one-way flow information flow between organism and environment, (the anti-Lamarckist move *par excellence*) did not succeed in making it clear that natural selection was the only important force in evolution, although it did show that natural selection only acted upon variation *after* it was created. And Mendel did tighten up the definition of heredity by providing a particulate mechanism, where traits combined in discrete units, but this did not lead to any particular notion of how natural selection acted upon heredity to create variation. In essence, we can say that these limitations on Darwinism only ruled out specific

⁶⁴ Depew and Weber, p. 217 Depew and Weber provide a useful and complete account of Mendelianism in Chapter 9 of *Darwinism Evolving*. See also Mayr, *One Long Argument* and David Hull in *The Philosophy of Biological Science* (Prentice Hall: New Jersey, 1974), Chapter 1.

mechanisms: those that are Lamarckist. They did not stop debates about which role each component was supposed to have in evolution. And as we shall see, the period of the Modern Synthesis did not solve many of these issues either, the metaphysics of neo-Darwinism was still up for grabs, but the mechanisms which were considered allowable began to fall into place.

2.3 The Modern Synthesis

The Modern Synthesis describes the development of what is now called neo-Darwinism. Neo-Darwinism is usually characterised as the marriage of modern genetics and populational genetics with Darwinism. This characterisation receives much discussion,⁶⁵ but for the purposes of this discussion I would like to concentrate only on the way in which neo-Darwinism as embodied in the Modern Synthesis deals with the issues already covered, variation, heredity and natural selection. To many writers, the most important debate in the Synthesis focused on what many have called the issue of "hard" versus "soft" inheritance.⁶⁶ Closely related to this issue, is of course the role of natural selection. In 'soft' inheritance, the organism is thought of as actively responding to the environment and changing toward it. Thus variation occurs before natural selection acts upon it, and this could occur through use and disuse, or the inheritance of acquired characteristics. In 'hard' inheritance, all changes in the organism arise purely by chance, and natural selection then acts upon these changes afterwards. One of the most important features of the Modern Synthesis was to reject soft inheritance completely. When hard inheritance was agreed upon, this in turn changed the nature of natural selection.

As we shall see, it was still possible to disagree over whether natural selection was the only important force in evolution, but the rejection of 'soft' inheritance, as an extension of Weismann and Mendel's limitations on Darwinism, did have the effect of making neo-Darwinism explicitly anti-Lamarckist. That is, certain Lamarckist mechanisms were ruled out. The adoption of the Weismann Barrier as a theoretical entity which prevented the organism from actively changing itself to suit its

⁶⁵ For instance, see Mayr, *One Long Argument*, Maynard Smith *The Theory of Evolution* (Cambridge: Cambridge University Press, 1993)

⁶⁶ Mayr, *One Long Argument* ch. 8

environment and then passing on these changes to its offspring meant that change had to come from other avenues. Mendelianism allowed these changes to come from latent traits in the hereditary material of the organism, as well as from statistically random mixing of these traits during recombination.

In 'soft' inheritance, natural selection could be quite weak as an evolutionary force, since the active changes in the organism while responding to the influence of the environment could provide the needed evolutionary change. In 'hard' inheritance, since all evolutionary change occurred by the action of natural selection *after* variation was extant in the organism, natural selection could be considered as the only speciating force available, and therefore became much more important as an agent of evolutionary change. Yet equally important is the reappraisal of the role of chance in evolution necessitated by the acceptance of hard inheritance. If organisms could not actively change themselves in response to their environments, then all change in them had to be a matter of chance. In fact, all variation had to be due to chance. The Mendelian use of statistical methods to look at the distribution of traits in an organism gave chance a still more prominent role. But even this did not lead to any consensus on whether natural selection was the only important force in evolution.

M.J.S. Hodge notes that the introduction of population genetics to neo-Darwinism by R.A. Fisher, Sewall Wright, and J.B.S. Haldane had the effect of altering what was meant by natural selection.⁶⁷ These three contributors to the modern synthesis had different beliefs about the role of natural selection. R.A. Fisher was interested in marrying genetics to evolution by way of probability; he was convinced that models from statistical mechanics and thermodynamics could be imported into evolutionary biology. His interpretation of evolutionary biology in this probabilistic spirit led him to claim that natural selection could be divorced from factors that changed variance in other ways, for instance Mendelian dominant factors. His conclusion was that though there may be other factors that influence evolution, these were relatively unimportant, and natural selection therefore was the most powerful force in evolution. Fisher in effect agreed with Darwin insofar as Darwin claimed that natural selection could only occur when variation was present. However, he disagreed with Darwin's equation of Malthusian competition with natural selection. The

⁶⁷ Hodge, M.J.S. "Natural Selection" in *Keywords in Evolutionary Biology* p.215
Discussions of Fisher and Wright can also be found in Depew and Weber, *Darwinism Evolving* and Mayr, *One Long Argument*

introduction of probabilistic reasoning into evolutionary theory meant that in Fisher's view, Malthusian competition was best interpreted as a limit, rather than a law or force in itself. Fisher eventually claimed that Malthus was a special case, or consequence of natural selection. Selection was everything, in Fisher's programme.

Wright, on the other hand interpreted natural selection somewhat differently. He believed that Fisher's recasting of evolutionary biology into the thermodynamic model did not solve the issues regarding the possible causes of evolution; it did not permit the inference that natural selection was paramount, while Mendelian dominance, random drift etc. were unimportant in evolving populations. Wright claimed that Fisher's version of evolutionary biology was too idealised; real populations, he argued, were apt to change in ways that were not reducible to statistical mechanics. He believed that real, isolated, imperfect populations were able to change by means of random drift, without reference to natural selection. In effect, Wright downplayed the role of natural selection, and believed random drift, migration, mutation and other factors were much more apt to affect population change. Wright, therefore, believed natural selection was less important in evolution.

Thus were the battle lines drawn, (and interestingly, they are drawn along the lines of Britain versus America, a gap that may still persist to some degree today). However, Depew and Weber remark that the issue in the background is one that has to do with the status of laws in the biological sciences; they see Fisher as a proponent of a kind of reductionism where the 'law' of natural selection is analogous to the laws of physics, accepting that such laws are inherently statistical in nature. Wright, on the other hand, tends toward a view of science where laws are in the explanatory background, and parameters and models are more important in explanation.⁶⁸ Yet important issues for neo-Darwinism were already in effect in the Fisher/Wright disagreement: to what extent could one distinguish drift from natural selection? What would it mean to even compare causes of evolution in this way, if natural selection was an omnipresent background assumption? These issues will be discussed in detail in the following chapter.

But for now we may conclude that the Modern Synthesis of neo-Darwinism did put some limitations on the types of mechanisms that were permissible in terms of evolutionary theory. The adoption of the Weismann Barrier as an anti-Lamarckist

⁶⁸ Depew and Weber, p. 284

theoretical construct, or mechanism, meant that the organism did not adapt *toward* an environment, as the more teleologically oriented followers of Darwin might wish. Rather, natural selection was a process by which the organism was passively moulded by the environment. Such considerations, however, still left the question of what exactly natural selection is open to question. Furthermore, the ways in which the three components interacted with each other made it possible to debate the question of whether natural selection, if only a culling process which preserved variations after they were generated, by means of mechanisms other than the inheritance of acquired characteristics, could be said to be the most important force in evolution. This question still concerns the philosophy of biology, as we shall see in chapter 3. The Weismannian contribution toward the anti-Lamarckist, anti-teleological character of neo-Darwinism did serve to constrain the flow of information to a one-way flow: from germ to soma, never the reverse. But this move did not do much to elucidate just what sort of information was being transmitted in heredity. And the Mendelian inclusion of statistical methods to describe the frequency of discrete particulate units which were the basis of the variational traits of organisms did make the notion of chance, randomness and probability more prominent in evolutionary thinking. Yet here again, it was not clear just what role chance or randomness was to play in living evolutionary systems. Questions such as these, which were raised but largely unanswered during the shift from Darwinism to the Modern Synthesis of neo-Darwinism, will be addressed in the next chapter.

Chapter 3

Contemporary Neo-Darwinism and Philosophy of Biology

The previous chapter examined the three elements of evolutionary theory by tracing their development through their initial formulation by Darwin, through the limitations placed upon them by Mendel and Weismann, and through their development in the Modern Synthesis. Changes in their interpretations were noted, as well as the inherent ambiguities in how they are to be understood. This development and reinterpretation continues in the context of contemporary biological research today. This chapter will examine some recent controversies in biology in the three areas of natural selection, variation and heredity with a view to showing that these three elements, though central to evolutionary theory, remain problematic with regard to their proper role in evolutionary theory.

These three elements are fundamental to evolutionary theory, and each focuses on questions that are not only empirical, but also philosophical in nature. That is, each element's interpretation is largely governed by the way in which it is instantiated in terms of mechanisms, yet these mechanisms themselves entail wide-ranging implications in philosophical or metaphysical terms. Thus natural selection, treated as a force or mechanism, is interpreted in varying ways for reasons to do with the types of evolutionary systems under enquiry. Yet the notion of force or cause in evolution is always subject to philosophical interpretations. Similarly, variation as a 'random' process has links to an understanding of evolutionary systems as stochastic in some sense, and this in turn relates to concepts such as 'chance' and 'randomness'. Finally, heredity is connected with an empirical determination of the mechanisms of reproduction, but is also connected with a notion of 'information' which is conserved in the element of heredity.

This chapter will therefore discuss the interrelation of these three elements of evolution in terms of their empirical interpretations and their philosophical implications. Section 3.1 will discuss natural selection as a force, and investigate the role of fitness in the interpretation of natural selection. Natural selection will also be examined with reference to the controversy regarding adaptationism, a position that holds natural selection to be the most powerful, or even the sole, force in evolution.

The claim that natural selection is a perfecting or 'ordering' force distinct from mere chance will lead into the discussion in section 3.2. This section will examine the role of chance in evolutionary theory, as either a characterisation of novelty or as a constitutive aspect to evolution in the larger sense. The third section will examine heredity and its relations to information and selection in the context of the "unit of selection" debate.

In the case of each of the three elements, we will see how the metaphysical underpinnings of the neo-Darwinist research programme as a whole are expressed in the way the mechanisms of the theory of evolution are understood. In addition, it will be shown that the three elements must be interdefined - they all three come as a package. Attempts to define any element on its own, without reference to its interaction with the other two, inevitably lead to a skewed or incomplete characterisation of neo-Darwinism as a research programme. Finally, this chapter will allow a characterisation of neo-Darwinism as a research programme, which in turn will allow us to assess how challenges to neo-Darwinism, or alternative research programmes, can be evaluated.

We can present the results of this chapter as follows: Natural selection, as the first element of neo-Darwinism we will examine, is variously interpreted as a force, a cause, a law of nature, a result of the interaction between organism and environment, etc. Yet in order for natural selection to serve more than a merely metaphysical role, in order for it to be given any empirical grounding or predictive ability, it must function in conjunction with both variation and heredity. It must either 'act on something', upon a 'unit of selection', or act *via* something, a measure of fitness perhaps, in order to be incorporated in a mechanism. Thus, the question "Is natural selection the most important force in evolution?" which is at the heart of the "adaptationist debate", inevitably presupposes that natural selection can somehow be decoupled from the other two elements of variation and heredity. This, I will show, is impossible. And moreover, I conclude that natural selection, variation, and heredity are interdefined in such a way that selection is uncorrelated with the generation of variation. We shall see that natural selection is treated as an anti-Lamarckist constraint on evolution where it cannot be a creative force, acting toward an adaptive goal or plan of nature, but rather it is understood as a means of change that functions in an essentially stochastic way.

This 'stochastic' aspect of neo-Darwinism leads us to the conclusion that in the

case of variation, which is often described as random, we may say that this randomness is not truly random, but only random with respect to evolutionary advantage. Again, this second element of variation cannot be characterised alone, without reference to natural selection and heredity. This can be shown by example of the "drift controversy" which attempts to evaluate the difference between "evolution due to random factors" and "evolution due to natural selection". It will be shown that there is no way to distinguish these hypotheses either experimentally or theoretically within the confines of the neo-Darwinist research programme. In the end, variation cannot be characterised as random *per se*, but only as random with respect to evolutionary advantage. This also is an anti-Lamarckist constraint expressed as a mechanism.

Lastly, in the case of heredity, I will show that the role of heredity as a part of neo-Darwinism cannot be divorced from the way natural selection and variation operate. Since heredity serves the role of a 'copying system' to preserve evolution as a conservative process, it is natural to characterise the third element of heredity as an 'information carrier'. But the application of the concept of information to heredity is problematic, since at base the function of heredity is closely associated with natural selection, as the "unit of selection problem" will make clear. For a reductionist approach to biology allows heredity to be closely allied to natural selection. Moreover, even if heredity is conceived of as an information carrying system, it is still expressed as a mechanism in such a way that the flow of information through it is constrained as one-way flow only. This mechanism, which took the form of the Weismann Barrier, is now enshrined in the Central Dogma of Biology as the strict one-way information flow from DNA to protein, never the reverse. Thus natural selection and variation are also implicated; their role as anti-Lamarckist elements which act only to preserve adaptations, not to induce them, is assured by the 'simplex' informational flow constraints of heredity. Even if the concept of information itself is somewhat problematic in application to biology and evolutionary theory as a whole, it is the mechanism which expresses the *flow* of information which serves as an anti-Lamarckist constraint. With this summary in mind we now may turn to natural selection.

3.1 Natural Selection

The contemporary period of research and discovery in evolutionary theory really begins with what has been called the "molecular revolution". One of the crucial events in the molecular revolution was Crick and Watson's elucidation of the molecular structure of DNA. (see appendix 2) This elucidation reinforced Weismann's definition of heredity: information flowed from the germ (DNA) to the soma (proteins) via the translation mechanism of RNA. This so-called Central Dogma of Biology has never been seriously disputed. The main thrust of the molecular revolution was to try to show how Mendel's laws and Fisher and Wright's various added dimensions to population genetics could be tied to the physical mechanisms of heredity. Weismann's influence led to a search for the nature of this physical mechanism. The separation of germ from soma caused a change in the focus of research leading to the demand that heredity itself must be examined. Mendel's discoveries showed that heredity was particulate in nature. Thus it was thought that discovering the nature of heredity in its physical manifestation would show the means by which this physical mechanism would be made manifest in the phenotypic traits of the organisms themselves, and furthermore would show how these traits would be distributed in a population of organisms.

It was thought that an elucidation of the nature of heredity would lead to uncovering the way in which variation functioned in evolution. This variation, whatever its source, was then supposed to be acted upon by natural selection. On this approach, there was no question as to the ability of natural selection to create variation or adaptations, as the tensions outlined in the last chapter suggested. Rather the physical nature of heredity itself was examined to see how variation was provided as a kind of 'raw material'. Natural selection simply acted upon this variation after its generation. Elliott Sober characterises natural selection in this way: "The process of natural selection has two components. First variation must arise in the population; then, once that variation is in place, natural selection can go to work..."⁶⁹

However, this approach to the importance of heredity in variation could still lead to varying approaches to research. On the one hand, since the physical basis of heredity was seen as integral to the generation of variation, one might think that

⁶⁹ Sober, *The Philosophy of Biology*, p. 37

heredity had its own means of generating variation, and that these means may be structural properties of DNA itself, or organisational propensities, or a host of other variation-generating mechanisms. On the other hand, it might be thought that natural selection was all important, the *only* force in evolution, and could be decoupled from variation-generation in the mechanism of heredity itself. Therefore, it might be the case that change in the hereditary material itself was random with respect to natural selection. Of course, these two interpretations are not mutually exclusive. However, I would note that a strong belief in the second will entail that any other factor in evolution will be random *definitionally*. This will be considered later in section 3.2. For the moment let us examine the claim that since natural selection can be decoupled from mechanisms that provide the generation of variation, natural selection is the only *force* in evolution. This will be discussed in the context of the adaptationist debate, which recalls some of the issues raised in section 2.3, in the discussion of R.A. Fisher and S. Wright's ideas concerning the power of natural selection.

3.1.1 Adaptationism

The adaptationist controversy highlights some of the problems that surround the conceptual definition of natural selection in terms of its proper characterisation as an element of neo-Darwinist theory. I will not attempt to resolve these difficulties here, as such an endeavour is outside the scope of this thesis. However, I wish to note that, even if issues surrounding the proper characterisation of natural selection in terms of the criteria for explanation in scientific theories remain unresolved, evolutionary theory can still use the notion of natural selection without thereby attempting to define it in isolation from its interactions with other components of neo-Darwinism, variation and heredity. In this regard the adaptationist controversy centres on the relative importance of natural selection in comparison with other evolutionary mechanisms, but does not concern the definition of natural selection in itself. Though it is equally clear that a dispute over the relative importance of natural selection does appeal in some part to a characterisation of natural selection, I would argue that this characterisation need not be constrained by the criteria usually required by the philosophy of science in treating theoretical terms.

It was noted in chapter 2 that Neo-Darwinism designates natural selection as a mechanism of change in organisms over time. However, this designation has sometimes been extended to the belief that natural selection is by far the most powerful force in evolution, this belief is known as *adaptationism*. The most outspoken opponents of adaptationism are Stephen Jay Gould and Richard C. Lewontin, and their 1979 paper on "The Spandrels of San Marco and the Panglossian Paradigm"⁷⁰ outlines their concern that adaptationism was 'dominating' English and American evolutionary thought. They recommend a more pluralistic approach to evolutionary theory, one where factors other than natural selection are given more considerations as agents of evolutionary change. As they see it, evolutionary theory fails to investigate other possible explanations of genetic change in favour of an adaptationist approach that tends to support simple explanations based on the isolation of adaptive traits and the establishment of processes which could have led to this selection, which may appear plausible, but are liable to be false.

Elliott Sober notes that adaptationists do not necessarily deny the existence of other evolutionary casual mechanisms, such as mutation, migration, and drift, but rather they downplay the importance of these mechanisms. Adaptationists do not deny that drift, mutation, pleiotropy⁷¹ or other factors can affect the course of evolution.⁷² Yet Sober recognises that there are several senses in which the adaptationist claim "Natural selection is the most powerful force in evolution" can be taken. If it is taken as "Natural selection is a more powerful force than mutation" then Sober's response is that this is a legitimate question that can be answered by comparative analysis. At this point Sober's larger concerns in the philosophy of biology become apparent. Sober's view is that evolutionary theory is a "theory of forces" in much the same way as physics, and he is furthermore concerned to explicate exactly how causation works

⁷⁰ Gould, S.J. and Lewontin, R.C. "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme" *Proceedings of the Royal Society* vol.B205 (1979) 581-98

⁷¹ Pleiotropy is a term that describes a situation in which one gene can have many different phenotypic effects, some of which are advantageous and some of which may be disadvantageous. Because of this, it is harder for selection to weed out disadvantageous traits, as such traits have "hitchhiked" onto advantageous traits that selection would presumably preserve. Pleiotropy has therefore been mooted as an alternative, opposing force to that of selection.

⁷² Sober, Elliott. "What is Adaptationism?" in *The Latest on the Best* ed. John Dupré (Cambridge MA: MIT Press, 1987) pp. 105-118

with regard to neo-Darwinism. Sober's treatment of adaptationism is thus useful in illustrating the concerns that the philosophy of biology has with natural selection, and it is worth pointing out that there are some unresolved issues surrounding natural selection from this standpoint.

Sober believes that evolutionary theory is a "theory of forces"⁷³ and that the adaptationist debate is "not a claim about the power of selection in evolution, but about the power of certain simple models of evolution."⁷⁴ In a theory of forces, the forces must be decomposable for identifications of the relevant causal force to be possible. This means that, in order for a model which reflects these forces to function, the nature of the functional entities must be well-defined. In the case of adaptationism, the difficulty lies in deciding *which* factor is the cause of evolutionary change. Sober claims that mutation and selection are common currency in terms of their effects on a genome, therefore it is possible to decompose their effects and thus determine their relative causal contribution. Local facts about the population under study will determine which causal factor is more important in such an analysis. Therefore, natural selection *as opposed to* mutation can be investigated comparatively, but the same cannot be said for natural selection *as opposed to* drift. Natural selection as opposed to pleiotropy is similarly difficult to investigate, because Sober argues that situations of drift and pleiotropy are marked by non-local facts, which give little information about the causal factors involved. Here of course Sober is focusing on the use of the concept of cause to denote a relevant predictive factor, and thus concludes that questions about the relative force of natural selection that do not allow the decomposability of causal factors are predictively, and therefore explanatorily useless. We will investigate this line of thought further in section 3.2.

It is clear that the issues raised by the adaptationist debate are related to issues in the larger area of the philosophy of science, if only in the sense that what would count as an answer to the question of whether natural selection is the only cause in evolution is subject to a principled decision about what would constitute a causal explanation. This is in fact evident in Gould and Lewontin's attack on adaptationist accounts as unverifiable, or pseudo-explanations, what they call "just-so stories".⁷⁵ M.J.S. Hodge notes that this is an issue that is inadequately addressed. "A quite

⁷³ Sober, Elliott. *The Nature of Selection* (Cambridge MA: MIT Press 1984), ch. 1

⁷⁴ Sober, "What is Adaptationism?", p. 116

⁷⁵ Gould and Lewontin, "Spandrels of San Marcos"

general issue has still received no canonical treatment: what kind of thing is natural selection, anyway? A law, a principle, a force, a cause, an agent, or all or some of these?"⁷⁶ There is a sense in which it may seem more appropriate to talk of natural selection as being the 'constraints' on evolution, in the sense that it is what allows some variants to get through to reproduce, and keeps others from getting through. Similarly, it could be seen as the 'result' of the interaction of the organism with the environment which exerts selection pressures upon it. This option though, might be heading straight into the 'tautology trap'; that is, that since natural selection is "survival of the fittest", and the fittest are the survivors, then this type of definition of natural selection is circular.

3.1.2 The Tautology Problem and The Propensity Interpretation of Fitness

The possibility that natural selection is not really a force in the way other scientific theoretical terms such as gravity are, is important to consider. If natural selection simply selects out organisms through environmental constraints on these organisms, then in what sense can it be said to 'cause' evolution or change? After all, if natural selection is merely the result of environmental constraints, then this does not sound much like a force or cause. And what exactly does natural selection 'select' anyway? If natural selection does not really actively select anything, but is simply the result of the interaction between organism and environment, and simply describes the "survival of the fittest" then it cannot be an agent of change in any causal, predictive, or explanatory sense. For instance: What does natural selection allow to survive? The fittest. And what makes these the fittest? The fact that they have survived. In order for natural selection to have any status as a causal or explanatory force, it would seem that it is necessary that natural selection act upon some property or other of the organism for it to be a selective force.

The "tautology problem" has long been a topic of interest, probably since the publication of the *Origin*. Popper famously retracted his own statement that evolution by natural selection was a mere tautology, he later claimed that it was a metaphysical

⁷⁶ Hodge, M.J.S., "Natural Selection" in *Keywords in Evolutionary Biology* ed. Evelyn Fox Keller and Elisabeth A. Lloyd (Cambridge MA: Harvard University Press, 1992) p. 218

research programme in its own right, and blamed his earlier misreading on the fact that many prominent evolutionists had purposely framed the principle of natural selection in a tautologous fashion, notably C.H. Waddington, and R.A. Fisher, J.B.S. Haldane, G.G. Simpson.⁷⁷ The "tautology problem" is thought to be an important issue in many senses. Of course, there is the usual horror of admitting to the scientific community that natural selection is tautologous in the sense of a mere platitude, such an admission would be obvious ammunition for creationists, 'creation scientists' and others of their ilk seeking to show that evolutionary theory is unscientific. Furthermore, the tautology problem seems to occupy philosophers of biology who wish to make evolution a "respectable scientific theory",⁷⁸ and explain the mechanism of natural selection. Natural selection would then need a causal story of some kind to distinguish it from trivial selection processes, for instance, sorting mechanisms of the kind found in geology. The prevailing tendency among philosophers of biology is to claim that there is some sort of causal connection between the organism and environment, since this in some way gets them out of the "tautology problem". That is, to avoid the identification of natural selection with "survival of the fittest" in its most trivial sense, it is important to ascribe to natural selection the status of some kind of causal process. There must be some property of the organism that is selected by natural selection, or which is conserved by natural selection.

This property in evolutionary theory is called "fitness". It is related to the issue of whether or not natural selection as survival of the fittest is tautologous in the following way. As Mills and Beatty characterise the relationship: "The concepts of fitness and natural selection are closely linked, since it is through the process of natural selection that the fittest gain predominance, according to the theory of evolution."⁷⁹ "Fitness" is a term that refers to an organism's survival success or reproductive success, or its *relative* success. Now notice that defining fitness as the *actual* reproductive success of an organism would also lead us into the tautology trap. If we

⁷⁷ Popper, Karl. "Natural Selection and its Scientific Status" in *Popper Selections* ed. David Miller (Princeton: Princeton University Press, 1985) p. 242.

⁷⁸ Robert Brandon claims that this is his aim. He has worked with John Beatty on working out the status of fitness as a dispositional property, though he somewhat confusingly calls this property "adaptedness". See Brandon, R. *Concepts and Methods in Evolutionary Biology* p. 11

⁷⁹ Mills, S and Beatty, J. "The Propensity Interpretation of Fitness" *Philosophy of Science* 46 p. 264

designate the fitness of an organism according to whether it *happened* to survive or reproduce, then we risk treating fitness as the "dormitive virtue" of evolutionary theory.⁸⁰ So if fitness is to be defined in a non-circular manner, it must have more of a casual explanatory role. "The idea is that adaptedness is related to fitness i.e. reproductive success, in much the same way that solubility is related to dissolving." as Robert Brandon has put it.⁸¹ Mills and Beatty formulated the "propensity interpretation of fitness", which treats fitness as a dispositional property.⁸² That is, the fitness of an organism is that propensity for it to survive and reproduce, and therefore is the property that natural selection selects. Fitness thus becomes a measure of an organism's *potential* to survive and leave offspring. This makes fitness an empirical property, and allows natural selection to have some kind of causal or explanatory place in evolution.

The propensity interpretation of fitness is thus intended to give natural selection some causal story via fitness as a dispositional property. But if a propensity interpretation of fitness is necessary to give a causal story for natural selection, what can it tell us in terms of explanation? Defining fitness dispositionally allows biology to be an empirical science with limited prediction, and the Principle of Natural Selection then has some explanatory force. But is this really a solution? Hodge's question of what sort of thing natural selection is remains unanswered. Yet this question needs some answer, for it is clear that in order to answer the question of whether or not natural selection is completely fundamental to evolutionary theory, it is necessary to provide some reasonable characterisation of what natural selection is. This is the very question that the adaptationist debate seeks to answer. Later in this thesis, when we address some challenges to neo-Darwinism which disagree specifically with the adaptationist claim that natural selection is fundamental in evolution, it will become clear that such challenges cannot be assessed without first addressing the extent to which neo-Darwinism depends upon natural selection as an evolutionary force.

⁸⁰ See Scriven's example in his 1959 (Scriven, Michael. "Explanation and Prediction in Evolutionary Theory", *Science* 130, pp. 477-81). There are two identical twins, one of whom is struck by lightning before he has a chance to go on and have children. Scriven argues that if fitness is defined as actual reproductive success or actual survival, we would have to assign the surviving twin a greater fitness, though they are identical in every respect.

⁸¹ Brandon, *Concepts and Methods in Evolutionary Biology*, p. 49. Again, Brandon uses different terminology, but he is talking about what everyone else calls fitness.

⁸² Mills, S and Beatty, J. "The Propensity Interpretation of Fitness" pp. 263-286.

The adaptationist controversy is concerned with the relative power of natural selection in evolution. Some have thought that natural selection is relied upon too heavily as a source of change, and they would rather that evolutionary theory pay more attention to the possibility of change through the action of variation and heredity by themselves. They counter adaptationists who insist upon natural selection as being the only force in evolution by pointing out that such a position is in some sense 'unfalsifiable'. That is, as Gould and Lewontin point out, "the rejection of one adaptive story usually leads to its replacement by another, rather than to a suspicion that a different kind of explanation might be required."⁸³ In order to provide criteria by which these different kinds of explanation might be appraised, philosophers of biology have tried to show that there is a way in which natural selection can be compared with explanations that refer to mutation or pleiotropy, for instance. However, this has led to a recognition that natural selection must be more precisely defined in order for such explanations to be properly distinguished from each other. Characterisations of natural selection that are precise about the status of natural selection in terms that the philosophy of science would accept have been rare. Philosophers of biology seeking to avoid the 'tautology trap' of natural selection as "survival of the fittest" have tried to give at least the concept of "fitness" itself more causal power by treating it as a disposition. Yet even this has not resolved the issue of in what sense natural selection is a causal agent, or the related issue of how one could characterise it as a force or law, or principle.

3.1.3 Defining Natural Selection

In conclusion, I want to draw attention to the difficulties caused by evolutionists and philosophers of biology alike in attempting to define natural selection formally, outside any considerations of the other mechanisms in evolution. First, the constraints of philosophy of science, strengthened perhaps by Popper's initial indictment of natural selection as tautologous, have been largely interpreted as a demand to include the principle of natural selection within some kind of causal framework, and thus to make it into a respectable scientific law. The approaches discussed above are only representatives of the type of endeavour philosophy of biology has found itself

⁸³ Gould and Lewontin, p. 79

engaged in: an attempt to give natural selection its own causal relationship to organisms, in effect to define it on its own with reference to how it 'causes' organisms in an environment to change over time. Critics of adaptationism bring this problem into sharper relief: their position seems to be: "if you can't tell us what natural selection is, you can't properly contrast explanations of change due to natural selection from explanations due to different causes, and everything will end up being claimed to be an adaptation due to natural selection". Resulting attempts to tighten up the definition of natural selection have seemed to have a different effect. By formalising the definition of natural selection so as to distinguish it from other forces like random genetic drift or pleiotropy, natural selection as a cause seems to have lost much of its force.

For this reason, I suggest that natural selection can only be interdefined, or defined with reference to, the other two components of evolution, variation and heredity. Attempts to define natural selection in isolation from these other components will not so much be doomed to failure, and cause a skewed picture of the function of research programmes in biology. This skewed picture will make it impossible to interpret what parts of evolutionary theory are in conflict with neo-Darwinism and which are merely augmentations of previously accepted orthodoxy, a project I wish to pursue in the Part II of this thesis. It will be seen in the next two sections of this chapter that the same effect occurs with the components of variation and heredity.

There is one further issue to be recognised in the adaptationist controversy. Part of the claim that natural selection is the most important force in evolution might involve the notion that natural selection provides the sole source of *order* in evolution. Given what we have seen about the interplay between variation and natural selection, it is clear that natural selection as a culling mechanism can be conceived of as a sorting device that removes unfit variations from the gene pool. In chapter 2 we saw that evolution through variation, natural selection, and heredity is a process that conserves certain forms by means of reproduction and heredity, and that without the hereditary component, evolution would be nothing but constant disorganised change. We also saw that the rejection of Lamarckism meant that variation was random with respect to adaptational advantage. Natural selection can be conceived of as providing order by sorting through these random variations. This could also be interpreted so that evolution describes a process that creates order out of chaos, and natural selection is the most important element in this process.

It has been argued that this interpretation of natural selection as the sole source of order is predicated on two beliefs about evolution.⁸⁴ First, it rests upon the idea that variation as undirected, or as uncoupled from adaptive advantage, means that variation can occur in any direction. Second, it rests upon the ideas borrowed from thermodynamics and statistical mechanics (heavily relied upon by population geneticists) that systems left to their own devices will tend toward entropy or disorder. Natural selection provides the "Maxwell's Demon" in this type of analysis. Both of these claims have at their heart a characterisation of the role of chance, or chaos as opposed to order, and this opposition deserves further discussion as we turn to the role of chance in evolutionary theory.

3.2 Variation

The concept of randomness plays a key role in evolutionary theory. But what is the exact nature of this role? There are, as Sober has noted, two roles that chance can have in evolutionary theory. First, evolutionary theory, as we have noted, claims that natural selection acts upon variation in the hereditary material, and furthermore all variation in this hereditary material occurs at random, that is, unconnected with adaptational advantage. As Francis Crick has put it, "Chance is the only source of true novelty".⁸⁵ Crick therefore views chance as a characterisation of variation that then becomes available to natural selection. Second, we could say that randomness is part and parcel of evolutionary theory itself, through the functioning of natural selection as an agent of change. That is to say, evolutionary theory, as a statistical, probabilistic theory, necessarily incorporates an element of chance. But, as I will show, it is not easy to see an important difference between these two interpretations in terms of the neo-Darwinist research programme. Both interpretations fail to define the exact role of chance in evolutionary theory.

We have seen that the Modern Synthesis and its understanding of the nature of natural selection required that any variations in the genome of the organism be statistically independent, meaning that such variations or mutations are not directed by

⁸⁴ Kauffman, p. 8.

⁸⁵ Crick, F. *Life Itself: Its Origin and Nature* (New York: Simon and Schuster, 1981) p. 58

the influence of the environment in any way. Natural selection plays no role in the generation of variation by the organism. The environment preserves or rejects the phenotypes influenced by new variant genotypes *after* such variance has been generated. This is part of the anti-Lamarckist constraint of evolutionary theory as we saw in chapter 2. And it is in this way only, I will conclude, that evolutionary theory regards the concept of chance. That is to say, chance as an aspect of variation, the second element of neo-Darwinism, while it invites some further metaphysical considerations, is always interpreted in such a way that chance is incorporated in terms of mechanisms that serve to retain the fundamental anti-teleological basis of neo-Darwinism.

3.2.1 Randomness and Indeterminacy

The issue of randomness or chance is a perennial problem in the philosophy of biology. To evolutionists, it proves to be a source of constant confusion, whilst to philosophers, a source of constant argument. To begin with, it is clear that in the historical context of debates about biology and nature before Darwin, the role of chance was already a very tricky issue. It has been argued that mechanists, vitalists, and teleologists all denied the importance of chance, yet nevertheless were prepared to enlist chance as a weapon in the context of ideological debates.⁸⁶ Mechanists, in their opposition to vitalism, denied that anything was due to chance, given that they were Laplacian determinists. But these same mechanists, in opposition to teleologists, were quite happy to affirm chance as an antidote to Creator-driven design. There were some vitalists that denied chance, but there were some vitalists who were also indeterminists. The theologist/teleologists in the tradition of Paley designated chance as mere absence of design, that is, they did not construe chance in any positive way. It seems that the choice of one's metaphysics does influence one's view of the role of chance, but not in a particularly predictable way.

Yet, in many ways it makes little difference to the practice of biology which commitments one has with regard to determinism. For instance, both Wright and Fisher were indeterminists, but clearly they both had quite different interpretations of the role of chance in biology, as we have seen. Furthermore, they were both happy to

⁸⁶ Gigerenzer, et al., p. 132

use determinism-laden theory in their quest to understand the laws of population biology. Wright himself claimed that his indeterminism made no difference at all to his views on biology.⁸⁷ We can safely say that the issue of determinism and indeterminism is not important in biology, insofar as it does not seem to influence the direction of research programmes in any obvious way.

Although determinism or indeterminism as a high-level metaphysical commitment has no impact on research programmes, the role of chance, construed in a more subtle way, does. We will see how one's view of chance can influence the direction of research programmes by examining some definitions of randomness in evolution through Jablonka and Lamb's appraisal of the role of randomness.⁸⁸ Earlier it was noted that it is difficult to reconstruct Darwin's own view of the role of chance in evolution, though it is at least clear that he did not think it particularly influential in the generation of variation. But in the Modern Synthesis, the acceptance of hard inheritance meant that 'chance' was conceived of as uncorrelated with adaptive benefit. That is, variation in living things was due to chance, in the sense that variation arises randomly with respect to adaptational advantage. Now some variations are more adaptive, they may become more dominant because of this, and their selection is therefore not due to chance. But the fact that such variations that aid survival become dominant is not the reason they occur in the first place.

The Modern Synthesis dictated that all new heritable variations were randomly produced. This is in opposition to the view that mutations could be *directed* by the influence of the environment, which would be a Lamarckist view of mutation. But of course, there is a sense in which mutations or adaptations are not unconditionally random, they are random with respect to something. Dawkins suggests that random should be understood as "...random with respect to adaptive advantage, although it is non-random in all sorts of other respects. It is selection...that directs evolution in directions that are non-random with respect to advantage."⁸⁹ This serves to place the non-random on the side of natural selection. Mutation is random in the sense that it

⁸⁷ Gigerenzer, et. al., p. 161

⁸⁸ Jablonka, Eva and Lamb, Marion J. *Epigenetic Inheritance and Evolution* (Oxford: Oxford University Press 1995)

⁸⁹ Dawkins, R. (1986) as quoted by Jablonka and Lamb in *Epigenetic Inheritance and Evolution* p. 56

does not correspond with improvement or adaptation. However, Jablonka and Lamb have suggested that this is not what most evolutionists mean by random.

Another possible definition of mutation and randomness that Jablonka and Lamb suggest is that "mutation is random because it is not possible to predict which new variation will be produced at any moment".⁹⁰ This definition of random is of course more closely tied to predictability and indeterminism. These two definitions are quite different with respect to what types of mutations can be called 'non-random' or 'directed'. It appears that Jablonka and Lamb's definition allows wider scope for things to be designated as 'directed' where Dawkins' allows nearly everything to be random. For instance, Jablonka and Lamb suggest that Dawkins' definition requires that even induced mutations through the influence of a mutagenic agent be called random, whereas most biologists would not see this as random, but rather as caused by the mutagen and hence directed in some fashion. On the other hand, Jablonka and Lamb's definition poses similar problems in scope. For them, randomness is simply linked with predictability, or at least ignorance of which variations will be produced. Therefore presumably if we know the likelihood of certain mutations given the influence of a certain mutagenic agent, then any mutational changes here are non-random, and hence, 'directed'.

Sober notes in his discussion of randomness that "randomness of mutation does not mean that mutations are inherently unpredictable...Facts about the environment...concerning the presence of certain chemicals and kinds of radiation [mutagens]...make some sorts of mutation far more probable than others."⁹¹ If Jablonka and Lamb's criticism is to be taken seriously, this is precisely where Dawkins' definition of randomness comes unstuck; it seems to make everything seem random, even events that have some known probability or predictive possibility.

Thus one's definition of randomness does have a lot to do with what role one assigns to natural selection. Dawkins, the arch-Darwinist, does tend to ascribe nearly all change to the action of natural selection, therefore his definition of random is intended to dispel any Lamarckist ideas concerning the way in which variation is generated. Thus, "Variation is generated at random, but selection among variants is non-random"⁹² is the position that Sober gives on the issue of randomness. This

⁹⁰ Ibid., p. 57

⁹¹ Sober, Elliott. *The Nature of Selection*, p. 104

⁹² Sober, Elliott. *Philosophy of Biology*, p. 38

definition is the same as Dawkins' given earlier; the emphasis is on randomness as uncorrelated with selection pressures.

3.2.2 Random Drift vs. Natural Selection

We must now turn to the second role played by chance in evolutionary theory, as a necessary component in evolution by natural selection understood as an intrinsically statistical, probabilistic theory. Earlier it was claimed that determinism and indeterminism did not influence the choice of research programmes in an obvious way in biology. However, determinism does play some limited role in delineating research programmes in terms of whether or not chance is seen as an alternative to 'natural selection' as an agent of evolutionary change. We will now examine this claim by discussing the debate between random drift and adaptationism.

Random drift hypotheses were formed to combat the "neo-Darwinian notion that natural selection is an all-sufficient agent of evolution", that is to say, the adaptationist position.⁹³ In the 1930's and 40's, the period before the 'hardening' of the Modern Synthesis, random drift hypotheses were often invoked. They were intended as explanations of the continued existence of traits that differed from the norm but had no obvious adaptive significance. In section 2.3 the dispute between Fisher, an ardent adaptationist, and Wright, a champion of the role of random drift in evolution, was described, and we saw that each came down differently on the issue of random drift. Biologists like Wright were convinced that certain traits could take hold in populations not due to their adaptive significance, but rather due to changes in the size of populations from generation to generation.

For instance, let us take two traits in a population that are different, but not necessarily adaptively significant (i.e. blood types). The idea is that natural selection is 'blind' to these traits since they do not confer any advantage to their possessors. In each generation, one of these traits may take hold in the population simply because more copies of it are passed on by chance, and in a Mendelian inheritance model this is more likely. In an ideal Mendelian population model, with two heterozygous parents *Dd*, the number of *Dd* offspring will converge to 50% (see appendix 1) but in a real

⁹³ Beatty, John. "Random Drift" in *Keywords in Evolutionary Biology* ed. by Evelyn Fox Keller and Elisabeth A. Lloyd (Cambridge MA: Harvard University Press, 1992) p. 274

population, the number of offspring is limited, it may be that there are fewer or more heterozygotes, and in the long run this 'chance' distribution will affect the allelic makeup of the population. Thus, proponents of random drift hypotheses found it possible to explain some allelic differences by random drift alone.

The chance element here is related to the idea of natural selection as a stochastic process. We saw in section 3.1 of this chapter that fitness can be treated in terms of propensities. That is to say, a fitter organism will leave more offspring than a less fit one, *in the long run*, and fitness merely implies the likelihood of specific outcomes. If natural selection is a stochastic, rather than deterministic process (where fitnesses are real and logically imply future distribution of organisms) then we can say only that the distribution of fitter offspring will converge upon a limit. In a coin-flipping example, an infinite run of flips of a fair coin will be likely to converge on 50% Heads, 50% Tails according to Bernoulli's Theorem, otherwise known as the Law of Large Numbers. But the actual frequency of Heads in a limited run of flips is not deducible from the fact that the coin is fair.⁹⁴ In a limited run, the frequency of Heads to Tails is not likely to be 50/50, and the smaller the run, the more likely the distribution will diverge from the limit. This is a kind of 'sampling error' (although, as we will see in a moment, it is not the same kind of 'sampling error' that occurs in statistical analysis). In the Mendelian example above, the idea is that small population size makes it more likely that there will be a divergence from the expected distribution of alleles, and thus random drift can have a powerful role in shaping evolution.

Notice, however, that the requirements for a drift hypothesis to be applicable were that the traits in question had to be 'invisible' to natural selection, in the sense that they could not be adaptively significant. In the 50's and 60's, during the 'hardening' of the Synthesis, many examples of drift were subsequently reinterpreted as cases of natural selection at work. In the example of blood groups, biologists realised that blood type could affect an individual's susceptibility to disease, therefore blood type was not neutral and distributions of blood groups could be due to the action of natural selection. There was a resultant shift away from the use of drift hypotheses. As Mayr put it, "[The biologist] must first attempt to explain biological phenomena and processes as the product of natural selection. Only after all attempts to do so have failed, is he justified in designating the unexplained residue tentatively as a product of

⁹⁴ And it is possible that even in an infinite run, the frequency need not converge.

chance."⁹⁵ Yet Sober has noted that the distinction to be made is somewhat difficult here. He argues that since natural selection is by nature a stochastic process, it includes by necessity an element of chance. The question is not whether chance plays some role in evolution, but rather how important this role is, and what precisely this role is.

Beatty investigates the distinction between "drifters" and "selectionists", that is, between those who believe that adaptations are the result of random drift, and those who think that such adaptations can be explained through the influence of natural selection.⁹⁶ He believes that since drift is meant to be stochastic, those who study the action of selection pressures often use it as the null hypothesis. However, he argues that the drift hypothesis cannot be treated as the null hypothesis, because of the nature of the 'sampling error' in null hypotheses and drift hypotheses. We saw above that the drift explanation depends upon chance change in a small finite population through a kind of "biological sampling error". However, Beatty notes that if one is to use a drift hypothesis as a null hypothesis (i.e. the hypothesis that the result is due to chance), then sampling error enters into the picture in a totally different way. When one is using a null hypothesis and one finds differences between the populations that are not explained by the hypothesis being tested, one generally puts this difference down to 'sampling error'.⁹⁷ That is, only very large differences between the sampled populations are considered to be strong enough evidence to support the significant hypothesis, small differences are put down to sampling error. But as we have seen, the drift hypothesis itself depends upon sampling error as the means of change in the population.

As Beatty argues, "One way of expressing the difference is to point out that investigators invoke random drift hypotheses in order to *account for differences* between the groups under investigation, while investigators invoke the standard null hypothesis in order to *deny differences* between the groups under consideration."⁹⁸ Sampling error simply does not play the same role when one considers the drift

⁹⁵ Mayr, E. *Animal Species and Evolution* (Cambridge MA: Harvard University Press, 1964)

⁹⁶ Beatty, John. "Natural Selection and the Null Hypothesis" in *The Latest on the Best* ed. John Dupré (Cambridge MA: MIT Press 1987) pp. 53-75

⁹⁷ The null hypothesis states that there is no difference between the populations sampled. The null hypothesis must be disproved for the significant hypothesis to be supported.

⁹⁸ Beatty, "Natural Selection and the Null Hypothesis", p. 63

hypothesis separately, and when one considers the drift hypothesis as the null hypothesis. Therefore the drift hypothesis is an *alternate* hypothesis to that of natural selection, and should be treated accordingly experimentally. Beatty denies that selectionists are saying anything about the role of random drift because drift and selection are alternative hypotheses, not two sides of the same coin. That is, an investigator who claims to have disproved the presence of drift in a population has not then proven that selection is present. Beatty recommends testing both alternative hypotheses (selection and drift) in parallel, yet it is difficult to see how the alternative hypotheses of drift and selection could be qualitatively distinguished if his argument is correct. It seems that in order to test the two alternate hypotheses in parallel, one would need two experimental situations: one where selection is tested against its null hypothesis (which might read "no change due to selection forces, any observed change is merely random") and another where random drift is tested against its null hypothesis ("no change due to random drift, any observed change is merely random"). Although Beatty is careful to point out that the drift hypothesis should in no way be used as a "baseline" that selection forces are to be measured against, his recommendation of "testing the two alternates in parallel" seems inadequate. After all, are we not trying to discover how much of a random element there is in evolution? Testing selection against random drift might be pointless, but surely testing random drift against random drift is senseless. I am not suggesting that random drift is not a hypothesis, the point I am trying to make here is that it is unclear what type of null hypothesis is needed in order to answer any questions about the role and extent of random processes in evolution.

Since drift hypotheses tend to depend on traits that are not adaptively significant, and often it happens that these supposedly neutral traits turn out to have significance, it is difficult to tell whether or not one is justified in using a drift explanation. Mayr's methodological recommendation is an obvious response to this problem. Wright himself was uneasy with the 'either/or' view of drift and selection, he also believed that the real question was not 'is this change due to random drift or selection?' but rather 'to what extent is this change due to drift, and what extent natural selection?' Thus, he also thought that the two hypotheses must be tested in parallel. However, once again, it is hard to see how this could be done.

3.2.3 Defining Variation

The controversy over drift still exists, even after the move away from the use of drift hypotheses in the Synthesis.⁹⁹ The discussions of chance mentioned are important in biology with reference to variation in two senses. First, chance is seen as the character of variation, once the latter is decoupled from natural selection. Anti-Lamarckist moves made it impossible for natural selection to affect variation and adaptation directly, therefore variation was conceived of as due to chance, and natural selection acted upon it only after it was generated. Second, chance is important as an explanation of evolutionary change in that it is constitutive of natural selection as a process. Whether or not this means that chance can be seen a force in contrast to that of natural selection, as was seen in the random drift controversy described above, remains a difficult issue.

To return to the problematic set up earlier, regarding the characterisation of variation as random with respect to advantage (that is, the anti-Lamarckist requirement of neo-Darwinism), we can see that the characterisation of one of the components of evolution by natural selection, that of variation, is constrained by the requirement of randomness. This may be phrased as 'random, not directed'. To define variation as inherently random with respect to advantage, one must be careful to distinguish this sense of random from other uses of the term. But equally we have seen in terms of the debate over random drift, that randomness must be defined with relation to some other force or comparative base-line. This might be phrased 'random, not selected.' If one agrees with Sober's characterisation of evolution as *by nature* a stochastic process, necessarily entailing a certain element of chance, then it becomes difficult to locate this chance element at the level of mechanism or causal sequence, in just the same way as it is difficult to compare drift and selection hypotheses in parallel.

As was noted in the earlier discussion of Jablonka and Lamb, one's definition of randomness is closely related to one's understanding of the nature of natural selection. If one believes natural selection is the sole source of order out of 'chaos' then all variation will seem to be 'random'. On the other hand, if one sees natural

⁹⁹ For instance, Motoo Kimura's "neutral hypothesis" also recommends the importance of chance in evolution. Kimura, Motoo. *The Neutral Theory of Molecular Evolution* (Cambridge: Cambridge University Press, 1983)

selection as less important in the production of evolutionary novelty than the tendencies of variation itself, as Jablonka and Lamb seem to, then 'randomness' becomes a term which refers to probability and predictivity, and hence will only be applied to situations about which we have imperfect knowledge. And in the end, one's definition of the randomness with respect to variation and the relative role of natural selection will come down to how seriously one takes evolution as a 'stochastic theory' or process.

Evolutionary theory can be seen as either a theory with a strong element of chance built into it, in the sense that it is a statistical theory dealing with numbers of populations (not organisms) under change, or it can be seen as an explanatory framework that explains or predicts the reasons how and why organisms change over time. These perspectives may be compatible with each other, but either perspective entails strong beliefs about the role of randomness and chance in evolutionary change. These two perspectives on neo-Darwinism are not necessarily identifiable with indeterminism or determinism, though they may initially appear to correspond with these metaphysical beliefs. Rather, an interpretation of evolutionary theory that grants a strong chance element can often be played out empirically as a research programme intending to discover the 'laws' that direct this chance into ordered forms, and conversely, empirical research into the prevalence of randomness may be carried out by researchers who strongly believe in the power of deterministic laws of evolution.

So, although the role of randomness in evolutionary theory is difficult to locate precisely, it is clear that the notion of 'random' serves the role of making certain that variation remains uncorrelated with adaptive benefit. Whether this notion of random corresponds with the stochastic notion of 'chance' remains a somewhat difficult issue. Perhaps again we must conclude that neo-Darwinism has great difficulty giving a precise formulation of variation in evolutionary theory, even though it does agree that variation must be undirected, random with respect to advantage, in order for neo-Darwinism to remain an anti-teleological theory. It should be clear that the adaptationist characterisation of natural selection (section 3.1.1) and the hypothesis of random drift (3.2.2) involved identical issues. It appears that it is very difficult for neo-Darwinism to answer the question of whether chance or natural selection is more important in the process of evolution, given its own minimal definition of the

mechanism involving these two elements. Perhaps the role of heredity, the third element, can be more easily delineated by neo-Darwinism.

3.3 Heredity

We saw in chapter 2 that the concept of heredity had been refined by Weismann and Mendel, and both served to constrain the functioning of heredity so that it did not violate any of neo-Darwinism's anti-Lamarckist strictures. Yet many aspects of the nature of heredity were left unresolved by these moves. For instance, it was clear that heredity conserved the traits of the parent organism and passed them on to the offspring with some fidelity, and this necessarily meant that some kind of information was being transmitted, but what kind? And it was clear that the Weismann Barrier meant that natural selection could act on the organism, but not directly on the genes themselves. This meant that the actual hereditary material was only indirectly available to the action of selection. If this was the case, then was it also the case that heredity itself was nothing more than a copying mechanism? Could it too have properties that created variation? We saw earlier that the Mendelians certainly thought so. What role did heredity, as conceived of genes or DNA, have in evolution? I would now like to address some of the issues surrounding this question by looking more closely at the notion of information. I will conclude by placing these issues in the context of Dawkins' work and the "unit of selection" debate. I will argue that behind the reductive scheme in Dawkins' answer to the unit of selection problem, there lies a commitment to Weismannism, the anti-Lamarckist prohibition enshrined in neo-Darwinism. And furthermore, I will argue that this anti-Lamarckist prohibition comes not from the idea of genes, or *heredity* in themselves, but from the inappropriate use of certain metaphysically overdetermined metaphors concerning the idea of *information*.

3.3.1 Heredity as a mechanism

In section 2.1.3 Darwin's ideas concerning heredity were discussed, and it was noted there that Darwin's own theory of heredity, Pangenesis, was intended to explain how offspring were more or less similar to their parents, yet also how they were different. Fidelity in evolution is important, but not perfect fidelity, for without some variation,

there would be no material for natural selection to act upon. Darwin's early attempts to propose a physical mechanism to explain how this fidelity functions should show us that the functioning of heredity, the third component of Darwinism and neo-Darwinism, is unlike that of the other components. In the cases of natural selection, and of variation, these concepts were (and are) delineated by use of more metaphysical conceptions. That is, historically natural selection has been defined as either an 'active force' somewhat akin to a metaphysical force of nature, or conversely, it has been given the characterisation as the 'result' of the interaction of organism and environment, which itself has a decidedly mechanistic metaphysics behind it. Similarly, variation, with its constraint as 'random' in neo-Darwinism, has been particularly open to metaphysical characterisation, if only for the reason that the concepts of 'randomness' and 'chance' have varying interpretations and importance to both determinists and indeterminists, materialists and teleologists, mechanists and vitalists. Furthermore, as has been argued above, 'random' has important definitional ambiguities that stem from mathematics and statistics themselves, and even if these subject areas are not generally seen as arenas for 'metaphysical' debate, there is no denying the impact of Newton and Laplace on these issues, not to mention Democritus and Zeno.

But heredity seems somehow different. For issues concerning heredity, historically at least, seem to have been decided on more physical grounds, that is, in terms of the delineation of certain mechanisms. From Pangenesis, through Weismann, and all the way to Crick and Watson, the characterisation of heredity has been an elucidation of *mechanism*, rather than anything else. How do traits get transmitted through a lineage or organisms? Through the blood, through "gemmules", through the "germ line", through the transcription and translation of DNA, of course. It seems nothing could be simpler, and today it seems that there is nothing that DNA cannot explain. But things are not so simple, in fact heredity has been influenced by metaphysical considerations, and these influences have in turn found expression in anti-Lamarckist mechanisms.

There is no shortage, of course, of detractors of DNA-mythologising, from scientists to ethicists. There are many criticisms: ranging from claims that the interaction between genes and environment is of an order of complexity which we could never even begin to fathom, to claims that DNA itself is less important in

heredity than other cellular or environmental factors. I would like to set aside such 'empirical' arguments against the straightforward understanding of the nature of heredity in order to address a different issue: that of the interdefinition of heredity with the other components of neo-Darwinism.

Heredity needs a notion of fidelity, of 'copying', and this notion is associated, for most biologists, with the physical mechanism of transcription and translation of DNA. But this act of transmission, or copying also requires a notion of 'genetic information' as the stuff that gets transmitted. And here, I would like to argue, is where things are more complicated than the cut-and-dried physical manifestation of heredity might lead one to believe. This is related to the unit of selection debate as well. Darwin's Pangenesis, we might notice, does not have the same constraints, it does not posit any template, or unique entity in which the hereditary information resides, but rather it has particles from the organism moving around the body and collecting in the sex organs to generate a new organism. Rather than one mechanism, it postulates many. So although Pangenesis seeks to explain fidelity, why organisms resemble their parents, it does not deal with 'copying' in quite the same way as a physical mechanism which must 'transcribe' or 'transmit' *genetic* information from one generation to the next. So information is presupposed by any hereditary mechanism which it thought to copy information from one parent organism to its offspring. But 'genetic information' in biology today is used more extensively, even if these usages are not consistent with each other.

3.3.2 Heredity and Information

It would be worthwhile to look for a moment at why and how 'genetic information' as a concept came to be used in modern biology. There are several reasons for this, one of which is the discovery of the structure of DNA, which seems to lend itself to a 'digital' interpretation. Shortly before Watson and Crick delineated this structure, John von Neumann had already published an influential paper titled "The General and Logical Theory of Automata" in 1951.¹⁰⁰ In it, he examined the notion of a "self-reproducing machine", one capable of building itself according to a pre-specified

¹⁰⁰ See von Neumann, John. *Theory of Self-reproducing Automata*. Posthumously ed. Arthur Burks (Urbana, Illinois: University of Illinois Press: 1949)

program or blueprint. These automata needed a kind of warehouse which contained the parts with which the machine was constructed, as well as a blueprint which detailed the way in which they themselves were constructed. Von Neumann concluded that in order for each automaton to reproduce itself it would need to read its own blueprint, then construct another automaton according to these instructions. This new automaton would have to be provided with its own blueprint to enable it to reproduce itself, and so on. After Crick and Watson showed the structure of DNA, it seemed natural for many to see DNA as the 'program' or 'blueprint' that the organism executed, and each base pair might be seen as a 'bit' of information.¹⁰¹ And the living organism was perhaps as von Neumann had described, it had its own blueprint for construction (DNA), as well as a warehouse of proteins from which it constructed itself, and this blueprint was also passed on as part of the constructed organism. The transcription and translation of DNA might operate in much the same way as a reading frame in a Turing machine, moving up and down the strand and 'decoding' the information contained there. Thus 'information' came to be used in biological metaphors, in terms of 'computability'. In chapter 2 it was already made clear that the Mendelians had treated heredity as particulate, and it should be clear that this move allowed units of heredity to be treated as logically discrete. Once genes or DNA base-pairs were treated as discrete logical units, or bits of information, it was possible to apply computation-oriented descriptions to heredity as a system.

George Kampis notes that there are several properties inherent in speaking of 'genetic information' in the above sense. "(1) it is sequential, (2) it has an alphabet, (3) it can be transcribed letter to letter, and (4) it can be 'decoded', or translated, piece by piece." Kampis concludes by noting that these properties also define a transformational, formal language.¹⁰²

Because of this emphasis on 'decoding' an informational 'message', it was not long before Shannon entropic information (language borrowed from physics to characterise a mathematical theory of communication) was enlisted in the attempt to

¹⁰¹ The quantification of information as "bits" is founded on the work of Shannon, Claude E. and Weaver, Warren. *The Mathematical Theory of Communication* (Urbana, Illinois: University of Illinois Press, 1949)

¹⁰² Kampis, George. *Self-Modifying Systems in Biology and Cognitive Science: A New Framework for Dynamics, Information and Complexity* (Oxford: Pergamon Press, 1991) p. 421

describe living things in terms of 'information'.¹⁰³ These efforts, though not in the end successful in giving any sensible characterisation of genes or organisms formally, were nevertheless highly influential. It seems that biology has long since given up trying to define the information content of any genome, but the idea of 'gene as program' has not yet been abandoned. The approach that treats genes as programme has also been called neo-preformationist by some commentators, for instance Mahner and Bunge.¹⁰⁴

So information still has strong associations with the neo-Darwinist conception of heredity for historical and theoretical reasons alike. Far from being characterised entirely in terms of physical mechanism, heredity was invested with metaphysical concepts from its modern inception. The physical nature of DNA lent itself readily to a computational paradigm, and this has not been completely abandoned. To see why this is, we may now turn to the "unit of selection" debate.

3.3.3 Heredity and the Unit of Selection

The debate centres on the level at which natural selection is supposed to act. The question at the root of the unit of selection debate is whether traits evolve because they benefit individual organisms or because they are good for the group in which they occur. Darwin's original formulation suggests that he believed that natural selection operated only on individuals; poorly adapted individuals would lose out to better-adapted individual in their species. Controversy was attracted by "group selectionists"

¹⁰³ See for instance Gatlin, Lila. *Information Theory and the Living System* (New York: Columbia University Press, 1972). These attempts ended in "sheer nonsense" as Kampis remarks, not only because these "informational contents" were non-specific between living and dead cells, for instance, but also because the Shannon notion of information, measured by reference to entropy, is nothing like the information described in computational models. Furthermore, Shannon entropy (upon which information is defined in a communicating system with a sender and receiver) is already a corruption of the definition of entropy in physics. A critical discussion of the notion of information in Shannon is provided in Kampis pp. 406-10, and in Tor Nørretranders' *The User Illusion: Cutting Consciousness Down to Size* (New York: Penguin Books, 1998) pp. 23-41, Kampis points out that the application of Shannon information to living systems was fundamentally flawed, and Nørretranders examines the various confusions surrounding the equivalency of Shannon entropy and entropy in physics.

¹⁰⁴ Mahner, Martin and Bunge, Mario. *Foundations of Biophilosophy* (Berlin: Springer Verlag, 1997) p. 280

(specifically V.C. Wynne-Edwards and others)¹⁰⁵ when they suggested that natural selection could act upon groups of individuals and species as a whole.¹⁰⁶ Species for them would play the role Darwin set aside for individuals; they too would lose out to better-adapted species. In essence, what was being suggested was that if the unit of selection was only the individual organism, then nature could only be selfish and competitive. If the organism is the exclusive unit of selection, then adaptations that were 'altruistic', or good for the group of organisms, could never evolve. Richard Dawkins provided a third alternative by suggesting that selection could act at the level of genes, and individuals should be viewed as mere receptacles for these genes.¹⁰⁷

The unit of selection debate, although it appears to be focused upon a fairly narrow debate concerning the evolution of altruism, is much more fundamental. Dawkins believes that it is of central importance to any theory that proposes to explain adaptations and to what end they are directed.

Are they for the benefit of the individual organisms, for the benefit of the group or species of which it is a member, or for the benefit of some smaller unit inside the individual organism? Adaptations for the good of the group will look quite different from adaptations for the good of the individual.¹⁰⁸

¹⁰⁵ Dawkins, Richard. *The Extended Phenotype* (Oxford: Oxford University Press 1982) p.82; also Maynard Smith, John. *Did Darwin Get it Right?: Essays on Games, Sex, and Evolution* (New York: Penguin 1993) p. 54

¹⁰⁶ Group selection in the evolution of social behaviour is a complex issue in its own right, and there is much literature on the subject and on the wider subject of sociobiology. A criticism of group selection formulated in this way can be found in George C. Williams's *Adaptation and Natural Selection* (Princeton: Princeton University Press 1966). More discussion can be found in works by J.B.S. Haldane such as *The Causes of Evolution* (London: Longman's Green.1932; Reprint Princeton University Press 1990) and W. D. Hamilton, for instance, "The Genetical Evolution of Social Behaviour" *Journal of Theoretical Biology* 7 (1964) pp.1-16;17-52. Group selection is claimed to be at odds with neo-Darwinism primarily because it seems to evade the usual element of selfish competition for limited resources. More importantly, it is claimed that it does not provide any mechanism for such adaptations, at least not in the straightforward phenotypic sense. Because this formulation of group selection is concerned with complex social behaviours and sociobiology, and not necessarily the question of the status of units of selection in themselves, it is outside the scope of this thesis. However, "Altruism" and approaches related to it will be discussed further in chapter 4.

¹⁰⁷ Dawkins, *The Selfish Gene, The Extended Phenotype*

¹⁰⁸ Dawkins, *The Extended Phenotype* (Oxford: Oxford University Press 1982) p. 81

Furthermore, as will become clear, the unit of selection debate concerns the role of mechanisms in evolutionary theory, as well as the role of explanation in neo-Darwinism. The "unit of selection" (or the "unit of evolution" which Maynard Smith suggests is more appropriate) as the 'thing that selection acts upon' will have to have something to say about how selection functions as well as how we describe this functioning and the mechanism involved.

The unit of selection debate is thus concerned with the utility of isolating certain functional entities in evolution. The point I would like to make in this section of the chapter is that the unit of selection debate is primarily concerned with denoting what the 'individual' should be in evolutionary theory, and this will have profound implication for not only the third component of evolutionary theory, heredity, but for the other two as well. Dawkins' contribution is surely very useful in showing that 'the organism' need not end with the skin or with the outer membrane of the biological entity in question. However, it is possible that his recommendation of "genic selectionism" simply replaces the individual organism with the individual gene without resolving any of the issues inherent in an 'individualist' approach in biology.

Dawkins managed to offend nearly everyone, scientist and non-scientist alike, with his book *The Selfish Gene*. On the one hand, its title misled non-scientists into believing that Dawkins was claiming that it was in our genes to be selfish. His true claim, that genes themselves were the target of selection forces, and that organisms were only vehicles for the propagation of these genes, incensed biologists, who thought it both needlessly reductionistic and counter to common sense. If genes are the replicators and not organisms, then why should organisms adapt for survival, and not the genes themselves?

Dawkins' claim is that genes are the replicators (that which gets copied) while the organisms are the vehicles for their transmission. David L. Hull sees Dawkins' use of "vehicle" as running counter to common sense, since if the individual is a merely neutral vehicle, then why should it change as a result of selection, and not the replicators themselves? Hull recommends that individuals should be called "interactors" since this would retain their role as a unit that is itself influenced by the

environment. However, Hull believes that Dawkins is right to place emphasis on the replicator, and not concentrate so much on the individual organism.¹⁰⁹

Sober notes that this is the most valuable aspect of Hull's and Dawkins' contribution, that it disentangles the unit of *heredity* from the unit of *selection*. That the gene is the "replicator", the thing that gets copied from one generation to the next, is uncontroversial. But for Hull and Dawkins, anything that carries these replicators around is unimportant, it is not the vehicle or interactor that is selected, it is the replicators themselves. So Hull and Dawkins would like to have it.¹¹⁰ Therefore, the selfish gene hypothesis is intended to function as a unifying idea. Since the unit of heredity is the gene, why not let it be the unit of selection as well? For Dawkins the question is about whether we should call the gene or the organism the functional unit of evolution. Dawkins appears to think that both descriptions will turn out to be compatible¹¹¹ though Sober is not so sure of this.¹¹² Kitcher and Sterelny explicitly claim that "Dawkins's genic selectionism offers a *more general theory* of evolution."¹¹³

This in itself should give some clue as to the underlying ideals behind Dawkins' work on this issue. Many anti-Dawkins arguments are aimed at the issue of 'needless reductionism' which the selfish gene view of evolution is supposed to entail.¹¹⁴ Since Dawkins is clearly trying to reduce all evolutionary explanations to those dealing with genes, this is so. His belief is obviously that any successful explanations in evolution which refer to organisms can be stated in a way so that they refer to genes. However, an issue which I believe gets obscured by this charge of reductionism is an issue about the status of *heredity*. I myself would like to leave aside the issue of reductionism in biology in favour of a more precise inquiry into how heredity is conceived of in

¹⁰⁹ Kitcher and Sterelny, "The Return of the Gene" *Journal of Philosophy* 85 (1988), pp. 339-361

¹¹⁰ Although Sober suggests that Hull is not quite so keen as Dawkins to have the gene as the *exclusive* unit of selection. Sober, Elliott and Wilson, David Sloan "A Critical review of Philosophical Work on the Units of Selection Problem" *Philosophy of Science* 61 1994 pp. 534-55

¹¹¹ Dawkins, in *The Extended Phenotype*, claims that explanations in terms of genes and in terms of organisms will be equivalent, by use of his example of the Necker Cube. However, in the preface to the 1989 edition of *The Selfish Gene*, he extends this metaphor and suggests that the "gene's eye view" of evolution can explain more than an organism's-eye view.

¹¹² Sober, *Philosophy and Biology*, p. 107

¹¹³ Kitcher, Philip and Sterelny, Kim. "The Return of the Gene" pp. 339-361.

¹¹⁴ Dawkins deals with some of these objections by Rose, Lewontin and Gould in chapter 2 of *The Extended Phenotype*

evolutionary theory, though it is clear that some of my discussion of this issue will be pertinent to the more broad issue of reductionism.

It has been noted that Dawkins' and Hull's proposal in the unit of selection debate was to make the unit of heredity, the gene, the same as the unit of selection (selection acts on the gene not the organism, and the gene is the unit of heredity). That is, they claim that since the gene is what is copied, then it should also be what is selected. For them, the individual can be treated as a mere receptacle for the genes. For the individual organism itself dies, but its genes are passed on if the organism has reproduced. Thus the gene ought to be treated as the functional unit in evolution, for it is what is copied from one transient generation to the next. We ought here to be reminded of Weismann's *Continuity of the Germ Plasm*.¹¹⁵ Although Dawkins' proposal seems to be a more general move referring to the types of explanation that evolutionary theory should provide, we can see that it is little more than a reaffirmation of the Weismannian, anti-Lamarckist requirement of neo-Darwinism. For Dawkins, the 'information' resides in the genes, as the immortal element and as Kamps puts it, for Dawkins "Every phenotypic event (i.e. every evolutionary event) is recorded in the genes."¹¹⁶

So we may have to view Sober's pronouncement, that Dawkins and Hull have disentangled the unit of heredity from the unit of selection, with some suspicion. For they have made them the same thing, with the neat result that all selection events (phenotypic events) are describable as heredity events (genotypic events). Mahner and Bunge remark that this move makes sense only in the context of the Modern Synthesis.¹¹⁷ As was noted in chapter 2, the population genetics strand of the Modern Synthesis, typified by Fisher and Wright, saw evolution in terms of changes in gene frequency. Selection for the population geneticist is seen only in terms of these changing allelic frequencies, and making selection work only upon genes can be seen as an extension of this approach to evolution. This then, as was hinted at earlier, is a way to give greater consistency to the neo-Darwinist Modern synthesis. Explanation of biological events can be given either in terms of genes or in terms of selection, offering a "more general theory of evolution" as Kitcher and Sterelny have it. Thus explanations of selection and heredity can be given in the same language, they function

¹¹⁵ see fn. 58

¹¹⁶ Kamps, p.471

¹¹⁷ Mahner and Bunge, *Foundations of Biophilosophy* p. 117. p. 338

by use of the same currency, which is genetic information. This, as I have argued, lends itself to a computational metaphor, where DNA is the 'programme' that controls the eventual characteristics of the organism. Thus the DNA genotype causes the phenotype much as the programme causes the computer to calculate. DNA is treated as a formal language. What nicer result for the true mechanist, or true determinist? Not only does the hereditary component cause the organism to develop, it even formally defines its characteristics. Mahner and Bunge also argue that if one treats the gene as that which is selected, then this cannot mean that the actual physical structure of the DNA itself is selected, but rather that the information encoded in the gene is selected. This information is what supposedly 'benefits' from the 'survival' conferred by replication, in Dawkins' terms, and they deem this "good old Platonism in modern informational garb"¹¹⁸

So there is a strong tendency to see DNA, or the gene, as a programme with informational content, as a type of formal language. But a formal language must have a pre-established syntax, the eventual states of the computer are defined by this, but these eventual discrete states can never rewrite the syntax of the formal language. This is where the anti-Lamarckist constraints of Dawkins' position become clear. For it is not so much a question of equating information and heredity, or information and DNA, as taking information-oriented metaphors too seriously. There are no metaphysical constraints in heredity as such, nor in the mechanism of DNA or genetics as such, but there are many metaphysical constraints lurking in the often ill-defined notion of information.

So even if Dawkins' genic selectionism has made evolutionary theory simpler, or more general in terms of explanation, by equating selection with heredity, (and it is not wholly clear that it has, since selection still acts upon the same 'individual' as the organism, under the description of the organism's 'complete genome') it has done something else as well. It has, by treating the genetic hereditary component as a 'programme' which is executed to cause the development of the organism, postulated a one-way flow of information as well. By treating the transcription of DNA as a mechanism analogous to the transcription of a formal language, one in which the rules of syntax are pre-established and unalterable, and also claiming that selection can be described wholly in terms of genetic information, Dawkins has curtailed the possibility

¹¹⁸ Mahner and Bunge, *Ibid.*

of feedback from genes to environment. If the 'information' in DNA is the only thing that is available to selection, and the organism effectively disappears from evolutionary explanation, then there is no way for an organism or genome to alter its own 'blueprint'.

Thus heredity is defined as non-Lamarckist in evolutionary theory. But this is not because of the actual physical mechanism of DNA transcription and translation, it is also a result of some strong metaphysical constraints associated with the notion of information. These come from the application of computational metaphors to biology. The unit of selection debate concerns the functioning of entities in evolution, and the move to establish hereditary units (genes) as the units of selection has allowed us to see how the function of heredity has been constrained by metaphysical considerations. And, just as in the case of natural selection and variation, it is quite impossible to give an adequate characterisation of one of the components of evolutionary theory without reference to the others. The way that heredity is to be understood is implicated in the way selection is thought to act. And this result may come as a surprise to those who believe that the function of heredity, since it is so closely tied to an actual physical mechanism, is unproblematic in evolutionary theory.

We have concluded that the third component of neo-Darwinism, heredity, is closely tied to the definition of mechanisms that rely heavily on a notion of information. Yet we have also seen that this concept, information, is, to say the least, somewhat problematic. However, the difficulties related to giving an adequate characterisation of information as a concept in evolutionary theory have not prevented it from being a cornerstone of neo-Darwinism as an anti-Lamarckist constraint. For with the advent of neo-Darwinism, and the introduction of such concepts as the Weismann Barrier, along with the discovery of the structural properties of DNA as a replicating molecule, there has been a concomitant application of the term information to the function of biological entities at the cellular level. Information is used to denote the possible vectors of information flow in biological systems. Thus, the Weismann Barrier postulates that information can never flow from soma cells to germ cells, and the Central Dogma postulates that information can never flow from proteins to DNA. Although it may not be clear what exactly this information 'encodes' or 'contains', it may be said that 'information' as a concept has been operationalised by neo-Darwinism as part of neo-Darwinism's anti-Lamarckist constraints.

In effect, neo-Darwinism, although it is made up of the three elements of natural selection, variation, and heredity, is largely defined by being a theory that is *anti-Lamarckist*, which is to say, *anti-teleological*. The functioning of its three elements is characterised by disallowing Lamarckist modes of evolution. This occurs, in some part, because they are all three mutually dependent, or defined by way of the functioning of the others. But the net result of this is that neo-Darwinism is an expression of the *constraints* on how biological entities can function. The second part of this thesis will address how this neo-Darwinist model of evolution interacts with some approaches to evolution which have been characterised as *non-Darwinist*, or even perhaps *anti-Darwinist*, such as symbiosis and bacterial evolution. But, given the conclusion above, if these approaches are anti-Darwinist, then must they also be Lamarckist? For if neo-Darwinism is defined by its exclusion of Lamarckist modes of evolution, then to what extent must all challenges to it be dependent on the modes of evolution which neo-Darwinism proscribes? In other words, the second part of this thesis will explore the interplay between Darwinism and Lamarckism with reference to some challenges to neo-Darwinist orthodoxy. In order to establish the extent to which these are true challenges to neo-Darwinism, we must be able to discern which aspects of them are truly at odds with neo-Darwinism, and inevitably these challenges will bring us to the issue of neo-Lamarckist mechanisms.

Part II

Symbiosis and Prokaryotes: A Challenge to Neo-Darwinism

"Lamarck has been so systematically laughed at that it amounts to little less than philosophical suicide for anyone to stand up in his behalf."

--Samuel Butler, *Evolution, Old and New* (1882)

Introduction to Part II

Part II of this thesis, chapters 4 and 5, will address the approach to evolutionary theory that seeks to criticise neo-Darwinism in a different way than the debates we have already addressed. The symbiosis-based research programme criticises neo-Darwinism's account of evolution and individuation, and is thus a challenge of more interest than challenges to neo-Darwinism which merely seek adjustments to the theoretical apparatus of neo-Darwinism. Symbiosis has been used to characterise the evolution of early life on earth by proposing that early collective cells were symbiotic unions. Thus, it is not merely a different metaphysical perspective on evolution, but a programme of research which presents real mechanisms of evolution which might be different from those of neo-Darwinism. But in order to assess whether it is a successful fundamental challenge to neo-Darwinism, we must tease apart its different claims, and see whether these are fundamental challenges to the metaphysics of neo-Darwinism. Then the mechanisms which symbiosis proposed must be investigated to see whether these mechanisms violate the core metaphysical assumptions of neo-Darwinism. This analysis will constitute the discussions in part II.

Chapter 4

Symbiosis

4.1 Symbiosis-based research programmes

Symbiosis is claimed by its major proponents to be a long-neglected area of research within biology and evolutionary theory today. The most prominent proponent is probably Lynn Margulis, who proposed the Serial Endosymbiosis Theory in its modern form in the 1960's. There are now many other scientists who insist upon its importance in biology, including James Lovelock, Sorin Sonea, Stanley Shostak, W. Ford Doolittle, Fritjof Capra, John Maynard Smith, Humberto Maturana and Francisco Varela. More importantly for the purposes of this thesis, however, is the number of commentators on science who have embraced the concept of symbiosis as a 'new paradigm' of biological and evolutionary research, among them Jan Sapp, a historian of science, Kevin Kelley, Robert Trivers, and R. Axelrod. It is now quite common to find references to symbiosis in popular characterisations of biology. Authors and scientists who explicitly defend a 'symbiosis-based' approach have of course many different reasons for allying themselves with such a concept. However, what they do share is a belief that first, symbiosis is in some sense incompatible with neo-Darwinism, and second, that a symbiosis-based research programme is better suited to provide a correct characterisation of evolutionary processes.

This incompatibility is predicated on several claims about the status of neo-Darwinism itself. For instance:

"In these mathematic machinations of evolution, the number of individuals in a population or a species is taken as the basic measure. The usual interactions that are explored between individuals (or species) are competition (for resources, space, etc.) and predation...The incorporation of "cost-benefit analysis" methods borrowed from insurance practices has led to the biologically puerile numerology that systematically ignores chemistry, biochemistry, molecular biology, and

geology. Nevertheless such aseptic language dominates current evolutionary theory."¹¹⁹

Thus Lynn Margulis complains that neo-Darwinism is obsessed with competition, rather than cooperation, that it is heavily reliant on "mechanist" mathematicisation, as opposed to an "organicist" outlook. Furthermore, she contends that neo-Darwinism must by nature focus on the "individual" and cannot properly focus on the symbiotic complexes that are in her view so fundamental in biology and in our evolutionary past.¹²⁰ She also argues that neo-Darwinism has only one mechanism for the generation of novelty or evolutionary innovation: random mutation, random meiotic recombination, that is, the gradual accumulation of favourable random changes.¹²¹ And, finally, she claims that the "chromosomal theory of inheritance", as well as Mendelian analyses of "factors", are at fault for improperly designating the genes in the nucleus of the cell as the proper focus of enquiry into heredity.¹²²

So symbiosis is seen as incompatible with neo-Darwinism on several levels. But in what sense could it be said to provide a more correct characterisation of evolutionary theory? We can identify four separate claims made by the proponents of symbiosis which are related to this question, and they need to be carefully distinguished from each other. First, there is the broad claim corresponding with Margulis' complaint about "mechanist" as opposed to "organicist" models of evolution. It is a little hard to pin down quite what is being said here, but I presume that part of it has to do with the idea that using methods borrowed from statistics cannot properly describe biological things which are thought to be in some sense 'uncapturable' by these methods. That is, using such statistical analyses can only capture part, and a very small part, of living systems in all their complexity. This is, I assume, the 'reductionism versus holism' debate at base.

¹¹⁹ Margulis, Lynn "Symbiogenesis and Symbiogenesis" in *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis* eds. Lynn Margulis and Rene Fester (Cambridge MA: MIT Press 1991) p. 6

¹²⁰ Margulis, Lynn "Symbiogenesis and Symbiogenesis" p. 10

¹²¹ Margulis, Lynn "Symbiogenesis and Symbiogenesis" p. 11

¹²² Margulis, Lynn. *The Symbiotic Planet: A New Look at Evolution* (London: Weidenfeld and Nicolson, 1998) p. 21

Also there is in this a claim about "the whole being more than the sum of its parts" as organicism has elsewhere been characterised.¹²³ I assume that this is what is meant by the further claim that symbiosis can describe complex interactions, and is not entirely focused on individuals, as neo-Darwinism is said to be. Therefore symbiosis-based research programmes would provide a 'fuller' understanding of biological processes by placing complex entities at the forefront of enquiry. This further claim may also be addressing the issue of latent 'essentialism' in biology. The idea here, first explicitly addressed by Mayr, is that Darwinism replaced essentialist thinking (about species, individuals, or types) with "population thinking" and thus shifted the focus of evolutionary thinking from thinking about "types" with properties or essences, to thinking about populations of organisms with shifting traits determined by the dynamic interactions and behaviours of the populations.¹²⁴ I interpret Margulis's position here as an indication that she believes neo-Darwinism has insufficiently come to terms with this shift, by continuing to focus on individuals as the basic unit of measure for evolution at large. It is difficult to assess the impact of these types of claims on scientific theory using the methodology this thesis has adopted, for it is clear that claims which focus on organicism, reductionism, holism, essentialism and the like might be considered too general in scope as criticisms of any specific research programme. Of course, these 'metaphysical' criticisms surely do have some importance in the context of explanation in biology at large. We will leave this claim aside for the moment, until a fuller explanation of symbiosis is in place, and will return to it in the conclusion.

A second and separate claim in the 'symbiosis' position is that neo-Darwinism focuses on competition at the cost of cooperation, meaning perhaps that cooperation should be a central characterisation of evolution instead of "survival of the fittest". Margulis and Sagan have said elsewhere that "survival of the fittest" has been "warped to mean that only the most ruthless win out in the 'struggle for existence'",¹²⁵ so perhaps they argue only with this warped and highly politicised version of natural selection, not with a more sober version of natural selection. Indeed, they point out

¹²³ Capra, Fritjof. *The Web of Life* (New York: Anchor Books 1996) p. 27

¹²⁴ Mayr, Ernst. "Species Concepts and Their Application", in *Philosophy of Biology*, ed. Michael Ruse (New York: Macmillan 1989). Also see Mayr, *One Long Argument*,

¹²⁵ Margulis, Lynn and Sagan, Dorion. excerpt quoted in *From Gaia to Selfish Genes: Selected Writings in the Life Sciences* ed. Connie Barlow (Cambridge MA: MIT Press 1991) p. 59

that "fit" in evolution means "fecund", not strong. Yet we saw earlier in section 3.1.2 that the status of fitness as a measure in evolution is not without its problems. But I think it is important to recognise that it is not at all clear whether one can replace 'competition' with 'cooperation' in a straightforward manner without identifying what this change would mean for a characterisation of natural selection itself. In fact, it is not clear whether the neo-Darwinist focus on competition is a *result* of how natural selection is thought to work, or whether competition is integral to neo-Darwinism itself. Questions like these need to be answered if one is to distinguish properly symbiosis from neo-Darwinism.

A third argument that must be identified is the idea that symbiosis provides a source of evolutionary innovation above and beyond the sources that are provided by neo-Darwinism's theoretical apparatus. This is equally hard to pin down. First, it may be that "random mutation" is not thought to be a strong enough source for the many increases of complexity seen in evolutionary history, and symbiosis provides a better and more reasonable source. Or else it may be that random mutation is a source, just not a very important one. The same may perhaps be said of "gradual accumulation of random favourable mutations or changes", where Margulis appears to be arguing against 'gradualism' in favour of a more 'saltationist' evolutionary story, one where symbiosis is the source of the 'leaps'. Again, it is not clear whether a symbiosis-based research programme would entail a full denial of the importance of random mutation, or gradualism, or whether such a programme would merely supplement neo-Darwinism with another source of evolutionary change. Indeed, it is arguable whether neo-Darwinism itself is necessarily committed to 'gradualism' in this way (see section 2.1).

Fourth, the claim about the "chromosomal" theory of heredity must be examined in some detail, which introduces some interesting issues about the importance of research programmes in the historical sense. Jan Sapp has argued this point somewhat more forcefully than Margulis, claiming that what he terms the "nucleocentric" research programme in the early 20th century was the main reason that symbiotic research was ignored for the most part. This "nucleocentric" research position describes the belief that the nucleus was the controlling centre of the cell, and this position was associated with a Weismannian strong separation between the germ ,

or nucleus, and the soma.¹²⁶ Now this may be the case contingently, but what is not clear is to what extent neo-Darwinism fully embraces a "nucleocentric" position. It may be the case that it does have a strong notion of heredity which does actively prevent enquiry into non-genetic loci of heredity. However, this may reside in the essentially anti-Lamarckist requirements of neo-Darwinism rather than in the locus of experimentation. We are not yet in a position to answer the question of how heredity functions in symbiosis-based research programmes as opposed to how it must function in neo-Darwinism, but it is at least clear that the issue of heredity in symbiosis is quite complex.

Given these considerations, this chapter will use the structure adopted throughout this thesis to examine these last three aspects of symbiosis I have identified. That is, the various symbiotic positions will be grouped according to the three components of neo-Darwinism: natural selection, variation, and heredity. In the case of the component of natural selection, symbiosis disagrees specifically with the neo-Darwinist 'assumption' that natural selection is competitive. In the case of variation, symbiosis approaches claim that symbiosis provides a mechanism for evolutionary novelty above and beyond that provided by neo-Darwinism. Finally, in the case of heredity, symbiosis-based approaches explicitly argue against neo-Darwinism's supposed insistence upon a very limited notion of heredity, which is anti-Lamarckist and nucleus-oriented. These three claims will be discussed in turn in this chapter.

A historical introduction to symbiosis will now be useful in setting out what the issues of symbiosis have been in past and present scientific work. Much of the following discussion is commentary on Jan Sapp's excellent history of the subject, and is intended to introduce some of the issues that are raised by symbiosis, for instance, the metaphors of collectivity, and of the types of entities that symbiosis throws up for consideration. These issues will be important when we address the issue of whether symbiosis is a separate, or a subordinate research programme to that of neo-Darwinism.

¹²⁶ Sapp, p. 39

4.2 Historical Introduction to Symbiosis

4.2.1 Mutualism and Master-Slave: the early history

The first symbiotic relationships discovered in nature were those of the lichens, which are all associations of a fungus and an alga. In 1868, Simon Schwenderer, a Swiss botanist, first proposed that lichens, which had previously been inimical to Linnaean classification, were in fact two types of organisms locked in what he termed a 'master-slave' relationship. His 'dual hypothesis' as he called it, was not accepted fully until around 1900. Some of those who did accept the dual hypothesis were unhappy with Schwenderer's assertion that the relationship was a 'master-slave' relation. There was disagreement among botanists who worked with lichens over the degree of parasitism in these relationships. Some saw the master-slave metaphor as too politicised, and replaced it with a terminology based on parasitism. Yet some saw the relation as more cooperative, and complained that the terminology based on parasitism carried too many connotations of disease and plague.

In 1877, Albert Bernhard Frank, one of the first botanists to accept the dual hypothesis, proposed the introduction of a neutral term that did not presuppose any degree of parasitism and only described the co-existence of two species in or on one another: he recommended the term symbiosis.¹²⁷ The coinage of the term is usually attributed to Anton de Bary, yet he did not himself use the term until 1879. The introduction of this technical term did not, however, stop the debates over the degree of parasitism in such relationships. Pierre Van Beneden had earlier proposed the term "mutualism" to describe the same types of relationships. He believed that there was a continuum of relationships in nature from the "parasite" at one end of the continuum to the "free animal" at the other, with various degrees of mutual or symbiotic relationships falling in between.

Over time, botanists began to see more and more evidence of symbiotic associations in nature, ranging from complex plant and animal associations down to symbiotic associations between bacteria and viruses. Though the researcher's immediate communities accepted many such discoveries, the biological community at

¹²⁷ For this account of the early history of symbiosis see Sapp, Jan. *Evolution by Association* pp. 4-8, 35-39

large often did not accept them until many years later. More importantly, such discovered symbiotic associations were often acknowledged as specific adaptations in nature in special isolated cases, but were not considered to have any ramifications in theoretical biology as general themes.

In the late nineteenth century, researchers believed that the secrets of all life could be found by understanding the cell. It had already been discovered that all cells came from other cells, and that plant and animal cells were very similar in function and organisation. Thus, it was thought that research into the cell would shed light on all the functions of the higher organism. The single cell was generally thought of as an individual, self-sufficient organism, but the discovery of more and more organelles, or separate specialised structures within the single cell, led many to adopt explanatory metaphors using phrases such as 'division of labour' and 'cell-state' or 'cell-republic'. Researchers could be fairly specific about what the role and function of each organelle was, but they were unable to explain how such specialisation could have come about. The tendency was, therefore, to treat the entire individual cell as prior to any enquiry concerning the specialised functioning structures within it. Moreover, the cell itself was seen as the fundamental building block of higher organisms, so it was thought that an investigation into the cell would show much about the basic units of evolution.

There were, however, some researchers who wanted to treat individual cells as cooperative entities. Richard Altmann, in the late 1880's, suggested that the cell evolved through the conglomeration of bodies he called "bioblasts" into a collective colony. He believed that these bioblasts, which seemed to be present in all animal cells, were responsible for all cell metabolic activities. Altmann's work was severely criticised, and other researchers believed these bioblasts were merely artefacts of his staining process. The existence of bioblasts was later supported by the work of Alexander Benda in 1897; these bioblasts were what we today call mitochondria. But Altmann's theory of cell evolution was largely ignored.

We can see in this early history some of the tensions within symbiosis theorisation itself, as well as some tensions between neo-Darwinism and symbiosis. The early history of the term symbiosis has caused some difficulties for the usage of the term today. There has been a tendency to use the terms mutualism, cooperation and symbiosis interchangeably. Margulis has argued that the term symbiosis should be reserved for designating relationships between organisms of different species.

Furthermore, she believes that approaches which fail to make this important distinction are wholly inappropriate to dealing with symbiosis in its most important form. This will become important later when we examine some neo-Darwinist approaches to cooperative behaviour. Additionally, Margulis has recommended that terms such as "mutualism", "commensualism" and "parasitism" tend to obscure the genetic aspect of symbiotic systems, an aspect which she believes is fundamental in understanding symbiosis. This 'genetic' element will now be explained in more detail.

4.2.2 Nucleocentrism and Lederberg: extracellular genes

The development of theories for the evolution of the cell was soon eclipsed by the discovery of the importance of the nucleus as the carrier of genetic information. In chapter 2 we examined Weismann's ideas on the nature of heredity, and it was noted that Weismann's work was a significant constraint on the Darwinist notion of heredity. By claiming the germ line affected the soma, but never the reverse, Weismann effectively denied that Lamarckist inheritance of acquired characteristics could ever take place. Also, the identification of the hereditary material with the nucleus had the consequence of identifying the organism with its germ-line alone. In the words of Bergson, for Weismann the organism becomes an "excrecence, a bud caused to sprout by the germ..."¹²⁸ Weismann's work on this subject continued to gain support, and soon it was believed that the nucleus, as well as being the receptacle for genetic material, was itself responsible for the differentiation of cell organelles and their functions. It was noted earlier that Mendelian ideas about the particulate nature of heredity reinforced this belief to a large extent.

The assumptions behind what Sapp has called "nucleocentrism" are manifold, but are related to what has already been said about the nature of heredity and variation: one, that the nucleus contains the genetic material; two, that this material is the source of development for the differentiation within cells and the maintenance of their metabolic functions; three, that this genetic material is that which is passed between generations as heritable material; four, that genetic variability is gained through random

¹²⁸ Bergson, Henri. *Creative Evolution*. Authorised translation by A. Mitchell (Lanham MD: University Press of America 1983) p. 27

changes and reshuffling of this material alone; and fifth that this genetic material is self-contained and separated off from the external environment.¹²⁹

The discovery of DNA as the carrier of hereditary information merely continued this trend in a different guise: the DNA was seen to be the 'program' that the cell carried out, and was responsible for all cell functions, as well as all higher functions of the larger organism. Research into the evolution of cells themselves was generally pushed aside by this research program. Since it was believed that the nucleus or DNA was the 'program instructions for life' it was left to researchers to discover its origin, and the evolution of the cell would presumably be secondary to this.¹³⁰ Thus, research focused on nuclear genes as the entities that determined everything else in development, and the other components of the cell, the organelles, were considered simply as developments that the nuclear genes were responsible for. There was for many years little interest in understanding how these separate entities within the cell had come to be. They were thought, for the most part, to have been formed through slow accumulation of adaptations in the nuclear genotype itself, manifested in the cell and subjected to gradual selection.

However, the emphasis on researching the "universal code" of DNA and RNA also disclosed some interesting findings in the field of symbiosis. The discovery of bacterial genomes, as well as the discovery of viruses as "naked genes" led to research into the mechanisms by which these genes interacted with each other. Since it was known that viruses and bacteria were responsible for many illnesses, the research was driven by an attempt to understand the nature of pathology. The discovery of such extracellular genetic particles was itself shocking to investigators, who had previously relied entirely on a Weismannian model of inheritance where genetic material was separated off from the environment by the nucleus.

As was discussed earlier, inheritance and genetic variability was thought to proceed between generations of cells by mutation and random shuffling of genomes that were self-contained. It was not thought that extracellular genes could have any effect on genomes that already were held separately in the cell. Soon it began to be recognised that extra-cellular genetic particles, such as viruses, could alter the genome

¹²⁹ Sapp, p. 36

¹³⁰ This research program is still very much alive, and the work in the 1970's to construct a "primeval soup", as well as the work of Cairns-Smith and those working on the "RNA-world" theory attest to this.

of other cells by being incorporated into them. Research seemed to show that this process was almost always fatal to the host cell, and viruses were generally seen as worse than parasites, as harmful pathogens.

Joshua Lederberg's work in the 1940's began to show that the 'host-parasite' or 'pathological' picture of the virus-bacteria relationship was much more complex. He showed that viral DNA, once injected into its host, could be incorporated into the bacterial host's DNA as a harmless segment of DNA, called a prophage, which would then replicate along with the bacterium's own genetic material. The prophage seemed to confer resistance to infection from other external factors onto the bacterial host. Such prophages could stay inside cells for many generations, either staying inert and allowing the bacteria to do their replication for them, or else later become activated and kill their host, and be released to infect other bacteria. (see Appendix 3)

Lederberg realised that the relationship was hard to define. It seemed to be a host-parasite relationship since the viruses were using their bacterial hosts for replication. But on the other hand it could also be seen as a close symbiotic relationship, one which the infection-resistant host could not do without. He also realised that the difficulty of adequately defining such a relationship led to a larger problem having to do with the nature of the organism: how could one designate the 'normal' components of a cell when external supposedly 'pathological' factors were so closely integrated in a cell's normal functioning?¹³¹ Lederberg thought that prophages were an important source of genetic variation among bacteria, "a special form of sexuality".¹³²

Lederberg's research into the functioning of bacteria and viruses is important in the history of symbiosis, and makes certain theoretical aspects of symbiosis clear. First, the cell's own genome is not necessarily uniquely responsible for the functioning of the cell. Extra-cellular genomic factors can be implicated in normal cellular function. Second, the relationship in bacterial-viral associations is symbiotic, but also of evolutionary importance, because of the possibility of genetic change through these avenues. This has profound ramifications for taxonomy, as it makes it problematic to assume that bacteria evolved from one common ancestor, since their genomes change with such ease through the intervention of viruses. Thus, apart from the symbiotic

¹³¹ Sapp, pp. 158-161

¹³² Sapp., p. 160

relationships which subsist today between bacteria and viruses, there is also the fact that such relationships in the past may have been frequent, and may explain much about evolutionary relationships today. So we can see that symbiotic processes can occur at the level of DNA itself, as in the symbiotic relationship between viruses and bacteria. But symbiosis can also occur between different types of bacteria, each of which can form a cooperative relationship which persists as a functioning entity on a higher level or organisation. As we will see next in the discussion of Serial Endosymbiosis Theory, this type of 'cooperation' can in fact be significant from an evolutionary point of view.

4.2.3 Serial Endosymbiosis Theory

Lynn Margulis's serial endosymbiosis theory, or SET, now widely accepted by the scientific community, theorises that in fact all complex nucleated cells (eukaryotes) evolved as communities of interacting free-living bacteria (prokaryotes), which themselves already had the ability to fulfil the functions that the eukaryotic organelles now fulfil.¹³³ For instance, mitochondria, the energy producing organelles in animal cells, are thought to have been bacteria that had already developed an efficient oxygen-respiring ability, which were later incorporated into a cell host which provided protection against acidity and high temperatures. Thus, it is believed that eukaryotes, the basis of most complex plant and animal life on earth, were formed only through a mutually dependent relationship between various types of bacteria. (see appendix 4) The fundamental ideas behind SET were first proposed by the Russian biologist K.S. Merezhkovsky in the early 20th century, although Margulis herself was unaware of his contribution until the late 1980's. Thus her ideas were not particularly new in one sense, but she was the first to propose SET to a western scientific audience with the support of current research.¹³⁴

¹³³ Margulis, Lynn. *Symbiosis and Cell Evolution: Microbial Communities in the Archean and Proterozoic Forms*, 2nd Ed. (New York: Freeman 1993) p. 2ff

¹³⁴ The tale of how Margulis learned of her Russian counterparts in symbiosis research is a classic story of the state of science during the Cold War, and is told in L.N. Khakina's *Concepts of Symbiosis: A Historical and Critical Study of the Research of Russian Botanists* trans. Stephanie Merkel and Robert Coalson (New Haven: Yale University Press, 1992) Margulis now gives credit to these Russian scientists for most of the ideas in SET. I set out the major tenets of SET here with credit to Margulis as is

Margulis also discovered homologous structures in the centriole and basal bodies (to which flagella and cilia, (motility organelles) are attached) in both prokaryotes and eukaryotes. She interpreted the existence of these homologous structures as further evidence for SET. Margulis' work took several years to be accepted, since it was thought that the homologous equivalents she discovered were not in themselves enough evidence to support SET. The reasons for this had to do with Neo-Darwinism's conception of how and at what pace evolution occurs.

Earlier it was noted that symbiosis proponents claim that the neo-Darwinist synthesis, with its insistence on genetic change through random reshuffling of genetic material acted upon by natural selection, suggested that evolution could only happen slowly and very gradually. Some opponents of the SET insisted that eukaryotes could only have evolved gradually from prokaryotic ancestors. 'Gradualist' detractors of endosymbiosis expected to see a slow, gradual accumulation of adaptations rather than a series of endosymbiotic events. Though some agreed that SET was "aesthetically pleasing" they believed there must be a "missing link" as yet undiscovered, that would show the gradual transformation of prokaryote to eukaryote.¹³⁵ The homologous structures that Margulis had seen were interpreted as exactly what one would expect in a gradually transformed lineage from prokaryote to eukaryote. It is in this sense that symbiosis has been claimed to provide a source of evolutionary novelty that contradicts the gradualist assumption of neo-Darwinism. This claim will be considered in more detail in 4.3.2 below; I introduce it here merely as an example of historical reception of symbiosis theory.

But the most significant aspect of SET in terms of symbiosis is the fact that the collective nature of the eukaryotic cell means that there is more than one genomic component involved, and thus, in terms of evolutionary descent, that there is more than one common ancestor involved in eukaryotic cells. Since mitochondria have their own genetic RNA component, this means that there is an avenue of heredity distinct from the nuclear genetic component. Furthermore, the centrioles and basal bodies involved in cell motility have also been conjectured to have a genetic component, as they appear

the common custom with recognition that she is the proponent of these ideas most well known in the West.

¹³⁵ Sapp, p. 161

to be self-reproducing.¹³⁶ Thus, SET shows that the 'complete genome' as a characterisation of the organism, may be a very complicated position indeed. For instance, Dawkins' strong Weismannian commitments, and his genetic reductionism, seem to lead him toward a view which claims that the organism might be thought of as the genotype as far as evolution is concerned.¹³⁷ But which genotype? In effect, SET shows that all organisms are made up of more than the genetic component of their own particular species. Each eukaryotic cell has not only its nuclear DNA, but also RNA from its mitochondria and chloroplasts. Each living cell has *more than one* genetic lineage.

This brief history of symbiosis shows that the early investigation into cells as collective entities was overshadowed by the insistence on the importance of DNA in evolution at large. But as DNA came to the forefront of research programmes in evolution and biology, it revealed many findings that pointed to symbiosis as an important evolutionary phenomenon in its own right. And, in the end, research programmes returned to investigating cells as collective entities, but this time as collective entities that were the product of several independent genealogies, as in SET. Thus the history of symbiosis shows the many tensions between symbiosis and neo-Darwinism, first as cooperation versus competition, second, as variation through symbiotic genetic recombination versus incremental change, and third as an understanding of heredity that is not limited to vertical transmission of nuclear genes.

This tension between neo-Darwinism and symbiosis also shows how neo-Darwinism attempted to explain away the various examples of close cooperation that symbiosis represented. For example, SET was dismissed as "aesthetically pleasing" but largely unconfirmable for many years, indicating that orthodox neo-Darwinists believed that they had available to them other ways of explaining the facts Margulis presented. And also, in the early days of symbiosis research, it was often claimed that cooperation was rare in comparison with competitive behaviours among organisms. How in fact does neo-Darwinism explain cooperation? It is important to address the ways in which cooperative behaviour is explained by orthodox neo-Darwinism before we can assess to what extent symbiosis can challenge neo-Darwinism as insufficiently 'cooperative'.

¹³⁶ Although this has been contested by Maynard Smith and Eörs Szathmáry in *The Major Transitions in Evolution* (Oxford: Oxford University Press, 1997) pp. 142-145.

¹³⁷ Or, as Henri Bergson put it, Weismannism leads to a position "as if the organism itself were only an excrescence", Bergson, Henri. *Creative Evolution*. p. 27

4.3 How does neo-Darwinism deal with cooperation?

Sapp's outline of the history of symbiosis notes that in the early days of plant biology, where some of the first symbiotic systems had been recognised, the debate about symbiosis was, on one level, a debate about how terminology should be applied to such systems. Yet, on another level, it was marked by political polemics regarding the nature of human society. The very term 'symbiosis' was introduced to designate a relationship that was neither strictly parasitic nor strictly mutualistic. In plant biology at the end of the 19th century, a flurry of terms were introduced, all describing various kinds of relationships along the continuum running from parasite to cooperative whole. Yet although the terms to describe these distinctions were available, the prevailing view was that most symbiotic relationships in plants were simply *apparently* mutualistic. In fact, they were cases of parasitism, where one party benefits at the cost of the other. The definition of parasitism could, perhaps, be broadened so that the host could gain some small benefit from the parasite, but this broadened definition did not entail that the relationship was in any way mutualistic.

The assumption behind this view was the belief, based on Darwin's use of Malthus in no small part, that the key to evolution was selfish struggle for limited resources. This principle alone was thought to be the best way to understand the complex relationships between species. The idea that a party in a symbiotic relationship was not, upon closer inspection, an invidious parasitic thief was anathema to Darwinism's 'struggle for resources' ecological principle. More broadly, it was thought that cooperation in the sense of combining resources was limited to human society. Those biologists that were more accepting of cooperative systems in biology still limited their discussions of symbiotic systems to such metaphors as "master-slave", where there is a kind of cooperation, though still decidedly one-sided. The core of Darwinism, at that time, limited the kinds of perspectives that could be used to view symbiosis. The most important limitation was the prevailing belief that evolution *demand*ed that organisms struggle against each other for limited resources.

Let us look for a moment at what this approach to cooperation leads to, in terms of its understanding that evolution is competitive at base.

4.3.1 Altruism, Reciprocal Altruism and Group Selection

One group of general approaches to the evolution of cooperative behaviour can be roughly grouped under the heading of altruism. Altruism, in its broadest form, is the exhibition of a type of behaviour that increases the fitness of another at the expense of one's own. It is thought to run counter to Darwinism since any behaviour that reduces fitness is maladaptive and hence should be selected against in the long run. Thus the research programme that deals with altruism seeks to explain how such cooperation can be explained given the assumption that nature is essentially competitive in the neo-Darwinist paradigm. This research programme broadly includes such terms as reciprocal altruism, altruism, group-selection, kin selection, and evolutionary game theory. Each term will be explained in context in this section.

Reciprocal altruism, a thesis proposed by Robert Trivers in 1971, claimed that natural selection operated in a way such that acts of kindness would be recognised and repaid in kind later on, so that 'altruistic' acts were actually selected for by natural selection. Trivers specifically invoked the concept of symbiosis as an adjunct to his theory: "Reciprocal altruism can also be viewed as a symbiosis, each partner helping the other while he helps himself."¹³⁸ V.C. Wynne-Edwards had earlier proposed the group-selection hypothesis, which caused controversy by claiming that cooperation could be explained by the possibility that evolution could work at the level of the group of individuals as a whole, at the level of species, rather than at the mere level of individual organisms, thus suggesting that the group or species could be seen as the "unit of selection". It was claimed that 'cooperative' strategies enlisted by species as a whole would be adaptive for the continuance of that species on an evolutionary level.

4.3.2 Kin Selection

The thesis of group selection has been discredited and explanations of altruism have been replaced with explanations that are based on the idea that the unit of selection is

¹³⁸ Trivers, Robert. "The Evolution of Reciprocal Altruism", *Quarterly Review of Biology* 46 (1971) as quoted in Sapp, p. 199

either the gene or the individual.¹³⁹ Maynard Smith, in his own attack on group selectionism, pointed out that cooperation is an unstable strategy; introduce a competitive element into a cooperative group and the competitors will soon take over the cooperators. For this reason, it was thought that altruism at the intraspecies level ought to be explainable by Hamilton's famous kin selection hypothesis. In the kin selection approach it is claimed that if evolution occurs at the level of the genotype, then any strategy that maximises the number of genes passed on will be an adaptive strategy. Strategies that do this may appear to take the form of altruism since parents will care for any members of the group which carry some of the parental genes into the next generation. The idea is that an individual's own fitness will be sacrificed to ensure that its offspring will be increased. On this approach, as J.B.S. Haldane remarked, one would be prepared to give up one's life for exactly two brothers, or eight cousins.¹⁴⁰ However, it seems that any kin selection hypothesis must have some kind of kin recognition system in order for it to work, since there must be some way for members of a species to identify related members so that they can protect them. Thus the reciprocal altruism and kin selection approaches, by assuming competition as the rule, must also account for the generation of recognition in order to explain cooperation.

4.3.3 Evolutionary Game Theory

A related area of discussion which is closely related to kin selection and reciprocal altruism has its origins in game theory. It also is concerned to explain how cooperative strategies arise in an essentially competitive world. Maynard Smith is credited with introducing game theory to the domain of biology, by using classical game theory to

¹³⁹ The discrediting of Wynne-Edwards and group selection began almost immediately upon the suggestion that species themselves could be "units of selection", and is now considered complete. However, it is hard to see why this suggestion met with such outrage, if all it suggests is that cooperation is a useful strategy for a group of animals, as well as for an individual animal. It seems that, at least in Dawkins case, the problem was not so much that Wynne-Edwards was promoting cooperation as assuming it. Dawkins thought that cooperation must be explained, not assumed, and furthermore, it must be explained from the individual (or gene) point of view. (See R. Dawkins, *The Selfish Gene*) This means that groups cannot be units of selection, and if a group seems to have been selected against as a whole, this is simply because all or most of its individuals have been selected against. I have to admit that this distinction does not seem especially profitable. see footnotes 106, 139

¹⁴⁰ Maynard Smith, John. *Did Darwin Get it Right?* p. 187

disclose evolutionary stable strategies (ESS). This approach was designed to answer his own objection mentioned earlier, namely, that a cooperative strategy was highly vulnerable to being invaded by a competitive strategy, and was thus not a stable strategy. Evolutionary game theory was devised to show how it was that cooperation could be shown to be a stable strategy. However, the results actually showed that cooperation and competition were equally stable strategies.¹⁴¹ And again, because it depends upon a recognition system, game theory approaches to are confined to species that can recognise other individuals and remember how they act. This move makes it more clear what the assumptions behind evolutionary game theory are. The obvious problem is exactly the same as for reciprocal altruism and kin selection theories: how does the recognition get generated? In kin selection, it is clear that kin selection cannot work unless there is a kin recognition system. In reciprocal altruism, there must be a means by which individuals can both recognise and remember a 'kind act'.

Axelrod and Hamilton attempted to show that the evolutionary game theory results were not confined to complex animal societies.¹⁴² They explicitly claim that their approach deals with "symbiosis".¹⁴³ They attempted to show that a simple life form like a bacterium could form a cooperative relationship if it was limited to

¹⁴¹ Classical game theory ranks individual preferences for different outcomes on a linear scale. Evolutionary game theory sees these preferences as differences in fitness. The paradigm game for altruism is the Prisoner's dilemma. In classical game theory, the player's preferences are ranked according to the best outcome, which would be for the player to do whatever the other player does. The best outcome is for neither to confess, the next best is for one player to "rat out" the other. In evolutionary game theory, the game is iterated, that is, played over and over, each play affecting the next. Results given by this iteration show that there are two "stable" strategies (in the sense given by Maynard Smith as the least "invadable" by other strategies) and they are called "Defect" and "Tit-for-tat". Roughly they go as follows: In Defect, the payoff matrix shows that it is better for player 1 to defect, no matter what player 2 does. Also, it is better for player 2 to defect no matter what player 1 does. Though it would be better for both to cooperate, neither wants to run the risk of being a "sucker" when the other player decides to defect. In Tit-for-tat, the strategy is to cooperate at first, and from then on do as the other player did in the last game. Since both strategies are equally stable, the question becomes why cooperation should evolve as a strategy at all. Maynard Smith supposed that the early stages of the evolution of a cooperative strategy would have to be something like reciprocal altruism, and claims that this is what Trivers' original hypothesis could be used for. Maynard Smith, *Did Darwin Get it Right?* pp. 192-201

¹⁴² Axelrod, R. *The Evolution of Cooperation* (New York: Basic Books, 1984)

¹⁴³ Axelrod, R. p. 90, 91, 101, 219n

continuous contact with only one other organism. This would eliminate the need for a recognition system:

When an organism is not able to recognise the individual with which it had prior interaction, a substitute mechanism is to make sure that all of its interactions are with the same player. This can be done by maintaining continuous contact with the other. This method is applied in most mutualisms, situations of close association of mutual benefit between members of different species... Another mechanism for avoiding the need for recognition is to guarantee the uniqueness of the pairing of individuals by employing a fixed place of meeting.¹⁴⁴

Thus the explanation of how associations between different species can be cooperative in the absence of a recognition system seems to appeal to the fact that such associations have certain characteristics: continuous association with one partner, a fixed spatial meeting place. But surely the evolution of these characteristics is what needs to be explained by evolutionary game theory. Noting that such situations are stable does little to explain how they can come about. Certainly it is the case that symbiotic partners do in fact have continuous association in a fixed spatial area, but surely why this association begins is that which must be explained.¹⁴⁵ The 'early stages' in the evolution of such stable associations are not addressed by the evolutionary game theory approach. Given that the competitive strategy is as stable as the cooperative strategy no matter what the probability of continuous interaction in future, the problem of how cooperative behaviour evolved is still an issue. And again, evolutionary game theory appeals to another associated type of cooperation, kin selection, to explain the early stages.

In fact ALL D ["Defect"] is evolutionarily stable no matter what the probability is of interaction continuing. This raises the problem of how an evolutionary trend to cooperative behaviours could ever have started

¹⁴⁴ Axelrod, p. 100

¹⁴⁵ And quite why such a spatio-temporally restricted situation would have any bearing on the need for recognition at all is interesting; perhaps it is a case of familiarity *not* breeding contempt. Also, there is no such thing as a single bacterium in nature.

in the first place...Genetic kinship theory suggests a plausible escape from the equilibrium of ALL D..."¹⁴⁶

But kin selection theory *itself* depends on a kin recognition system of some kind, precisely what Axelrod and Hamilton were concerned to avoid the necessity of. In addition, remember that Axelrod and Hamilton are trying to explain how non-genetically related organisms could cooperate given that they have no complex intelligence. Kin selection could never work as an early stage in the evolution of such a system, since the parties involved are not genetically related. This is the whole point of symbiosis, that the partners are completely different from one another in the sense that they have different requirements for survival, and are yet involved in a close association. For members of the same species, cooperation may appear to be cooperation in the interest of some shared goal¹⁴⁷ for both parties, but in symbiotic associations between vastly different organisms, these goals may well be different for each partner.

It seems that all three of these approaches, kin selection, reciprocal altruism and evolutionary game theory, depend on each other for support, since they all presuppose each other. Maynard Smith appeals to reciprocal altruism for support to explain how cooperation could evolve in the early stages.¹⁴⁸ Axelrod and Hamilton appeal to kin selection to the same ends. Kin selection appeals to reciprocal altruism to explain how non-genetically related partners might come to behave in altruistic associations. All of them seem to presuppose a complex social intelligence, since all need a recognition system to work. They are thus confined to cooperation between members of the same species, and this must be a highly socially competent species. When trying to explain cooperative behaviours among distantly related species, they all seem to end up appealing to intra-species explanations for the early stage of the evolution of such associations.

There are several points worth drawing out of the above analysis. First, both the altruism and game-theoretical approaches are based on the assumption that nature is competitive, and cooperation is a strange case that needs to be explained. The

¹⁴⁶ Axelrod, p. 96

¹⁴⁷ Though I use this term without any teleological intent; I wish only to show that cooperation has some functional aspect.

¹⁴⁸ See fn. 141, also Maynard Smith, *Did Darwin Get it Right?*

presence of this basic assumption causes these approaches to be based largely on same-species considerations, resulting in the claim that cooperation is explainable by the attempt to ensure that one's genes survive into the next generation. All the interesting things are seen as occurring between members of the same species, not between widely divergent species which have neither any obvious competitive interest in each other, nor overlapping 'goals'. Axelrod and Hamilton are forced into their absurd hypothesis (that bacteria can side-step a kin recognition system by being in contact with only one other organism) by the notion that cooperation can only occur when an organism can remember a kind act and thus repay it, or remember a defection and retaliate. Second, the cost-benefit analysis approach that Margulis complained of earlier is obvious. This is also a product of the assumption that nature is essentially competitive. Above I have shown any approaches which assume competitiveness are also forced, when dealing with 'cooperative' situations, to deal only with genetically related individuals, and can say nothing about associations between different species.

Thus neo-Darwinism encounters real difficulties trying to explain how cooperation comes about if it takes it for granted that evolution operates in such a way that nature is essentially competitive. And this, perhaps, is the reason that symbiosis seeks to challenge neo-Darwinism on this point. But what is not clear is whether this 'competitive' nature is an account of natural selection *itself*, or if it is a result of a misinterpretation of natural selection. It appears that neo-Darwinism does deal poorly with cooperation, but this may not have anything to do with the question of whether natural selection is wholly dependent on competition. Moreover, even if neo-Darwinism is fundamentally competitive, it is up to symbiosis to recommend an alternative interpretation that improves upon neo-Darwinism in terms of explanation.

4.4 Symbiosis: three criticisms of neo-Darwinism assessed

4.4.1 Natural Selection: Cooperation, not competition?

We may now turn to the question of to what extent neo-Darwinism's component of natural selection depends upon competition rather than cooperation. In this section I will argue that first, natural selection does not depend necessarily upon competition as a mechanism for change, as the symbiologists would have it. Second, I will argue that

even if this were the case, the idea that cooperation as a replacement for competition does not have any theoretical advantages for viewing biological systems more appropriately. At best, it is a simple reverse description of the mechanism of competition, not a separate and more refined component.

Earlier in section 3.1, the first component of neo-Darwinism, natural selection, was addressed, with a view to discovering exactly what sort of thing natural selection is. It was argued there that this endeavour was doomed as long as natural selection was discussed on its own, divorced from its interaction with the other components of neo-Darwinism, variation and heredity. And earlier in section 2.1.2 it was noted that Darwin himself dealt with the tension in natural selection between its role as an active mechanism and a passive sorting system. We must now return to these considerations in order to address the question of to what extent natural selection is a fundamentally competitive mechanism.

Let us examine some characterisations of natural selection that seem to stress its competitive nature. It is possible to break down these definitions into two strands, which could be characterised as 'natural selection as author' and 'natural selection as editor'. These might correspond roughly with the active and passive roles assigned to natural selection discussed earlier in this thesis. On one view, natural selection is the author of adaptations in the sense that natural selection is the primary mechanism by which certain adaptations become more prominent in any population of organisms. On the other view, natural selection is the editor of adaptations, such adaptations are generated by other mechanisms, and natural selection is the mechanism by which certain variations become prominent in the sense that it preserves or rejects these adaptations as appropriate to the environment. Both characterisations rely upon the existence of a population of organisms, which is winnowed down by the demands of the environment and its limited resources. In this sense, natural selection is dependent on competition as a generative mechanism for adaptations. But is natural selection competitive? And if it is, then does symbiosis provide a non-competitive alternative? And if it is possible that natural selection could be characterised as non-competitive, then is an alternative needed?

I think it is uncontroversial to suggest that all evolving systems operate under constraints of one kind or another. This is the sense in which evolution by natural selection is marked by competition. We might say that in evolutionary theory, all that is

presupposed is that the organisms exists in an environment, and this environment is the constraints on the organism in question. A population of organisms that is unsuited to the environment will be culled, regardless of whether or not there are other organisms around that compete with them for resources. Of course, it may be the case that there are other organisms in this environment, some of which may be in a 'competitive' relationship for the same resources, but in terms of evolutionary theory, these can be thought of as part of the environment, or as constraints just like any other. Neo-Darwinism does not presuppose 'competition' between organisms in the sense of organisms battling it out between each other for resources, it only presupposes that there are limited resources, and organisms must deal with these constraints as best they can. And of course, these resources need not even be limited for them to act as constraints. If competition is simply a term that reflects the existence of constraints on evolving entities, then it is not wholly clear why this should be regarded as an inappropriate characterisation of evolution by natural selection.

If it were the case that symbiosis offered a distinct characterisation of evolution by natural selection, it might be an alternative of note. But it is not clear that it does this. As above, Margulis claims that symbiosis represents a challenge to neo-Darwinism in that neo-Darwinism, with its insistence on competition, tends to see cooperation as the exception, rather than the rule. She objects to the fact that competition is built into any models of evolution that use the population biology approach, which views all evolutionary changes as changes in gene frequency:

In these mathematic machinations of evolution, the number of individuals in a population or a species is taken as the basic measure. The usual interactions that are explored between individuals (or species) are competition (for resources space, etc.) and predation. A simple reversing of the signs of the interaction coefficient in the Lotka-Volterra model turns a "competition model" into one of "mutualism"¹⁴⁹

I take it that here the suggestion is that neo-Darwinism sees competition in everything, and its use of mathematical models which prioritise predation and competition tend to

¹⁴⁹ Margulis, Lynn "Symbiogenesis and Symbionticism" p. 6. Margulis refers to Boucher, D.H. *The Biology of Mutualism: Ecology and Evolution* (Oxford: Oxford University Press, 1985) in the remarks I cite here.

obscure any other characterisations of evolution. But how, then, can 'symbiotic' approaches which seek alternative characterisations of evolution (which might prioritise cooperation, for instance) use precisely the same mathematical models? An alternative approach to evolution which seeks to deny the importance of competitive natural selection must do more than describe the same basic mechanisms differently. It is not enough to turn competition 'upside down' and call it cooperation, if it is the case that the very same constraints on evolving systems are being described in this move. And Margulis' example of Lotka-Volterra models seems to confirm this. A reversal of the fundamental mechanisms of evolution must do more than force a change in terminology. But can symbiosis-based approaches do more than redescribe 'adaptations due to competition' as 'adaptations due to cooperation'?

What would be the ramifications of cooperation-based descriptions for evolutionary theory in the larger sense? If it could be shown that cooperation provided an explanation of the generation of adaptations above and beyond an explanation that relied upon competition, then this might be an important alternative. Let us take two explanations of adaptation and compare them. In one explanation, two organisms compete for the same resources, one has an advantage, natural selection selects for this advantage, the organism survives and the other does not (this example also might describe a population of organisms, some of which have the advantage, of course). In the other explanation, two organisms require the same limited resource, they cooperate in order to get it, and this 'symbiotic' cooperative relationship is selected for and persists. Now two things are clear about this comparative example: one, natural selection is serving exactly the same role; it preserves an adaptation in both cases. Two, what is at issue is not the mechanism of adaptation in terms of the characterisation of selection itself, but the mode by which these adaptations come to be generated. I hope it is clear that here cooperation versus competition has nothing whatever to do with natural selection as a mechanism for evolutionary change in the sense suggested by Margulis above. That is, it is hard to see what advantage the second explanation has over the first in terms of treating natural selection as a mechanism.

Similar to my own examples above, though still somewhat distinct, is the argument offered by George Kampis in his *Self-Modifying Systems in Biology and*

Cognitive Science.¹⁵⁰ Kampis criticises "dynamical" models (models which track changes in a system's state over time, where this system is deterministic and all its initial states are known) by examining the differences between neo-Darwinism and another "challenge" to neo-Darwinism which he labels "coevolution". As he describes it, neo-Darwinism assumes that the organism and the environment are sufficiently independent for the organism's evolution to be determined by "external" factors, i.e. the environment as a separate, external entity. In coevolution, the causes of evolution are more "internal", as coevolution claims that selection pressures come not from the external environment as such but from the selection forces acting within and between populations of organisms, in terms of relative "fitness".

[Coevolution] tells how the numerousness of populations and the evolutionary forces depend on the network of interactions in which the populations occur. Typical models deal with host-parasite, predator-prey, etc. interactions.¹⁵¹

Kampis goes on to show that these two approaches, in terms of the variables they intend to capture and track, are formally equivalent to one another. "From a formal perspective, we have the same structure with two, equivalent, interpretations."¹⁵² Thus, they are mathematically and structurally identical, and hence predictively and explanatorily identical. This result should make it more clear that 'challenges' to orthodox neo-Darwinism are not always quite what they seem; it often happens that the novel approach they seem to bring often disappears when they are revealed as 'reversals' or redescriptions of the terms of neo-Darwinism. For them to be a real challenge to neo-Darwinism, they must demonstrate more than this.

Notice also that for the symbiosis-based approach to natural selection, natural selection is sufficiently decoupled from the generation of variation so that it fits perfectly well with the neo-Darwinist, anti-teleological interpretation of evolution where natural selection works upon variation *after* such variation has arisen. The question of cooperation versus competition as a characterisation of natural selection

¹⁵⁰ Kampis, George. *Self-Modifying Systems in Biology and Cognitive Science*, p. 14

¹⁵¹ Kampis, p. 14

¹⁵² Kampis, p. 15

posed by symbiosis, does not seem to call the anti-teleological, anti-Lamarckist, neo-Darwinist interpretation into question in any fundamental way.

Our two comparative explanations do, however, show something else about the symbiosis-based approach to evolution. The difference in the approaches focuses the dispute more on the modes, or perhaps mechanisms of variation that symbiosis might be thought to characterise more thoroughly than neo-Darwinism. It is to the question of what symbiosis has to say about variation as the second component of evolution by natural selection that we now turn.

4.4.2 Variation: Evolutionary Novelty through symbiosis?

Let us examine again some of Lynn Margulis' views concerning the role of symbiotic systems in generating variation:

...according to present-day neo-Darwinian evolutionary theory, the only source of novelty is claimed to be by incorporation of random mutations, by recombination, gene duplication and other DNA arrangements. As is emphasised by those using the term "syntogenesis", symbiosis analysis contradicts these assertions by revealing "Lamarckist" cases of the inheritance of acquired genomes...The standard textbooks on evolution catechize all species and higher taxa (genera, families, phyla) as having evolved in the same way: by gradual accumulation of favourable mutations...*Yet not a single example of the origin of such lower taxa (species) exists in the literature.* ¹⁵³

Leaving aside whether or not the specific genetic mechanisms mentioned really are the only ones admissible in neo-Darwinism, let us divide the ideas suggested above into three separate issues. One, the notion that symbiosis provides a means of variation generation beyond mere "random mutation". Two, that neo-Darwinism insists upon 'gradualism' in evolution, and symbiosis provides a means of the generation of variation which is not 'gradual'. And third, that symbiosis is in some sense

¹⁵³ Margulis, Lynn. "Syntogenesis and Symbiogenesis", p. 11

"Lamarckist". This third question will be dealt with in section 4.4.3, concerning heredity.

Many of the issues concerning 'randomness' were examined in the last chapter, and it was noted there that it is difficult to precisely locate the 'element of chance' in evolutionary theory. With no clear means of delineating the precise way in which 'randomness' functions in a theory of evolution with a strong stochastic element, it is not easy to evaluate quite how symbiosis-based approaches are at odds with the idea of variation through random mutations, as neo-Darwinism seems to suggest superficially.

In section 3.2, in the discussion concerning random drift, it was noted that for 'randomness' to make any sense at all as an element in evolutionary theory, it must be random *with respect to something else*. That is, random with respect to some ostensible or observed order in the evolutionary system. And we also saw that neo-Darwinism, as anti-Lamarckist, claims that mutations or adaptations are 'random' with respect to adaptive advantage, that is, adaptations do not arise because they will be useful in future, they merely arise 'randomly' and are culled by the forces of selection.

We can reconstruct the symbiotic position on randomness in two different ways. One, it could be that symbiosis provides a means of generation of variation that does not proceed by the gradual accumulation of random mutations or gene recombination. Or, two, it may be that symbiosis denies that evolution is random in the sense that symbiosis is Lamarckist in process. If the former is the correct reconstruction, then symbiosis-based approaches must rather be characterised as 'anti-gradualist' rather than simply 'anti-random'. For what seems to be at issue is the way in which evolution occurs on a phylogenetic level. In the case of the symbiotic origin of eukaryotes, it is clear that for proponents of symbiosis, the way in which eukaryotes formed is, perhaps, 'saltationalist' rather than 'gradualist', since the symbiotic union of prokaryotes to form the eukaryote cell happened 'all at once', and there was no "missing link" in a gradual transformation through the accumulation of piecemeal adaptations between prokaryote and eukaryote.

But there is an important distinction to be made here, for it is not the case that neo-Darwinism depends solely upon random mutation as a characterisation of variation generation; all it requires is that variation be random with respect to advantage. And even a symbiotic cooperative innovation does not appear to entail that this innovation be directed, or non-random with respect to advantage. Margulis then perhaps means to

say that evolution happens more quickly if it is characterised by cooperative symbioses, rather than slow mutation. But neo-Darwinism, though it is gradualist, is not gradualist by depending solely on random mutations in the sense of slow changes, but rather through its insistence that variations are not directed by the environment

If symbiosis is 'anti-gradualist' then it is not obvious that it is a true challenge to neo-Darwinism.¹⁵⁴ For it should be clear that none of the three elements of neo-Darwinism (natural selection, variation, heredity) are 'time-indexed' in any way. Neo-Darwinism does not provide any account of the rate of evolution in itself. Of course, there has been an enormous amount of research on the rate of genetic change in populations, on the macro- and micro-level, with a view to understanding what the general rate of evolutionary change must be. This information would be immensely valuable in evaluating the time at which species diverged, for instance. But a generalised rate of evolution or even of mutation rate, has been difficult to find. For example, Maynard Smith reports some of Haldane's estimates in his *Theory of Evolution*. These estimates proceed by assigning a value defined as the "intensity of selection" which is a measure of how many organisms in a population die because they are less fit than others; this value then can be used to calculate the number of deaths due to poor fitness in terms of the number of generations that must pass before an unfit trait is supplanted entirely by the fitter trait.¹⁵⁵ But these studies simply reference the rate of evolutionary change under certain conditions, work only for a small number of fitness traits, and are, to some extent, unreliable. There is no suggestion that these seek to provide an account of any underlying rate of change over time. Symbiosis may, on this account, deny that evolution happens as slowly as neo-Darwinism claims, but it must be conceded that neo-Darwinism in itself *has no account of any privileged time scale for evolutionary change*.

So if symbiosis is a criticism of gradualism, or neo-Darwinism's dependence on random mutation as the only source for variation, or if it is an attempt to show that evolution happens more quickly than neo-Darwinism might have it, it is not clear that it could be classed as a challenge to neo-Darwinism of great importance. If it merely queries the time-scale of evolution, and criticises neo-Darwinism's dependence on

¹⁵⁴ Maynard Smith makes a similar point in "A Darwinian View of Symbiosis" in *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis* eds. Lynn Margulis and Rene Fester (Cambridge MA: MIT Press, 1991) p. 37-8

¹⁵⁵ Maynard Smith, John. *The Theory of Evolution* p. 47, pp. 282-5

'random' mutation simply as an exemplar of neo-Darwinism's inherent 'gradualism', then it must be said that neo-Darwinism as a research programme has little to say about the time-scale of evolution in this sense. If a symbiosis-based research programme's assumptions have only this to say, then it is perfectly compatible with neo-Darwinism. At best, it might be said to be a sub-research programme, one that may dispute some of the more metaphysical core assumptions of neo-Darwinism (gradualism being perhaps one of them) but agrees with all of the mechanisms which instantiate neo-Darwinism's conception of the way in which its three components work together.

Of course, if symbiosis queries neo-Darwinism's characterisation of variation as 'random' for other reasons than the ones outlined above, this may be a more serious challenge. We have seen that 'random' ought to be read as 'random with respect to adaptive advantage' as a core mechanism of neo-Darwinism. If symbiosis disputes this particular reading of random, then it contravenes a significant mechanism of neo-Darwinism, as well as its metaphysical counterpart: that is, it would violate the anti-Lamarckist stricture of random, rather than directed, variation, and violate the anti-teleological metaphysical assumption of neo-Darwinism by allowing variation to occur toward an adaptive goal. This would constitute symbiosis-based research programmes as a separate research programme ^{from} ~~than~~ that of neo-Darwinism.

To return to the quote by Margulis offered above, I want merely to make it clear that there is some difficulty with disputing neo-Darwinism as postulating evolution through the accumulation of random mutations. The difficulty is that this characterisation may mean that neo-Darwinism is gradualist, and symbiosis is then in a sense 'saltationalist', or it may mean that neo-Darwinism is anti-Lamarckist, and symbiosis is Lamarckist. Clearly these are different, and the latter is far more of a challenge than the former. The remarks by Margulis perhaps mean to say that symbiotic evolution is 'saltationalist' *because* it makes use of Lamarckist mechanisms such as the inheritance of acquired genomes. If this is correct, then symbiosis is surely a challenge to neo-Darwinism, but now the question must be: Are the mechanisms described by symbiosis truly Lamarckist, do they themselves postulate a different means of heredity that is outlawed by neo-Darwinism, and do they entail teleological evolution?

4.4.3 Heredity: Is heredity in symbiosis Lamarckist?

We must first look at Lamarckism before we deal with Lamarckist aspects of symbiosis. Lamarck and the idea of the inheritance of acquired characteristics has already been introduced earlier when neo-Darwinism was characterised as an essentially anti-Lamarckist theory. There are, however, some more remarks that might be made about what Lamarckism consists of. Jablonka and Lamb note in their treatment of the issue of Lamarck and neo-Lamarckists that there are many important distinctions to be made within Lamarckism, for Lamarckism is more than simply the "inheritance of acquired characteristics", and there is more to even this simple phrase than meets the eye.¹⁵⁶

Lamarck himself had many sophisticated ideas about evolution and the nature of life in general, not all of which particularly concern us here.¹⁵⁷ Most important, perhaps, are his "two laws". The first postulates that changes in organisms and their structures occur through "use and disuse", that is, a given organ will strengthen if used frequently, and will diminish in function if it is not used. The second law postulates that, in evolutionary terms, these changes through use and disuse are heritable, they will be passed on to the progeny. In themselves, these ideas were neither new nor radical; as we have seen, even Darwin was in agreement with this characterisation of evolution to some extent. The most significant part of Lamarck for the purposes of this thesis is the fact that the environment directly produced variations that were adaptive for the organism. That is, an organism was not only affected by its environment, but actively changed to suit its conditions. For instance, a predator that preyed on fast-running

¹⁵⁶ Jablonka and Lamb, *Epigenetic Inheritance and Evolution: The Lamarckian Dimension* (Oxford: Oxford University Press, 1995) pp. 3-20

¹⁵⁷ Amongst Lamarck's ideas: a peculiar vitalist materialism where there is no distinction in principle between the living and non-living, but only a change in the organisation of living matter by which it is capable of self-organisation and progressing complexity. Spontaneous generation was thus not only possible, but ubiquitous for Lamarck. Living matter exhibited a tendency toward a gradual increase in complexity by means of the action under natural laws of the "subtle fluids" that living matter is composed of. For Lamarck, there were no extinctions in nature, rather, simple forms were transformed into more complex forms, giving the interesting result that simple living forms were created more recently than complex ones (since the simpler forms had not yet had time to transform, and the complex forms must have been around longer in order to transform).

animals would exhibit changes in its morphology that actually allowed it to run faster, and these changes were induced by using their legs more often. Since Lamarck did not provide any particular theory of heredity, there was no particular restriction on the actual mechanisms by which the environment could produce these changes through use and disuse.

Such restrictions on mechanism were provided by Weismann and later by the Central Dogma of DNA, as we have seen. The impossibility of "inheritance of acquired characteristics" by means of the Weismann Barrier or through proteins reprogramming DNA itself entailed some change in whether or not a certain mechanism was considered to be acceptable by neo-Darwinism. The inclusion of prohibitions forced a tighter definition of what could be considered a Lamarckist mechanism. By this I mean that things that were previously thought to be Lamarckist could now be assimilated by neo-Darwinism. For instance, the Weismann Barrier postulated that changes in the soma cells could never affect changes in the germ cells. Any mechanism where the soma directly affected the germ was deemed Lamarckist and therefore unacceptable. When the workings of hereditary material became more clear, and the Central Dogma was established, the situation changed. In a sense, as the Central Dogma superseded the Weismann Barrier, mechanisms which violated the Weismann Barrier were now considered acceptable, just so long as they did not violate the strictures of the Central Dogma. Now it was the case that the environment could affect the organism, and thence its progeny, in a heritable way, but it could not directly affect the DNA of that organism. The phenotype was available to environmental influence, but the genotype was not. So we can say that inheritance of acquired characteristics was possible, but only if these mechanisms did not affect the DNA itself. Much is made of this point by Jablonka and Lamb, and proponents of "epigenetic inheritance".¹⁵⁸

I here distinguish between two kinds of things that are thought of as Lamarckist by neo-Darwinism. One is a mechanism that breaks the Weismann Barrier,

¹⁵⁸ In fact, they present my argument here from exactly the other way round. They suggest that the more sophisticated Lamarckist and neo-Lamarckist theories become, the more possible it is to be a neo-Darwinist and still allow Lamarckist inheritance to occur as a parallel mechanism. I, on the other hand, suggest that the more narrowly neo-Darwinism defines what constitutes a Lamarckist mechanism, the more it can *assimilate* mechanisms previously considered Lamarckist, and thus treat them as if they were totally compatible with neo-Darwinism. In this way, for instance, acquired symbiotic partners can be inherited, but this is not Lamarckist since it does not entail any reprogramming of the host's genotype.

the other is a mechanism which reverses the direction of information flow of the Central Dogma. If we consider that the Central Dogma has superseded the Weismann Barrier in terms of the growth of microbiology as a discipline, we would have to conclude that anything that violates the Weismann Barrier is acceptable, just so long as it does not claim that the DNA of an organism can be 'reprogrammed' by the organism itself in response to environmental pressure. In this way, the inheritance of acquired characters is acceptable, just so long as it does not entail reprogramming of DNA and/or directed evolution toward a goal. If we view these mechanisms in this way, it becomes clear that there is the possibility of distinguishing several types of 'Lamarckisms'. But this level of discussion, while showing the ways in which mechanisms determine what can be ruled in and ruled out of a theory, tends to conceal the possibility that the metaphysics behind a research programme can have unintended consequences in terms of the programme's direction.

Earlier in section 3.3, we considered the "unit of selection debate" and found that the interaction of the three components of neo-Darwinism, in themselves giving no indication of what kind of thing natural selection acts upon, left it open to debate whether natural selection selects the organism, the species, or the genotype, or even individual genes or parts of genes themselves. Yet in order for evolution to proceed, selection must act upon some thing, and although the nature of this thing that it selects is somewhat open to debate, it is surely the case that natural selection must pick out some entity as that which survives, and reproduces, and it is to this entity that labels such as "fitness" are to be attached.

Although it is undoubtedly the case that neo-Darwinism is to a great extent defined by its anti-Lamarckist stance in terms of its allowable mechanisms, it is also true that the way these mechanisms are characterised forces neo-Darwinism to make a distinction between organism and environment, just so that the organism is selected by the environment. As was made clear in the unit of selection discussion, the 'organism' need not be considered as a certain animal or plant's phenotype, we could just as easily make the same distinction on another level, so that, as Dawkins does, we might think of the gene being selected by its environment. But whatever the nature of this entity that is acted upon by natural selection, be it gene, or part of gene, or actual complete organism, this entity must be a stable concept for neo-Darwinism. To be anti-Lamarckist really means having a stable distinction between organism and

environment, so that the organism cannot affect its own environment in a teleological manner, but merely adapt to it. And the two anti-Lamarckist mechanisms of the Weismann Barrier and the Central Dogma, though they may differ in terms of what is ruled in and ruled out, are both effectively means of claiming that the environment affects the organism, and the two are separate entities.

But if it were the case that there was a class of living things whose functioning called this distinction into question, and in this way was Lamarckist in nature, then they would point toward the way in which symbiosis can be a real challenge to neo-Darwinism, not simply in terms of heredity, but in terms of the way all three components of neo-Darwinism function. And there is such a class of creature: the prokaryotes, or bacteria.

In the next chapter I will introduce a discussion of the nature and function of what I will argue are the most Lamarckist organisms around: bacteria. By seeing how they function, we will be able to see two important things: one, that prokaryotes or bacteria are essentially outside the scope of neo-Darwinism for several reasons. Two, that the way in which bacteria function is an excellent example of how symbiotic processes can be seen to problematise the notion of the individual. And this, I will conclude, is the most important way in which symbiosis can be said to challenge neo-Darwinism. I will argue that symbiosis, and bacteria as an example of such symbiotic functioning, is not simply Lamarckist, but actually dissolves the entire Darwinist/Lamarckist dichotomy.

Symbiosis, I will argue, problematises the individual on every important level; it problematises the in principle distinction between the organism and environment, between the germ and soma, between DNA and protein in terms of the Central Dogma of Biology. We have seen that the anti-Lamarckist constraints of neo-Darwinism depend upon in principle distinctions between entities on these levels. In order for adaptations due to the action of natural selection to be 'undirected', adaptations must be selected by the environment, there can be no sense in which the organism 'selects' its environment, and there must by this account be a distinction between organism and environment. In the Weismann Barrier, germ cells cannot be affected by the soma cells of the sexually reproducing organism. In the Central Dogma of Biology, information flows from DNA to RNA to protein, never the reverse; the physical structure of the cell can never reprogram its own genetic instructions. Symbiosis problematises these ; x

very distinctions, it thus is not only a challenge to neo-Darwinism at this level, the level of heredity, but even more significantly, it means that neo-Darwinism is a theory with a very narrow application to a small proportion of life on this planet. The following chapter will thus introduce some of the ways in which these distinctions are problematised with reference specifically to bacteria.

Chapter 5

Bacteria and their place in evolutionary theory

5.1 Introduction to Bacterial Evolution

Bacteria account for 97% of the biomass of life on earth. They are the oldest and, by some accounts, the most successful group of organisms in biological history. Lately it has been discovered that they can live almost anywhere: salt lakes, alkali lakes, thermal undersea vents, fumaroles, geysers, polar ice caps. Not only are bacteria ubiquitous in our own environment, but these organisms seem capable of colonising environments which are known to be too extreme for any other more complex organisms.¹⁵⁹

Most complex organisms are highly dependent on bacteria, and could be said to be in a symbiotic relationship with them. Plants use them to take up nutrients from the soil; insects use them to digest wood (in fact, the latest technology in cockroach and termite extermination uses antibiotics to kill the intestinal bacteria of these insects, thus starving the insects to death). Without our own bacterial microflora, we would not survive—we could not metabolise our food, or fight off infection. In a sense, the organisms which we call ourselves do not end with our own body cells, we must also include the multitude of bacterial 'helpers' without which we could not survive in order to describe the totality of us as 'organisms'. And as Serial Endosymbiosis Theory has shown, even our 'own' genetic complement owes some of its material to a bacterial lineage (as mitochondrial RNA), not even our human genotype is entirely free of bacterial ingredients.¹⁶⁰

¹⁵⁹ These organisms, called extremophiles for obvious reasons, are now steadily being cultured by microbiology for exploitation in both genetically modified foods and other industrial markets. Those organisms which have resistance to extreme cold, heat, acidity and the like are being plundered for genes which can be inserted into other organisms, as well as being used for toxic spill cleanup and related technologies.

¹⁶⁰ Mitochondria, the "powerhouses" in each of our cells which convert chemical nutrients into energy, are important in themselves in terms of the use of genetic "fingerprinting" to disclose human evolutionary history. Since mitochondria are only passed on hereditarily in gamete fusion from the mother's side only, their genetic complement has been used to determine a "Mitochondrial Eve", the earliest human with the mitochondrial genes that we all possess today, giving a useful evolutionary clock for human evolution. See Dawkins' *River out of Eden* (London: Weidenfield & Nicolson, 1995) for an interesting summary of this work.

Yet these organisms and their importance in evolution are often ignored by traditional neo-Darwinism for a variety of reasons. They could even be said to be a difficult, or anomalous case for neo-Darwinism, for reasons which will be argued in this chapter. This chapter will examine the ways in which bacteria are different to the kinds of organisms that neo-Darwinism is concerned with. On both a micro and macro level, bacteria behave in ways that are fundamentally different to the concepts embraced by neo-Darwinism. This chapter will also show why neo-Darwinist theoretical concepts do not apply to bacteria. It will be noted that neo-Darwinism's conceptual inapplicability with regard to bacteria will mean that neo-Darwinism is a limited theory covering relatively few types of organisms. The importance of bacteria in evolution means that a theory of evolution must use concepts that apply to both bacteria and more complex organisms if it is to be fully explanatory.

5.2 Structural differences between bacteria and other forms of life

First I will discuss the structure of bacteria and how they differ from other organisms. Living organisms are taxonomically divided into two groups: the prokaryotes and the eukaryotes. The word "prokaryote" means "before nuclei", indicating that bacteria evolved without nuclei, and the nucleus was a much later evolutionary innovation involving the incorporation of one bacterial lineage into another, according to SET.¹⁶¹ The various sorts of bacteria comprise the kingdom of prokaryotes (again accounting for 97% of organisms), while the eukaryotes include all other organisms. At present it is estimated that only 5% of extant prokaryotes have been cultured.¹⁶² For simplicity's sake I will use the more general term bacteria to designate the prokaryotes.

Bacteria are asexually reproducing; that is, they do not reproduce through meiotic gamete fusion, and thus do not have available to them the reshuffling of genetic material that occurs in meiosis as a source of variation. Bacteria divide in a process called binary fission where each daughter cell contains a copy of the replicated plasmid, or circular bacterial chromosome. Since the bacterium simply divides in two,

¹⁶¹ Margulis remarks that "prokaryote" means "before nuclei", but "eukaryote" means "good nuclei", perhaps an interesting indicator of neo-Darwinism's enthusiasm for the Weismann Barrier. Margulis, Lynn. *Symbiosis and Cell Evolution*

¹⁶² *Modern Bacterial Taxonomy* 2nd ed., Fergus Priest and Brian Austin (London: Chapman and Hall, 1993) p. 139

all daughter cells are clonal; that is, they have identical genetic material. Thus the process by which bacteria make more of themselves is not really what we'd like to call sex, as it does not necessarily cause any generation of variants, but merely the replication of the parent cell. The means by which bacteria generate variation is very different. Because bacteria are asexual, variation is not primarily generated through random meiotic crossover, the cause of variation usually studied by neo-Darwinism. On the one hand, because they are clonal, bacteria have little variation. On the other hand, bacterial genomes are remarkably plastic, since, as we shall see, they recombine their genetic material in unusual ways. Thus, bacteria are immensely variable, but again, this variation comes from avenues that are somewhat unfamiliar to neo-Darwinism.

On a structural level bacteria are principally different in that their genetic material is not contained in a nucleus, whereas eukaryotic organisms all have their chromosomal genes enclosed in a nucleus. In bacteria, this genetic material may take the form of a linear chromosome, or else it may be in the form of a circular chromosome called a plasmid which is self-transmissible. The lack of a nucleus is not merely a structurally distinctive characteristic, but in fact reflects a fundamental reproductive difference. As we saw in Part I, the Weismann Barrier, structurally enshrined in the nucleus of the cell, is a theoretical barrier to the inheritance of acquired characteristics and is thus a proscription against Lamarckism. The Weismann doctrine states that the germ (or sex cells) cannot be affected by changes in the somatic (or body cells) in an organism. The Weismann doctrine, made familiar earlier in chapter 4 as the 'nucleocentric' cell theory research programme, is based on the view that the nucleus is the sole container of hereditary material, and nothing else in the cytoplasm of the cell can affect this hereditary genetic material. It thus imposes constraints on the information flow in evolution. Since this hereditary material is separated off physically by the nucleus in eukaryotes, and bacteria do not have a nucleus, the Weismann Barrier does not apply to bacteria. The lack of a nucleus marks bacteria out as non-Darwinist in this sense. Because there is no nucleus to contain or protect the genetic material, bacteria can acquire genetic material in ways that eukaryotic organisms cannot.

The lack of a nucleus to bound genetic material allows bacteria to engage in complex gene transfer. Bacteria exchange DNA and RNA in many different ways, customarily divided into three categories: transformation, transduction and

conjugation. An example of the practical importance of bacterial gene transfer can be found in the phenomenon of multiply drug resistant bacteria. Bacteria can acquire immunity to antibiotics, and this is becoming a major challenge for clinical microbiology. The widespread use of common antibiotics has led to a world-wide rise in bacteria which are resistant to them. Drug resistance in bacteria is most often acquired through transduction and conjugation. This kind of acquisition offers several advantages: First, bacteria can acquire several separate and unrelated drug resistance factors. Second, this way bacteria have the ability to spread resistance horizontally. Resistance acquired in these ways is thus not restricted to vertical propagation in progeny. By gaining drug resistance in these ways, bacteria can acquire novel resistance genes from distant members of the microbial world.¹⁶³ It appears that the only way to fight the bacterial strategy is to frantically keep producing new antibiotics which the bacteria have not yet met. Vertical transmission of genetic material means that the material is passed on through a lineage of organism from parent to daughter cells, where one cell divides into two, and each have the same complement of genetic material as the parent cell. Bacteria do, of course, propagate themselves in this way for the most part. However, they can also transmit genetic material *horizontally*, which eukaryotes cannot do. The significance of this will be discussed in section 5.4.

The area of drug resistance is a startling case of how different bacteria really are from the types of evolving entities that are usually delineated in neo-Darwinism. Historically, the phenomenon of drug resistance was thought of as being similar to adaptational changes in more complex organisms. In the early days of microbiology, it was thought that bacteria gained resistance from antibiotics through accumulated random mutations. These mutations were thought to be chance events, which were selectively advantageous, and so were selected for and spread throughout the population. These random mutations were thought to be point mutations, where only one base in the DNA chain was altered. These point mutations were thought to chemically alter the bacterium's sensitivity to drugs, and were conserved.

Up until very recently, bacterial populations were still treated much as other ideal populations of higher animals: that is, when a given population is poorly adapted, most will die, and those few that are left will carry on reproducing to restore the

¹⁶³ *Microbiology* 4 ed. ed. by Bernard D. Davis, Renato Dulbecco, Herman N. Eisen, Harold S. Ginsberg. J.B. Lippincott Co. (Philadelphia:1990), 220-221

population to a stable relationship with its environment. Since most members of a bacterial population are clonal, they all have the same genome, and the only possible members to have any variation must therefore be mutants. These mutants, according to traditional neo-Darwinism, are the only ones able to provide new adaptations. For this reason the mechanism of mutational strategies is the focus of much research at present. It was traditionally believed that the only sources of mutation in a stable genome were either through cosmic rays or radiation, or through copying 'mistakes' in the process of either transcription, translation, or both. However, some research has indicated that such mistakes are part of a highly complex process of DNA repair mechanisms, and are not necessarily random, as previously believed. The issue of DNA repair mechanisms is highly complex, and will not be dealt with here. However, the larger issue of mutational strategies is at the centre of the debate surrounding the ways in which organisms can adapt to their environments. It is this issue that exemplifies neo-Darwinism's attempts to deal with anomalies at the level of mechanisms which violate its metaphysical assumptions.

5.3 Directed Mutation Hypothesis: Lamarckist Bacteria?

Directed mutation, an idea proposed by John Cairns in 1988,¹⁶⁴ claims that organisms (specifically in this case *E.coli* strain MCS2) under stress from an unfriendly environment might experiment with their own genomes to try to come up with an adaptive mutation. Cairns based his work on earlier *E.coli* experiments by Luria and Delbrück,¹⁶⁵ who attempted to investigate the difference between "drifters" and "selectionists" (described earlier in sections 2.3, 3.1.1, 3.2.2) in terms of bacterial mutation rates. They had concluded that most, if not all, bacterial mutation was random, or spontaneous in nature. Cairns, in contrast, proposed that the *E.coli* would only experiment with that portion of their genomes that might possibly be effective if mutated. This proposal was included to explain not only the apparent rapidity of the appearance of adaptive mutations, but also the apparent narrowness of the mutation: only those gene sequences that affected the nutritional capability of the bacteria

¹⁶⁴ Cairns, J., Overbaugh, J. & Miller, S. "The origin of mutants" *Nature* 335 (1988), 142-145

¹⁶⁵ Luria, S.E. and Delbrück, M. "Mutations of bacteria from virus sensitivity to virus resistance" *Genetics* 28 (1943), 491-511

appeared to have altered, and in many cases this was a matter of a one-base frameshift. This aspect of directed mutation was seen as Lamarckist, as it appeared to claim that the bacteria somehow sought out exactly what was needed, without having to try out other strategies first. In this sense, the flow of information is reversed, as the bacteria get information from the environment that allows them to effectively and quickly adapt to it.

Molecular biologists, faced with this apparent contradiction to neo-Darwinism, displayed their customary ingenuity in proposing ways in which such adaptational mutation might occur without threatening conventional dogma. An alternative strategy for bacterial populations under stress was for a subpopulation to start mutating vigorously at random in the hope that a lucky mutation would arise that would relieve the stress on the population as a whole. This approach, as can be seen, allows the flow of information to remain unidirectional and retains the random element necessary to neo-Darwinist natural selection. This explanation for the apparent directed mutation of bacteria was favoured by Barry G Hall.¹⁶⁶ Work has been done by Pat Foster and others to recapture the experimental results obtained by Cairns (these experimental results themselves are also disputed by Mittler and Lenski) under this less controversial theory.¹⁶⁷ It appears that during times of nutritional stress, mutation rates are indeed unexpectedly high, and in particular, one-base frameshifts (exactly what was occurring in Cairns' work).¹⁶⁸ It therefore appears that the phenomena discovered in *E. coli* do not rule out either hypothesis, and can in fact accommodate both of them.¹⁶⁹

¹⁶⁶ Hall, Barry G. "Adaptive Evolution That Requires Multiple Spontaneous Mutations. I. Mutations Involving an Insertion Sequence" *Genetics* 120 (1988), 887-897; Hall, Barry G. "Spontaneous Point Mutations That Occur More Often When Advantageous Than When Neutral" *Genetics* 126 (1990), 5-16; Hall, Barry G. "Adaptive evolution that required multiple spontaneous mutations: Mutations involving base substitutions" *Proc. Natl. Acad. Sci. USA* vol.88 (July 1991), 5882-5996.

¹⁶⁷ Foster, P.L. "Directed Mutation: Between Unicorns and Goats". *J. Bact.* 174 (1992), 1711-1716; Foster, Patricia L. and Cairns, John. "Mechanisms of Directed Mutation" *Genetics* 131 (1992), 783-789.

¹⁶⁸ Mittler, John E. and Lenski, Richard E. "New data on excisions of Mu from *E. coli* MCS2 cast doubt on directed mutation hypothesis" *Nature* 344 (1990), 173-175; Mittler, John E. and Lenski, Richard E. "Experimental evidence for an alternative to directed mutation in the *bgl* operon" *Nature* 356 (1992), 446-448; Lenski, Richard E. and Mittler, John E. "The Directed mutation controversy and neo-Darwinism" *Science* 259 (1993), 188-193.

¹⁶⁹ Bridges, Bryn A., 'Hypermuation Under Stress', *Nature* 387 (1997), 98-90.

Sarkar's analysis of the experimental work in directed mutation sees the historical root of the controversy in work done in the 1920's and 30's to try to settle the question of whether the evolution of bacteria was Lamarckist or Darwinist.¹⁷⁰ The types of statistical methods brought to bear on experiments to settle this question are the same used by Cairns and others to support their directed mutation hypothesis. Sarkar is pessimistic about their conclusion, as he identifies several methodological flaws in the types of statistical analyses used. The experimental methodologies used by Luria and Delbrück were designed to test between the extreme position that either all mutations were random, or else all were directed. Sarkar argues that because the current methodology is the same, and can only test this extreme position, he believes that this allowed Cairns to resurrect the weaker position that most mutations were random, but some were directed. However, it is not clear that Cairns' position is in fact a weak one; surely any position which claims that directed mutation can occur at all is bold enough. Sarkar appears to be more favourably disposed to an explanation similar to Barry Hall's and John Maynard Smith's hypothesis.

The recent work of John Maynard Smith and others into mutational strategies examines a slightly different aspect of mutational rates.¹⁷¹ Maynard Smith's work focuses on mutational strategies at a populational level. Whereas directed mutation and nutritional stress theories are mainly concerned with how a single bacterium responds to a stressful environment, Maynard Smith asks how a subpopulation of bacteria can reduce their individual fitness to allow the population as a whole to benefit.

Neo-Darwinism predicts that mutation rates have evolved to be as low as possible, limited only by the cost of error/mutation-avoidance mechanisms, because most newly arising mutations are either neutral or deleterious. But it has been found that up to one percent of natural bacterial isolates are "mutator" clones with high mutation rates. These mutator clones appear to have turned off their antimutation mechanisms, such that they can mutate very rapidly. While such rapid mutation is often deleterious for this small subpopulation, when a favourable adaptation does occur, it spreads throughout the rest of the population by "hitch-hiking"; that is, when a

¹⁷⁰ Sarkar, Sahotra. "On The Possibility of Directed Mutations in Bacteria: Statistical Analyses and Reductionist Strategies" *Philosophy of Science Association* 1990 Volume 1, pp. 111-124

¹⁷¹ Taddei, F., Radman, M., Maynard Smith, J., Toupance, B., Gouyon, P.H., Godelle, B. "Role of mutator alleles in adaptive evolution" *Nature* 387 (1997) pp. 700-704

mutator clone is associated with a favourable mutation, it increases in frequency. Once the adaptation is spread, the mutator genotype can then revert to its normal antimutator mechanisms.

This proposal thus identifies two "tracks" in evolution by which a population can adapt to an environment. One is the standard neo-Darwinism "slow track" approach, where favourable mutations appear in a non-mutator background, by chance, and spread through the population through simple selection. The "fast track" approach takes place through the use of mutator clones, which can facilitate adaptation occasionally through the process described above. Maynard Smith clearly thinks that this scenario, which is much more orthodox in terms of its commitment to the neo-Darwinist view of heredity and natural selection, is a more likely explanation for the kinds of results Cairns identifies.

Cairns' directed mutation hypothesis claims that there must be a means for the bacterial DNA to reprogram itself that runs counter to the Central Dogma of Biology, and thus is Lamarckist in character. Thus, Cairns theorises that a mechanism must exist for the transfer of information from the protein back to the genome of the cell. However, Cairns has not yet disclosed a mechanism by which transmission from protein to genome can occur. Sarkar concludes that until this is done, the statistical methodologies purporting to show the existence of directed mutation are useless. The debate about the existence of directed mutation exhibits the kind of neo-Lakatosian dynamics that I have described throughout this thesis to accommodate the anomaly that directed mutations represents, neo-Darwinism puts the burden of proof on the claimant: a mechanism must be supplied in order for directed mutation to be taken at all seriously. But what kind of mechanism would be acceptable seems to be a matter of metaphysical taste. Maynard Smith's favoured explanation does not admit the existence of any mechanism that could allow the proteins to reprogram the genes. Thus the directed mutation that Cairns and his colleagues describe is anomalous in the sense that its existence would require a major auxiliary hypothesis to be added to neo-Darwinism, and this auxiliary hypothesis would in fact be inconsistent with the hard core of neo-Darwinism. Supporters of the nutritional stress explanation, like Maynard Smith, are trying to protect this hard core. The assumption that such mechanisms could not exist is derived from the hard core of the neo-Darwinist research programme.

The debate about whether bacteria are Lamarckist can also occur at the level of a discussion of randomness with respect to adaptive advantage. But I will argue that at another level of analysis, the Darwinist/Lamarckist debate about bacteria has even stronger implications for neo-Darwinism as a research programme. For at the level of bacterial horizontal gene transfer as a mechanism for the generation of variation among bacteria, the issue can no longer be thought of as strictly Darwin versus Lamarck. In fact, this whole dichotomy is dissolved, and this has profound implications for neo-Darwinism as an explanatory theory.

5.4 Horizontal Gene Transfer

In the 1950's and 60's, it slowly became clear that the selective conservation of favourable random mutations was not the means by which bacteria generated drug resistance. Rather than accumulated random mutations, bacteria instead obtained and spread drug resistance through a variety of other hereditary and cellular mechanisms which can be grouped under the term "horizontal gene transfer". Horizontal transfer implies that one bacterium can insert genetic material into another, unrelated bacterium or bacteria, through the mechanisms of bacterial 'sex'.

Bacteria are quite distinct from other forms of life in their sexual behaviour (although bacteria are technically asexual), where 'sexual' merely describes the mechanisms by which genetic material is transferred. I will call these processes "bacterial sex" to denote them as reproduction conceived of as the generation of variants.¹⁷²

The mechanisms of bacterial sex have led some to propose that the whole bacterial community must be seen as consisting in a single, heterogeneous, multicellular "organism" in which genetic material is in continual flux, moving from one group of cells to another, and where a single pool of genetic information is

¹⁷² For bacteria in general, I would recommend the use of the term "propagation" over "reproduction". For reason that will become clear, bacteria are not in the business of faithful copying of internally cohesive genetic material; they are much more in the business of stealing genetic information from their environments, by any means available. The term reproduction is not really applicable to bacteria, in the sense that bacterial division is reproductive only in the replicative sense.

accessible to virtually every bacterial cell.¹⁷³ This proposal is echoed in Margulis and Sagan's remark that "Evolution is no linear family tree but change in the single, multidimensional being that has grown now to cover the entire surface of Earth".¹⁷⁴ This consequence of the importance of bacterial horizontal gene transfer leads to some interesting possibilities in the area of taxonomy, for Sorin Sonea and Margulis have also recommended that "If the standard definition of species, a group of organisms that interbreed only among themselves, is applied to bacteria, then all bacteria belong worldwide to a single species."¹⁷⁵

¹⁷³ Amabile-Cuevas, Carlos F. and Chicurel, Marina E. "Bacterial Plasmids and Gene Flux" *Cell* Vol. 70 (July 24 1992), 189-199; Sonea, S. "Bacterial Evolution without Speciation" in *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis* pp. 95-105

¹⁷⁴ Margulis, Lynn and Sagan, Dorion. *What is Life?* p. 73

¹⁷⁵ Ibid. The difficulty of arranging an honest taxonomy of viruses and bacteria throws up many methodological and philosophical problems. The relationship between viruses and bacteria is complex, and they are traditionally set apart from one another taxonomically, since it is recognised that viruses need hosts to replicate, while bacteria are capable of self-reproduction on their own. However, it could easily be maintained that viruses are more closely related to their bacterial host/symbionts than to each other. The two basic schools of thought about taxonomy, the phenetic approach and the phylogenetic approach, both have difficulty accounting for the bacterial/viral axis of evolutionary relationships. The pheneticists seek to group organisms through an ordering of their external phenotypic characteristics. But the phenetic approach has largely been abandoned in the case of bacteria, which simply do not display a wide enough range of different phenotypic traits needed for such a taxonomic approach. The phylogeneticists, on the other hand, are more concerned that taxonomy reflect actual evolutionary lineage and "relatedness" of organisms. But the phylogenetic approach relies on two distinct criteria to assess this relatedness, both of which are inapplicable to bacteria and viruses. Some phylogeneticists rely on what is known of as the Biological Species Concept (BSC), which states that "species are groups of interbreeding natural populations that are reproductively isolated from other such groups." [E. Mayr. "Species Concepts and Their Application", in *Philosophy of Biology*, ed. Michael Ruse. (New York: Macmillan 1989) p.138] Asexually reproducing organisms like bacteria, along with their viral counterparts, cannot be said to be reproductively isolated in any real sense, since they swap genetic information so readily. The only way they *are* reproductively isolated is that they do not need other bacteria to mate with to reproduce, they simply divide. According to the BSC, then, *all* bacteria would be members of the same species. The second phylogenetic taxonomic criterion is monophyly, which is insisted upon in the cladist approach. The cladist approach claims that since taxonomy should accurately reflect evolutionary lineage, a species should be a lineage that shares descent from one common set of ancestors. High rates of genetic interchange among bacteria mean that this "unique common ancestor" might be very hard to determine. Insistence on monophyly would lead to the bizarre result that a species of bacteria, composed of a single bacterium and all its descendants, might last only for hours or minutes, and each petri dish in all the

So, for bacteria, horizontal gene transfer is not only available, but perhaps even ubiquitous. The mechanisms by which this type of gene transfer can occur each have different, but nevertheless considerable, consequences for neo-Darwinism as a research programme. We will now discuss the three mechanisms of transformation, transduction, and conjugation in turn.

5.4.1 Transformation

The first category of bacterial sex is called transformation. Transformation describes the uptake of genetic material in the external medium by a bacterium. This process seems to be fairly random, and any portion of the available genetic material, whether it is in fragmented form or as a plasmid, may be taken up and incorporated into the cell. This type of genetic exchange is perhaps not anomalous with regard to neo-Darwinism because of its random nature. The Darwinist story of evolution insists upon the random generation of variants that are selectively culled by the environment. At least in transformation, the uptake of extraneous genetic material is uncorrelated with adaptive benefit. It is therefore possible to regard transformation in two different ways. If we focus on the fact that this process seems to be random with regard to benefit—that is, that bacteria take up any extant genetic material that happens to be around—it can be argued that this process is perfectly compatible with neo-Darwinism in the sense that it does not entail that the bacteria are here evolving with any adaptive benefit in mind.

However, the fact that bacteria are here taking up genetic material from their immediate environment means that it could be seen as more Lamarckist in character, since the environment is directly affecting the genetic material of the organism in question. Transformation allows alteration of the bacterial genome through direct contact with extraneous environmental genetic material. This is ^akind of utilisation of the environment that is not usually thought to be present in the more complex

laboratories in the world would each contain separate monophyletic bacterial species. Bacterial taxonomy is today in a state of flux, under contention from not only systematists, but microbiologists, virologists, and pathologists. The discovery of "archaeobacteria", an ancient lineage of bacteria which have genes in common with both prokaryotes and eukaryotes, has caused further consternation about the traditional taxonomic distinction between prokaryotes and eukaryotes. How this matter will eventually be resolved should be of much interest, as it may have ramifications for neo-Darwinism itself as a theoretical framework. See for instance Dupré, Shostak and Hull (works cited in bibliography) for more on the issue of taxonomy.

organisms that neo-Darwinism describes. In transformation, bacteria are able to take up already existing genetic components from their environment wholesale. The neo-Darwinist constraint on evolution by the piecemeal accumulation of random variations is not present.

Even if this process is random with respect to adaptive benefit, it is a type of horizontal heredity that neo-Darwinism does not have much to say about. Given that there is no 'Weismann Barrier' in the form of the nucleus to break through in the case of bacteria, we might again conclude that since bacteria cannot violate a non-existent prohibition of neo-Darwinism they are perfectly compatible with neo-Darwinism. But the fact of horizontal gene transfer direct from environment to organism might make a clean distinction between 'organism' and 'environment' problematic, even if the organism is treated only as its genomic complement. The mechanisms of the Weismann Barrier and the Central Dogma both codify the direction of information flow; they both serve to schematise a distinction between the organism and the environment. This distinction is put at risk by bacterial horizontal gene transfer, so although bacteria may not violate any of the explicit mechanisms of neo-Darwinism, they may affect the metaphysical assumptions of the neo-Darwinist research programme.

Thus, bacterial transformation may problematise a distinction between organism and environment. If this is the case, then it is no longer a question of whether bacterial evolution is Lamarckist because it is in some sense anti-neo-Darwinist. If the mechanisms of bacterial propagation and variation are not specifically outlawed by neo-Darwinism, it may be that bacteria are simply outside the scope of neo-Darwinism. If this is the case, then the neo-Darwinist research programme needs only add an auxiliary hypothesis to accommodate them. But this auxiliary hypothesis would have to have the effect of allowing an organism/environment distinction to be blurred, in order to accommodate the fact that bacterial transformation means that the external environmental genetic material and the internal bacterial genome are capable of being united into a functional entity which is neither organism nor environment, but an uneasy fusion of the two. This type of auxiliary hypothesis would in turn problematise neo-Darwinism's metaphysical strictures against Lamarckism itself, or at the very least it might make the metaphysics of neo-Darwinism unstable.

If the organism/environment distinction is affected by transformation, then it is even more affected by transduction. In transduction, we see an even further confusion

of the supposedly stable entities of evolutionary theory, this time because of the possibility of symbiotic relationships which are more intimate than the types of relationships that were discussed in chapter 4.

5.4.2 Transduction

In chapter 4 it was noted that if symbiosis means nothing more than a recommendation of cooperation over competition, or a dismissal of the role of random mutations that is really a dismissal of the supposed 'gradualism' of neo-Darwinism, then it is not likely to be taken seriously as a real challenge to neo-Darwinism. Furthermore, if symbiosis is taken as mere 'mutualism' or a consideration of cooperation between members of the same species as "kin selection", then it has little to offer as a research programme other than a slight change in perspective. But if it were the case that symbiosis offered not only a reappraisal, but a disruption of the fundamental entities that form the basis of evolutionary explanation, then it would be a real challenge indeed. I will now argue that it can do this, specifically when we consider the symbioses that bacterial transduction entails.

The second category of bacterial sex is transduction. Transduction is the uptake of genetic material through viral vectors, and it seems to be the most common means of bacterial genetic exchange and recombination. When exposed to ultraviolet radiation, otherwise healthy bacteria may explode, releasing many tiny virus-like entities called prophages, which can spread genes to other bacteria.¹⁷⁶ Viruses which 'infect' bacteria donate genetic information to a prokaryotic cell, and this need not always be fatal. Bacteria are in a highly symbiotic relationship with viruses in the sense that the viruses are often the means by which bacteria obtain variation in their genetic material, and viruses are integral to bacterial 'sex'. Viruses can take genetic material from one host and transfer it to another, completely different host. Thus the process of transduction is able to move any sort of gene from one bacterial host to another.¹⁷⁷

¹⁷⁶ Margulis and Sagan, *What is life?*, p. 74. Margulis hypothesises that this type of transduction may have been more prevalent on the early UV bombarded earth, before the atmosphere was in place to protect against UV rays.

¹⁷⁷ Jacob, François and Wollman, Elie L. "Viruses and Genes" (*Scientific American*, June 1961) in *The Living Cell: Readings from Scientific American* (W H. Freeman and Co. San Francisco 1961) p. 23

This type of genetic exchange is an excellent example of the importance of symbiosis in evolution. Though the virus needs the machinery of the bacteria to reproduce itself, the virus is not necessarily in a simple parasitic relationship with the bacteria, although the bacteria are infected by the virus. The virus, through infecting the bacteria, is using the bacteria as a factory to replicate its genetic material. Yet the virus can also often confer beneficial genetic material on the bacteria. Viral genetic material can become active and cause the bacteria to make replicas of it and explode, releasing the copied virus, or alternatively it can behave as an inert part of the bacterial chromosome. When it becomes inert and integrated into the bacterial chromosome, it can confer upon its bacterial host a resistance to other viruses. Thus the bacteria can obtain immunity from viruses as a result of viral infection.

To recall some of the discussion in the previous chapter about symbiosis and the difficulty in treating this concept as merely an index of the relative 'altruism' involved in association between organisms, we can note that the nature of the symbiotic relationship in the bacteria/virus transduction situation is not obviously a strictly parasitic one. Neither is it one of simple altruism, nor one where each party gains equal benefit. The obvious question in such close symbiotic relationships is how to distinguish parasitic from altruistic symbiotic relationships. Any attempt to delineate strict definitions of the character of relationships in this domain will call into question the status of the 'organism' in such contexts. Since the genetic material is transferred between bacteria and viruses in this relationship, and this genetic material can play quite different roles in each, it is not quite clear whose genetic material it is, or even who gets greater benefit. If, as is often recommended, we define the organism in terms of its unique genetic identity, or genomic components, it is difficult to isolate the organism in such closely symbiotic relationships. Furthermore, it is clear that definitions like "parasitic" or "altruistic" have no place in these symbiotic relationships. Since the genetic exchange cannot be easily said to benefit one organism over another, it may be that these types of strategies are in the interest of a higher-level organisational plane, and indeed, may problematise the very idea of 'being in the interest of'.

Quite what the environment consists of in this type of relationship is similarly not immediately clear. Certainly it is different from the neo-Darwinist view of the organism/environment distinction. In neo-Darwinism, evolution is conceived of in

terms of the environment acting to select organisms, the organisms are relatively stable and the environment is the parameters or variables. In ecology, the environment is seen as the stable element, and the organisms that make it up are the unstable, relatively fast-moving parameter variables. In a closely symbiotic relationship, each organism *is* the other's environment. The easy separation between them that evolutionary theory calls for thus breaks down.

Again, transduction could be treated as compatible with neo-Darwinism, since it is not obviously Lamarckist in the sense of violating acceptable mechanisms in neo-Darwinism. But it is equally clear that neo-Darwinism does not really fully embrace any process through which the organism/environment distinction breaks down, or any of its functional analogues (i.e. a genotype/phenotype distinction). Furthermore, in this case, not only is the distinction between organism and environment blurred (as in the case of transformation) but the entities that natural selection is supposed to act upon are also made more complex by the addition of a symbiotic partner or host, whose own environmental parameters might be different from those of the symbiotic partner. The fact that the genome of each symbiotic partner is integral to the function of the other in terms of survival and reproduction makes it clear that the 'individual organism' is hard to individuate, and certainly this entity is far from stable in a bacterial/viral reproductive symbiosis. It might be thought that the symbiotic relationship between virus and bacteria could be simply explained away by neo-Darwinism by treating the symbiotic complex itself as a kind of individual which is available to selection as a whole. But since the bacteria can gain immunity from viral infections sometimes, and at other times these infections can be fatal, there is clearly no higher level stability available for this move to be made to accommodate symbiosis in this way. Additionally, horizontal gene transfer between viruses and bacteria entails mutual reprogramming of the genome in symbiotic viral/bacterial relationships, which also prevents this symbiosis from becoming stable enough to be treated as a kind of higher-level 'organism' in its own right.

Transformation and transduction both complicate things for neo-Darwinism, by calling into question the distinction between organism and environment, and by yielding an unstable symbiotic entity which is required by neo-Darwinism to be stable. Conjugation, the third mechanism of bacterial sex, has been immensely important in

evolutionary history, and yet its very existence is especially problematic for neo-Darwinism.

5.4.3 Conjugation

The third category of bacterial sex is conjugation. Conjugation is the process by which bacteria exchange genetic material through direct cell-to-cell contact. A small ring of DNA called the conjugation plasmid in the donor cell forms a sex pilus (a long tubular structure) that connects the recipient cell and the donor cell, and the genetic material is transferred by use of the pilus. The action of cell-to-cell contact activates replication of the DNA in the conjugation plasmid, and this DNA, once 'injected' into the recipient cell, replicates within it and then goes on to conjugate with other recipients.

This genetic material for the sex pilus is, importantly, self-transmissible. That is, the genetic material encodes the information for the construction of its own pilus to be used for its dissemination in other bacteria. Though the pilus plasmid is self-transmissible, it cannot necessarily replicate in every bacterial host. Some pilus plasmids are more promiscuous than others, however. In fact, the more promiscuous plasmids can engage not only other bacteria, but even more distantly related eukaryotes in conjugation. It has been conjectured that conjugation with its concomitant gene transfer may have occurred between species of different kingdoms. It has been argued that this process has been immensely important in the evolutionary history of life on this planet, not just for bacteria themselves, but between all types of life: bacteria, plants, and fungi.¹⁷⁸ This interkingdom reproductive relationship is definitely outlawed by neo-Darwinism, where the constraints on the vectors of genetic information are very controlled indeed. Conjugation is very worthy of interest, since it means that just about any organism can receive genetic components from any other. Not only this, but it seems to be a case of heredity that is quite unconnected with any known form of replication mechanism.

¹⁷⁸ Amábile-Cuevas, Carlos F. and Chicurel, Marina E. "Bacterial Plasmids and Gene Flux" *Cell* Vol. 70 (July 24 1992), 189-199; Dahlberg, C., Bergstrom, M., Andreasen M., Christensen B.B., Molin S., Hermansson, M. "Interspecies bacterial conjugation by plasmids from marine environments visualized by gfp expression" *Molecular Biology and Evolution* vol. 15 no. 4 (1998), 385-390

We have seen that the nucleus, and the doctrine of Weismann, requires that no extracellular genetic material can penetrate the nuclear barrier and reprogram the genome of the eukaryotic organism. The environment, then, can never affect the actual genes of the organism, but can only select the somatic components of the organism. But in conjugation the external environment is directly affecting the genome of another organism, and worse, conjugation is able to penetrate the nucleus of eukaryotes and insert itself into the genome, thus even violating the Weismann Barrier.

Because conjugation is somewhat like viral transduction, although not requiring a viral agent, the concept of the organism is further complicated by conjugation plasmids. Conjugation plasmids are self-replicating, but unlike viruses, they are not inert when not in contact with a bacterial host. Above it was noted that the symbiotic relationship between viruses and bacteria in transformation and transduction called the concepts of the organism as well as the concept of the environment into question. The case of conjugation similarly disturbs a definition of an organism, even if the organism is treated as its unique genotype alone. The plasmid is certainly a part of the bacterial genome in a way that viral DNA is not, but clearly the plasmid has its own agenda, which has little to do with the bacterium as an organism. The plasmid factor is simultaneously an internal part of the bacterial genome, and an external component that functions as an infectious agent. Neo-Darwinism has little to say about this type of heredity.

Conjugation can also be used in obtaining drug resistance, and this can happen even when living and dead cells are mixed together. It appears that even dead cells are capable of conjugation. I think it is safe to say that genetic exchange between living and dead organisms is somewhat outside the scope of neo-Darwinism. Jack Heineman puts the importance of conjugation in very clear terms:

Plasmids reproduce by horizontal transfer to organism of at least three different biological kingdoms--a microbiological 'bestiality' of sorts. The apparent promiscuity of plasmids violates teleological preconceptions about their function. In assuming that plasmids encoded sexual attributes of prokaryotes, the unexpressed expectation was that the potential for genes to transfer among bacteria, and from bacteria to eukaryotes, would be limited in the same way that recombination is

between multicellular creatures of different species. When genes were seen to exchange between prokaryotes of different genera, 'bacterial sex' was viewed as either altruistic (donation of beneficial genes, such as antibiotic or phage resistance, to potential competitors) or as understandable as an example of selfish plasmid replication. [...] The barriers to plasmid transmission have been routinely overestimated."¹⁷⁹

5.5 Conclusion

We can now see exactly how these three types of bacterial sex affect neo-Darwinism. In each case, it becomes difficult to pick out a stable entity that is an 'organism'. Worse, we cannot even pick out a unique genotype that might be a unit of selection, as Dawkins' genic selectionism recommends. As we saw earlier in the cases of transduction and conjugation, the genetic material in the form of the phage or plasmid is functioning in a very *external* manner. Though it is endogenous to the bacterium at certain stages, it is not really a permanent part of the genome, and thus is not in this sense a part of the organism. As an external element, it is not available as a target of natural selection in the same way a genotype or phenotype might be. And symbiotic relationships between bacteria and viruses, which occur at the level of the genome, similarly make it difficult to delineate a stable genome.

To conclude, we may recall the effects of these horizontal gene transfer events might have on neo-Darwinism as a theory. Because the Weismann Barrier does not hold for bacteria, since they do not have nuclei, we cannot say that bacteria are Lamarckist, since they do not violate this type of anti-Lamarckist stricture. But certainly they are not particularly Darwinist either, since what they do problematises some of the basic metaphysical assumptions of neo-Darwinism. One may conclude that they are outside the scope of neo-Darwinism. But if this is true, certain conclusions are unavoidable. If bacteria are outside the scope of neo-Darwinism, and bacteria constitute 97% of life on Earth, then neo-Darwinism is therefore a theory that has very limited scope, and describes only the evolution of a tiny proportion of organisms.

¹⁷⁹ Heineman, Jack A. "Looking sideways at the evolution of replicons" in *Horizontal Gene Transfer* eds. Michael Syvanen and Clarence I. Kado (London: Chapman and Hall, 1998) p. 14, 18

X But, if bacteria are *not* outside the scope of neo-Darwinism, and may be accommodated by it by the addition of certain auxiliary hypotheses which would explain them away, then the effects of these additional auxiliary hypotheses on the neo-Darwinism research programme must be examined. These auxiliary hypotheses would have to have the effect of allowing an organism/environment distinction to be blurred, since the fact of horizontal gene transfer makes the delineation of stable evolutionary entities problematic. If the stability of these entities is allowed to be called into question, the neo-Darwinist research programme might be rendered entirely unrecognisable as neo-Darwinism.

Chapter 6

Conclusion: Lessons for the Philosophy of Biology and Evolutionary Theory

6.1 Summary of the Results

We can now review the major points that have been raised by the inquiry of this thesis. First, let us review the results of part I, chapters 2 and 3, the analysis of Darwinism and the move to neo-Darwinism, using the methodology outlined in chapter 1. It was noted there that Darwinism itself was initially consistent with many metaphysical views concerning the nature of the living, some of which were teleological and finalist. These were eventually pushed to the side by the *mechanisms* neo-Darwinism increasingly began to depend upon, and these mechanisms ruled out any teleological or vitalist interpretations by prohibiting Lamarckist heredity. Thus, it was affirmed that natural selection was not a force that moved evolution toward any final goal, and it was not a creative force, or at least, it was only creative insofar as it preserved adaptations that were *already* created, by whatever means. In chapter 3 it was shown that this definition was all that neo-Darwinism had to say about what natural selection is: that is, it was defined by what it was not, in the sense that the ways the three elements worked in relation to each other (natural selection culling unfit variations after these variations were present) determined how natural selection acted. Natural selection could not be defined as a principle, or a law or a force in itself, this decision could only be made by reference to the interdefinition of natural selection with variation and selection.

Similarly, variation was initially able to fit within various metaphysical views of life; it could be seen as either the mere 'raw material' for natural selection to act upon, and variation or change toward an environment. Again, the neo-Darwinist prohibition of Lamarckist modes of evolution meant that the organisms could not invent variations that were better suited to their environment, there was no change in organisms through use and disuse. The anti-Lamarckist relationship between the organism and the environment took shape in the form the mechanism which postulated that the organism only passively responded to the environment, and did not react positively in any way.

way. This meant that variations had to be formed in a random, or chance way; variation had to be random with respect to adaptive advantage. The use of statistical methods to describe the frequency of variations in a population lent further credence to the view that evolution was in some sense a random process, or at least one with an inbuilt chance element. But this led to the drifter/selectionist argument during the formation of neo-Darwinism: was variation random, but natural selection non-random? Was natural selection itself a random process in some way? And could a random process really explain the complexity of life? This argument was considered in chapter 3, and there it was concluded that randomness was only defined as random with respect to adaptive advantage, whilst the precise location, function and importance of randomness was never fully agreed upon. Variation was generated in the organism through some kind of random process, since this variation could only be undirected. The environment through the action of natural selection directed the further progress of these undirected or chance changes.

In the case of heredity too, it was initially possible for heredity itself to actively work toward an environmental goal, in Lamarck, this was essential, through the action of use and disuse, and the inheritance of acquired characteristics. By these means, the changes that the environment required could be passed on to offspring in their totality, and evolution could, in theory, work much more quickly. If organisms could use changes inherited by their parents through the inheritance of acquired characteristics, then evolution could work in quick jumps, not through slow changes in each generation of organisms. However, these possible mechanisms of heredity were ruled out by the neo-Darwinist synthesis, when the particulate notion of heredity and the Weismann Barrier were adopted. This served to curtail the flow of information from organism to environment in such a way that reflected what has already been said about variation and natural selection. The Central Dogma of Biology, that information flowed from DNA to RNA to protein, but never from protein back to DNA, strengthened this one-way flow of information at the molecular level. The organism could not take up adaptive information from its environment and use it to change its own genetic code. In chapter 3, it was noted that information, a concept often depended upon for these kinds of interpretations of heredity, was by no means easy to define in itself. Information was necessary in the definition of heredity as a mechanism that copied and transmitted variations in an organism from parent to offspring, but it

was never fully defined, all that was settled was that information flowed directly from organism to environment, and only indirectly from environment to organism. The organism was passively selected by the environment, but it could not gain adaptations directly from it. Slow, gradual evolution through random changes acted upon by natural selection was the resultant interpretation settled upon through the changes to heredity.

Part II of this thesis attempted to address the symbiosis challenge to neo-Darwinism in the context of the characterisation of neo-Darwinism offered in part I. In order to do this, we teased apart some of the many claims of proponents of symbiosis in their criticism of neo-Darwinism. Symbiosis, because it takes cooperation as a prominent evolutionary process, criticises neo-Darwinism for its insistence on competition as a characterisation of natural selection. It was concluded that natural selection does not presuppose competition, as the symbiotic criticism claims, but it was also noted that cooperation between organisms that are of different, unrelated species is not addressed very effectively by neo-Darwinism. So although neo-Darwinism's construal of natural selection does not entail that natural selection works solely through competition, neo-Darwinism fails to come to terms with symbiosis as cooperative. But this, I concluded, did not mean that symbiosis offered a fundamental challenge to neo-Darwinism, since I argued that a cooperative and a competitive description of evolution would not be sufficiently distinct from one another. Each would offer an equivalent explanation of evolution, and for this reason this particular criticism of neo-Darwinism does not succeed as a new conception of evolution that neo-Darwinism could not accept. All that would be needed is for "organism" to be replaced with "cooperative symbiotic entity", both of these would be available to the action of natural selection as adaptations in the neo-Darwinist sense.

The symbiotic position, that symbiosis provided a source of evolutionary innovation above and beyond that accepted by neo-Darwinism, can also be dealt with in the same way: for neo-Darwinism does not have any strictures on where variation can come from other than the anti-Lamarckist constraint that these variations cannot come directly through the environment or through the inheritance of acquired characteristics. Symbiosis as the cooperative relationship between two related or unrelated organisms does not appear to violate neo-Darwinism on this level, at least. But if we say of a symbiotic entity that one organism is the other's environment, and vice versa, there

may be something in this. But as before, this symbiotic entity is itself available to natural selection as a unit of evolution, then the switch between the two terms of organism and environment might not make much difference. And if symbiosis claims that this source of evolutionary innovation consists of more than mere random mutation, then even this is not enough to challenge neo-Darwinism. Neo-Darwinism does not depend on random mutation, but it does depend upon randomness with respect to adaptive advantage. So neo-Darwinism can accommodate symbiosis as a source of innovation or variation, all it needs to do is replace "mutation" with "symbiotic innovation". This symbiosis criticism of neo-Darwinism, if it is no more than a claim about the speed of evolution, is not a challenge to neo-Darwinism, for neo-Darwinism itself does not claim anything about the speed of evolution on any time scale.

But if this claim about symbiosis as providing a source of evolutionary innovation actually means that symbiosis is more than random, but in fact is directed, or Lamarckist, then this would violate neo-Darwinism's fundamental metaphysical assumptions. Do symbiotic innovations involve Lamarckist heredity? They may, if it is the case that in any symbiotic complex one organism is the other one's environment, and if this means *more* than the postulation of an entity on a higher level of organisation. That is, if one is the other's environment, then this union might be treated as a kind of 'superorganism' which is composed of more than one part. But this relationship might rather blur the distinction between organism and environment in such a way that the neo-Darwinist anti-Lamarckist metaphysics becomes unstable. In order for neo-Darwinism to even *be* anti-Lamarckist and anti-teleological, then some separation between organism and environment must be in place, since this is the basis of its metaphysical commitments. In a sense, this is neo-Darwinism's account of *individuation*, and this, if threatened, would present a fundamental challenge to neo-Darwinism.

Chapter 5 showed that there are a large number of organisms that do this, and these organisms, bacteria, are not only good examples of symbiosis, but furthermore, the biological processes they exhibit seem to threaten neo-Darwinism on a fundamental level. Horizontal gene transfer in particular does this. There are two possible outcomes from this: ^{First,} we might conclude that neo-Darwinism is certainly useful for describing organisms which do not engage in horizontal gene transfer, for instance, complex

organisms like eukaryotes (although there is some evidence at present that horizontal gene transfer can occur even in eukaryotes). This would mean that neo-Darwinism, far from being a theory which explains evolution on any level, would instead be a limited and narrow theory which described only a small percentage of organisms. Second, perhaps it is the case that neo-Darwinism can accommodate these processes which seem to challenge it, by changing some of its commitments to deal with them. If this is the case, then what sorts of changes would be necessary? And what would these changes mean for evolutionary theory in terms of explanation? We may now address both of these possible conclusions.

6.2 The Limitations of Neo-Darwinism

The modern evolutionary paradigm of neo-Darwinism is increasingly relied upon in popular and technical literature alike to cast light on issues in disciplines as wide and varied as consciousness, sociology, history, psychology and many others. This in itself is nothing new,² contemporary readers of Darwin (as well as Darwin himself) used the power of the theory of evolution by natural selection to explain issues outside of the realm of the strictly biological. The popularisation of Darwin and neo-Darwinism has contributed to the extension of neo-Darwinist explanation to many wide and varied fields. Given this, this possibility that neo-Darwinism may be incomplete or of limited scope becomes more significant.

Of course, few people claim that neo-Darwinism is *really* complete; it is clear that neo-Darwinism is a changing theory, and probably not the final word on evolution. And as this thesis has showed, it is still the case that neo-Darwinism can admit of multiple interpretations, and such debate is not only inescapable, but healthy. And it is equally clear that just about every scientific theory has its theoretical shortcomings. This is not thought to be a problem by either science or philosophy. When a theory is incomplete, it does not need to be jettisoned, but only needs to be adjusted so that it may become more complete.

So perhaps it is not a question of neo-Darwinism being incomplete, and by this token potentially completable, but rather that neo-Darwinism is simply limited. If neo-Darwinism simply described the evolution of eukaryotes, then perhaps another theory is needed to describe what neo-Darwinism cannot: the prokaryotes. Maybe an

additional theoretical apparatus could complement neo-Darwinism in this way. But one must also ask whether the addition of this extra theoretical apparatus would change the fundamental metaphysical core of neo-Darwinism. If the addition of extra mechanisms affects the metaphysics of the theory, the theory itself might be completely transformed.

At this stage it would be worth addressing the field of biology which is most concerned with bacteria and see what types of theoretical contributions it might bring to such an additional theory. Microbiology, pathology, and virology are perhaps the main research areas which deal with the processes that bacteria exhibit, and we might ask what interest it takes in neo-Darwinism as a background assumption in biology. Furthermore, we might ask whether the field of microbiology shows any areas in which the themes of this thesis might become profitable.

It has already been noted that the asexual nature of bacteria does cause some problems for taxonomy, if taxonomy intends to categorise organisms through their inability to mate with other organisms. Nonetheless, it is worth recognising that bacteria are not generally thought to be inimical to taxonomy by microbiology or neo-Darwinism; it is simply recognised that they must be treated as a special case. The technology of microbiology today has made available many complete genomic maps of bacteria, and this information has been used to approach a taxonomy of bacteria and of viruses that is thought to accurately express evolutionary relatedness between organisms, in much the same way that "DNA fingerprinting" is used to establish relatedness among more complex organisms such as animals and humans. Furthermore, the technology of "gene-splicing" has become very prominent in microbiology, leading to the many industrial technologies such as oil-eating microbes, and also to the development of GM foods. It seems that microbiology does have a firm grasp on technology, and perhaps it is possible to state that microbiology's 'theories' are not those of neo-Darwinism, but more along the lines of those of engineering or any other applied science. Perhaps microbiology does not ask the question "how do we explain the evolution of these organisms?" except for the purpose of gaining information about how the evolution of bacteria might make available new technologies. If this is the case, perhaps microbiology no longer needs a neo-Darwinist explanation of evolution.

However, it is worth bearing in mind at least a few of the criticisms of these kinds of technologies. For instance, one of the major criticisms of GM food

technologies, apart from those criticisms which question whether eating GM foods might be actually harmful to humans, is the possibility that such 'unnatural' genes (which are often of bacterial origin), if inserted into plants, may spread of their own accord to other types of organisms, thus affecting the entire ecology of areas in which GM foods are grown. This is a question that cannot be answered by technology alone, nor can it be answered by neo-Darwinism alone, for reasons which I hope this thesis has made clear. For neo-Darwinism is not even in a position to admit that evolution can occur through such a horizontal, Lamarckist mechanism, much less can it assess the frequency of this mechanism on an evolutionary scale.

How can such questions be framed so that the risks of GM technologies can be assessed? At least, there must be more interest in finding out exactly how prominent horizontal gene transfer is in evolution as a whole, and this is obviously being closely examined at the moment. Moreover, this examination of the role of horizontal gene transfer must be looked at as an evolutionary strategy as well, and this means that it must be viewed as more than simply an 'adaptive mechanism' for bacteria or viruses. As this thesis has shown, the phenomenon of horizontal gene transfer involves organisms of different species, and it is not helpful to treat these organisms as merely 'hosts' or 'parasites'. Nor is it helpful to treat any relationships which involve symbiotic horizontal gene transfer as 'mutualist' partners, or as a 'cooperative whole', for this simply reverses the terms by which the explanation would function. As this thesis has argued, explaining an evolutionary strategy that involves symbiosis must do more than explain this as a host-parasite interaction, for it is clear that in many cases the relationship is not simply one-sided, and the 'host' often cannot survive without its 'parasite'. But it is also unhelpful to view these symbiotic relationships as 'cooperatives' unless one is able to explain how this 'cooperation' addresses the various strategies of its participants, for it is equally clear that these strategies may be directed toward different goals for each participant. If 'cooperation' rather than 'competition' is selected for, then it must be shown how and why this occurs, and neo-Darwinism seems quite unable to explain this.

Microbiology and virology are also concerned to understand the nature of pathology, that is to understand how bacteria and viruses work so as to lessen their impact in terms of disease. This too, is an area which has made great technological leaps, and again, it has been able to gain access not only to genome maps of bacteria

and viruses, but also to uncover information which gives insight into how viruses and bacteria interact between the bacterial cell wall and viral protein coats. The problem of drug-resistant bacteria shows the importance of having an understanding of horizontal gene transfer very clearly. Since bacteria can gain and transfer immunity to antibiotics with ease, then it is clear that simply attacking bacteria with multiple antibiotics will only exacerbate the virulence of these bacteria. Placing bacteria in unfriendly environments only encourages them to gain resistance by any means possible, the more antibiotics, the more multiply-drug-resistant bacteria.

So, if we cannot eliminate dangerous bacteria and viruses, perhaps we can disarm them instead. To do this would also entail more interest in the types of strategies viruses and bacteria enlist to deal with their environments and propagate themselves. And again, it is not advantageous to treat either bacteria or viruses as hosts and parasites, nor as cooperative partners which use the genetic information of the other to procreate. Instead, these symbiotic relationships work in a different manner than other symbioses between different organisms which cooperate, not least because of the fact that genes can be passed from one to the other in a fashion which seems quite external to either organism. Conjugation in particular seems an adaptive strategy which belongs to neither the donor or the recipient, and conjugation plasmids seem in a sense to have their own agenda. Treating bacteria as either selfish, as neo-Darwinism appears to, or cooperative, as the symbiotic approach seems to, would not capture this.

So we can see that the topics this thesis has addressed do have some importance in the field of microbiology, even if it is the case that microbiology does not have much interest in the metaphysics and mechanisms identified in this thesis. Neo-Darwinism may be simply a limited theory that explains only eukaryotic organisms. If this is the case, then perhaps a complementary theory is needed to address the prokaryotes and viruses. But this complementary theory must not share any of the pitfalls of neo-Darwinism if it is to be profitable. It must somehow have means of dealing with entities of evolution in a way that does not simply reestablish the limitations of neo-Darwinism. Nor can it be based on any alternative symbiosis-based research programme if this alternative programme simply identifies the same entities and mechanisms as neo-Darwinism under a different name. This thesis has shown that neo-Darwinism is essentially an anti-Lamarckist theory, and by this metaphysical

constraint it establishes mechanisms which serve to delineate the types of entities it uses for the purposes of explanation. It identifies organisms, living in environments, and these organisms have adaptive strategies, or fitnesses which are selected for by the environment. As an anti-Lamarckist move, it claims that the organism can never actively evolve toward an environmental goal. It also picks out entities like genes, which determine the phenotype. Anti-Lamarckism here is expressed in the claim that this phenotype can never reprogram the genotype. The organism/environment, genotype/phenotype distinction both expresses and requires the anti-Lamarckist constitution of neo-Darwinism as a theory. These distinctions also single out the operant entities in evolution for neo-Darwinism. We have seen that these distinctions are problematised by bacterial evolution and symbiosis. To be a general theory, and not just a limited one, neo-Darwinism must become more cognisant of such mechanisms of heredity, which it has heretofore viewed as Lamarckist. Thus, perhaps what is needed is a view of evolution which transcends the dichotomy between Lamarckism and Darwinism, and such a theory might make of neo-Darwinism a general theory that explains the evolution of all living things. But, since neo-Darwinism is defined by its anti-Lamarckist mechanism and metaphysics, transcending the Lamarckist/Darwinist dichotomy might well annihilate neo-Darwinism from the inside.

6.3 Transcending the Darwinism/Lamarckism dichotomy

It was argued in this thesis that part of the reason Lamarckist modes of heredity and evolution were ruled out by neo-Darwinism is because such mechanisms seemed to allow the possibility that organisms could actively evolve toward their environment in an intentional or teleological fashion. But why should this have been of such concern to neo-Darwinism? To begin with, it is perhaps because Darwin's theory was intended as a naturalistic theory of evolution that did not appeal to a Creator, or a preestablished plan of nature. Even this did not prevent many German biologists (and some English biologists) from interpreting natural selection as a kind of perfecting principle. This understanding of natural selection increasingly intersected with the belief in a 'living force' recommended by vitalism. And those concerned to establish a mechanistic view of evolution felt that this was incompatible with Darwinism. This interpretation claimed Darwinism as a theory which simply described the laws of life,

and such laws were analogous to Newton's laws. No vital force was necessary on this view.

But it is surely possible to have a vital force that does not operate as any kind of perfecting principle, and indeed it is possible to treat natural selection as a force which is not goal-directed, although it may still be described as if it were. Jacques Monod's "teleonomy"¹⁸⁰ is an attempt to show the latter. One could perhaps describe organisms as if they acted toward a goal, but this is just a manner of speaking; of course, natural selection is not really a teleological process. Perhaps neo-Darwinism can produce another such adjustment in the face of the issues raised in this thesis.

Perhaps neo-Darwinism can simply accept more of the types of mechanisms that it previously outlawed. For instance, it might retain the Central Dogma, and simply allow any mechanism that does not specifically violate the Central Dogma itself. Thus, 'Lamarckist' mechanisms would be allowed, but as they came to be assimilated, their Lamarckist 'sting' would be removed. Perhaps these mechanisms might even be given greater prominence, and perhaps even the role of natural selection could be downplayed. This then might make neo-Darwinism a more comprehensive theory. In this situation, we might say that neo-Darwinism could keep its metaphysics intact, by retaining the Central Dogma, but simply add a few extra mechanisms.

But, as I hope this thesis has shown, the kind of mechanisms that are admitted into a theory do have an effect on its metaphysical component. The inclusion of these extra mechanisms that were previously Lamarckist would entail some significant changes to neo-Darwinism. For if these mechanisms placed in question the definition of adaptations as random with respect to advantage, even if they did not specifically violate the Central Dogma, then neo-Darwinism would lose much of its metaphysical character. If neo-Darwinism were to allow horizontal gene transfer, and bacterial horizontal gene transfer is in fact much more 'directed' than 'random', then this change would have to be reflected in the metaphysical core of neo-Darwinism. What would a neo-Darwinism that allowed directed evolution look like? It might be unrecognisable.

Perhaps these mechanisms could be assimilated if one were to simply downgrade the role of natural selection. There might be less of a problem with 'Lamarckist' modes of heredity if it turned out that natural selection played a very

¹⁸⁰ Monod, Jacques. *Chance and Necessity: An Essay on the Natural Philosophy of Modern Biology* trans. by Austryn Wainhouse (Collins Fontana Books, 1974), chap. 2

small role in evolution, for then it would be possible to ascribe evolutionary change to the ways in which variation is created and managed. But what would neo-Darwinism be without natural selection? Downplaying the role of natural selection would leave the core of neo-Darwinism empty, for natural selection and variation need one another for evolution through the differential survival of variants to occur. And we have seen that it is difficult for neo-Darwinism to even distinguish between explanations that rely on natural selection and those that rely on the action of random variation. Giving up one of them might mean having to give up the other.

So, if it is not possible to assimilate these bacterial mechanisms and still retain the metaphysical core of neo-Darwinism, then maybe the metaphysics must be adjusted before these mechanisms can fully be integrated into a new theory. Neo-Darwinism is negatively defined with respect to Lamarckism, so anything that is not Lamarckist is thus acceptable to neo-Darwinism. Neo-Darwinism is so constrained by its anti-Lamarckist sentiments that it may be necessary to reevaluate the modes of evolution which are thought to be entailed by Lamarckist commitments. This thesis has shown that certain hereditary mechanisms that are present in bacteria do not fit into either of the categories that neo-Darwinism is so dependent upon for its very identity. They are neither Darwinist, nor are they Lamarckist. They do not so much violate Darwinism as fall outside it.

The fact that bacteria seem to fall outside, or even transcend, this dichotomy between Darwinism and Lamarckism might be of some interest in devising a change in the metaphysics of evolutionary theory. Bacteria might even be an exemplar of evolution at large, it may be possible that their evolutionary processes also apply to other organisms, and can be used to explain evolution more comprehensively. As Dawkins' position of genic selectionism shows, it is possible to have an evolutionary theory which is not committed to organisms, although this position is not without its limitations. Even though genic selectionism tries to replace the organism with the gene, it still retains the same distinction between a unit of evolution and a separate selecting environment. Genic selection treats genes as the units of evolution, but it still treats them as 'selfish' entities which obey the same laws of neo-Darwinist theory that organisms do. I do not propose a bacterial model of evolution which takes bacteria to be the units of evolution, for this would simply reestablish the same terms as neo-Darwinism. What would be more useful is to treat the processes and strategies of

bacterial gene flow themselves as paradigmatic mechanisms. The fluid and dynamic character of horizontal, as opposed to merely vertical, evolution could then be used to shed light upon other evolutionary processes.

Bacterial evolution makes use of symbiosis, but these symbiotic relationships are temporary and fleeting. Gene trading is rife among many kinds of bacteria, yet not all types. Why do some bacteria engage in temporary symbioses with viruses, and others conjugate? Why indeed do conjugation plasmids exist, and why do they propagate themselves in such a manner? Bacteria and viruses, as well as conjugation plasmids do seem to need each other for the generation of variation and for propagation. But what else is created by these relationships? There is more to such a relationship than a simple host-parasite relationship, and more than a cooperative whole. What kind of superorganism is created by such relationships, and what characteristics does it have?

Bacteria, as organisms that do engage in symbiotic relationships, exist as populations, not individuals. They form supercolonies which can behave just as a multicellular organism might. But even these relationships are temporary. We might ask how and why these relationships come into being and what characteristics they have. This might give insight into many of the processes of evolution that neo-Darwinism addresses today. For instance, treating organisms as members of a social group or population is more useful than looking at them as members of a species. Looking at evolution from the bacterial point of view might make available many different and new perspectives on life. Rather than looking at organisms as passively responding to their environments, perhaps a bacterial perspective would allow descriptions which transcend the organism/environment distinction. After all, *we are* the environment for many of these organisms. And our symbiotic relationship with other kinds of organisms raises the possibility that it is not our own organism that is of interest, but the nature of the symbiotic relations themselves.

But if neo-Darwinism must come to terms with the importance of these symbiotic relations themselves, and these symbiotic relations must be accommodated by the addition of certain auxiliary hypotheses which would explain them, then the effects of this on the neo-Darwinism research programme will be profound. To fully engage with complex symbiotic relationships and horizontal heredity, neo-Darwinism might have to allow the organism/environment distinction to be blurred, since the fact

of horizontal gene transfer makes the delineation of stable evolutionary entities problematic. If the stability of these entities is allowed to be called into question, the neo-Darwinist research programme might be changed beyond recognition.

Glossary *

Adaptedness The suitability of a structure or an organism for its environment or lifestyle, as a result of past selection.

Allele: Any of the alternative variants of a gene.

Binary Fission: in bacteria, the chief mode of division, in which a cell divides into two equal daughter cells, each containing a copy of the **plasmid**.

Chloroplasts: Organelles found in plant eukaryotes which convert light into energy through the process of photosynthesis. They are thought to have once been free-living prokaryotes, which are now in a permanent symbiotic relationship to other organelles in eukaryotes. See also **mitochondria**, **Serial Endosymbiosis Theory**

Clone: *adj.* Clonal; a group of genetically identical individuals or cells derived from a single cell by repeated asexual divisions.

Conjugation: transfer of genetic material between bacteria through a **pilus**

Eukaryote: Organisms with cells possessing a membrane-bounded nucleus which separates its genetic material from the rest of the cell. Eukaryotic cells also possess an extensive network of protein filaments which comprise its internal structure, as well as many membrane-bounded organelles in which its cellular functions are sequestered.

Genome: the genetic complement of a living organism or a single cell.

Genotype: the genetic constitution of an organism, which acting together with environmental factors determines a **phenotype**.

Germ cell: a reproductive cell; gamete; also **Germ Plasm:** a term coined by A. Weismann, to denote the idea of a protoplasm that is transmitted unchanged from generation to generation in the germ cells, as opposed to the inheritance of acquired characteristics.

Gradualism: A theory that evolution progressed by the gradual modification of populations, and not by the sudden origin of new types. It is contrasted with **saltationalism**

Lamarckism: the theory of evolution chiefly formulated by Jean-Baptiste Lamarck which embodied the principle, now taken as incorrect by Neo-Darwinism, that characteristics acquired by an organism during its lifetime can be inherited

Mitochondria: Small organelles found in animal eukaryotes, they are responsible for converting sugar into energy. They are thought to have once been free-living prokaryotes, which are now in a permanent symbiotic relationship to other organelles in eukaryotes. See also **chloroplasts**, **Serial Endosymbiosis Theory**

Monophyletic: also **Monophly** deriving from a common ancestor

Natural Selection: the process by which evolutionary change is chiefly driven, according to Darwin's theory of evolution. Environmental factors will lead to the preferential survival and reproduction of those members of the population genetically best fitted to deal with them. Continued selection will therefore lead to certain genes becoming more common, and over very long periods of time, will give rise to the differences between organisms.

Neo-Darwinism: the modern version of the Darwinist theory of evolution by **natural selection**, incorporating the principles of genetics and still placing emphasis on natural selection as the driving force of evolution

Phage: (also **prophage**) Bacterial DNA integrated into and replicating with the bacterial chromosome

Phenotype: the visible or otherwise measurable physical and biochemical characteristics of an organism, as result of the interaction of genotype and environment; also, a group of individuals exhibiting the same phenotypic characters

Pilus: a tubular structure that brings bacterial cells into contact during **conjugation**

Plasmid: genetic material in the form of a circular ring found inside certain bacteria. It is self-transmissible

Pleiotropy: ¹ Pleiotropy is a term that describes a situation in which one gene can have many different phenotypic effects, some of which are advantageous and some of which may be disadvantageous. Because of this, it is harder for selection to weed out disadvantageous traits, as such traits have "hitchhiked" onto advantageous traits that selection would presumably preserve. Pleiotropy has therefore been mooted as an alternative, opposing force to that of selection.

Prokaryote: Bacteria; unicellular organisms lacking a membrane-bounded nucleus to separate their genetic material, also lacking mitochondria, chloroplasts and other membrane-bounded organelles. Their genetic material is in the form of a circular molecule, or **plasmid**.

Saltationalism: Change owing to the sudden origin of a new type, that is, the production of a new kind of individual who gives rise to a new type of organism.

Serial Endosymbiosis Theory (SET): the idea, now generally accepted, that mitochondria and other chloroplasts, and possibly some other organelles of eukaryotic cells originated as symbiotic prokaryotic organisms

Somatic cell: body cell as opposed to cells of the germ line

Transcription: The process by which DNA is copied and an RNA template is made during cell division

Transduction: the transfer of genes from one bacteria to another by means of carriage in a virus

Transformation: the genetic modification of a bacterium by DNA which is external to the cell in the environment and is taken up by the cell and incorporated into the bacterium's own DNA

Translation: The process by which the RNA template is used to construct a protein chain.

Virus: an intracellular obligate parasite, consisting of a core of either DNA or RNA, surrounded by a protein coat. Viruses are unable to multiply or express its genes outside a host cell as they require host cell enzymes to aid DNA replication

Weismann Barrier: a theoretical construct relating to the continuity of the germ plasm and the non-transmissibility of acquired characteristics. It assumes that germ cells can affect somatic cells, but not the reverse. Its physical manifestation is the nuclear membrane

* Definitions taken from *Henderson's Dictionary of Biological Terms*, 10th ed. and 11 ed., ed. Eleanor Lawrence, (Longman Group, 1989) also from Mayr, *One Long Argument*, and some are my own.

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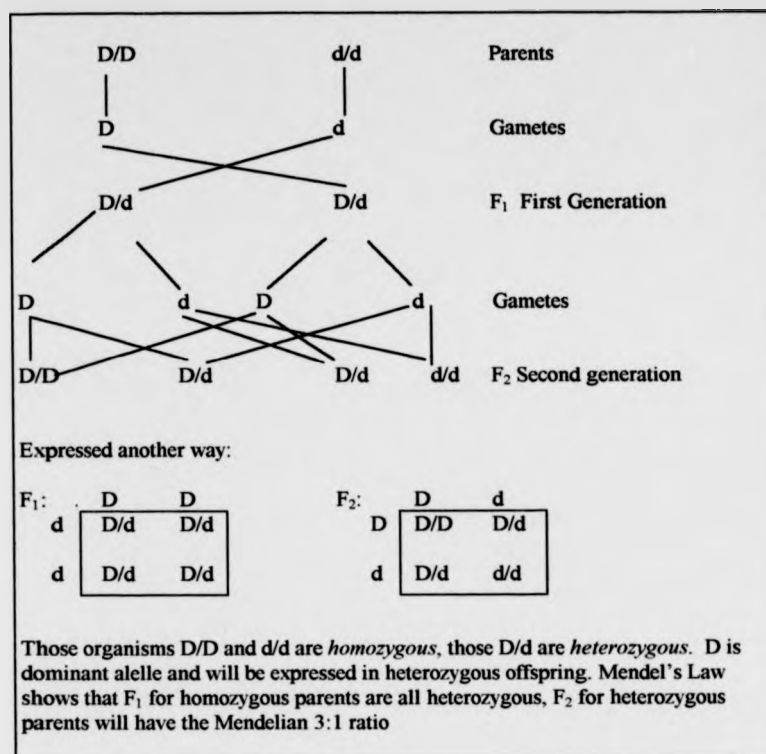
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Appendix 1

Mendel's Theory of Factors studies the genotype of sexually reproducing organisms in terms of their alleles, or traits. In meiotic sexual reproduction, each parent contributes to the offspring by donating one factor or allele to the gamete. These gametes fuse in the zygote, and they are expressed in the mature organism according to the relative dominance of the factor.

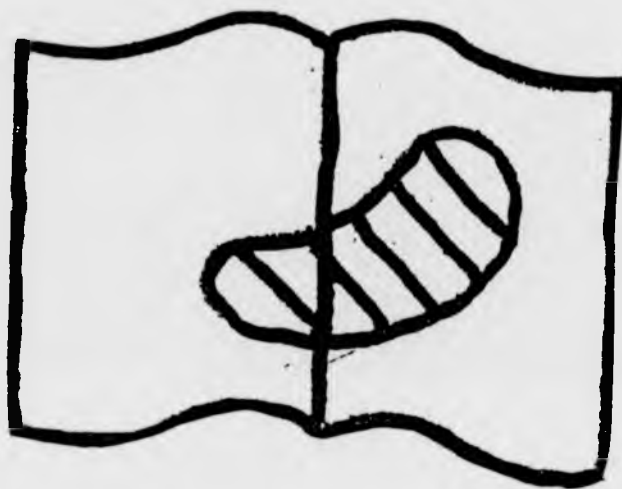


Appendix 2: Transcription and Translation

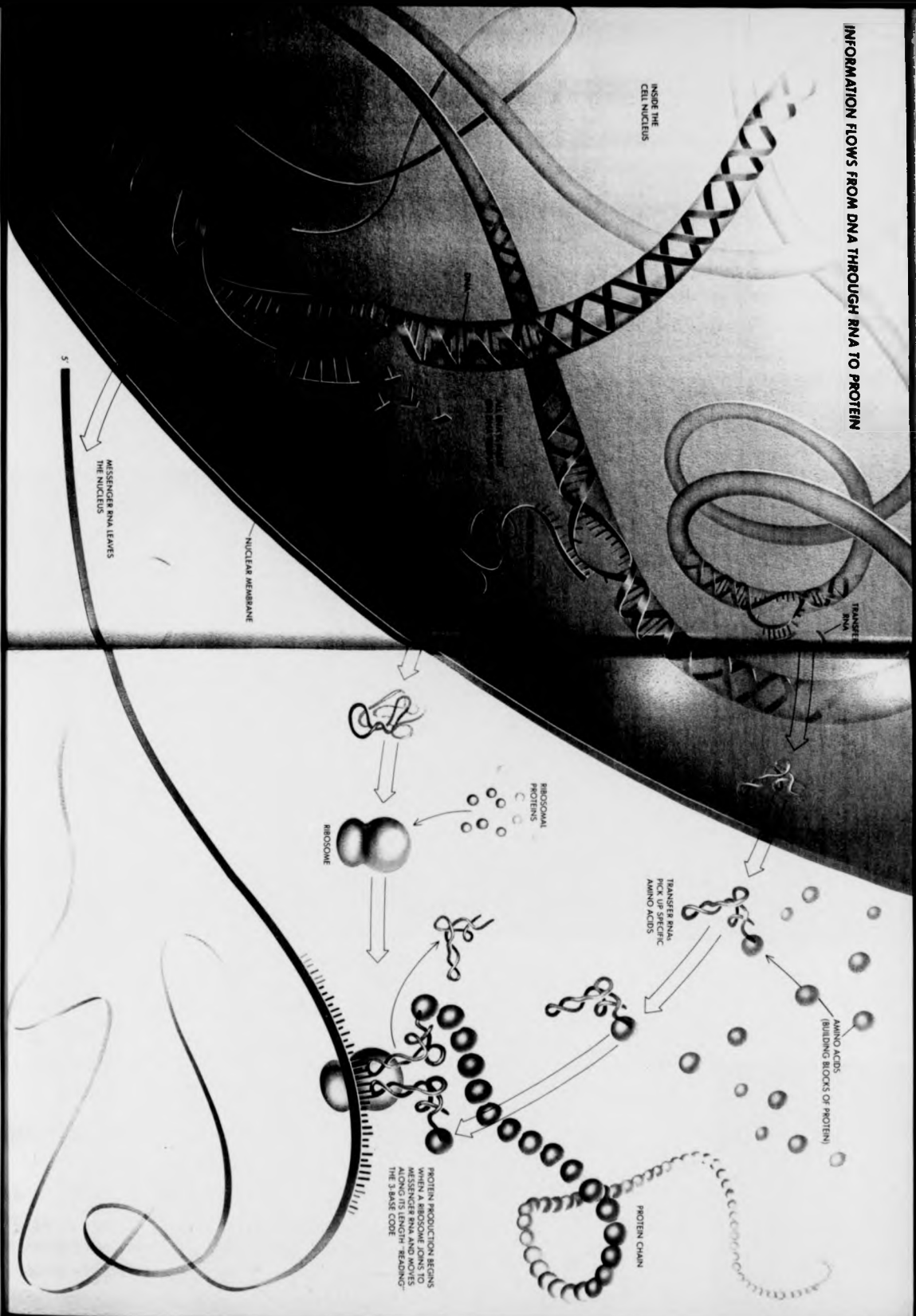
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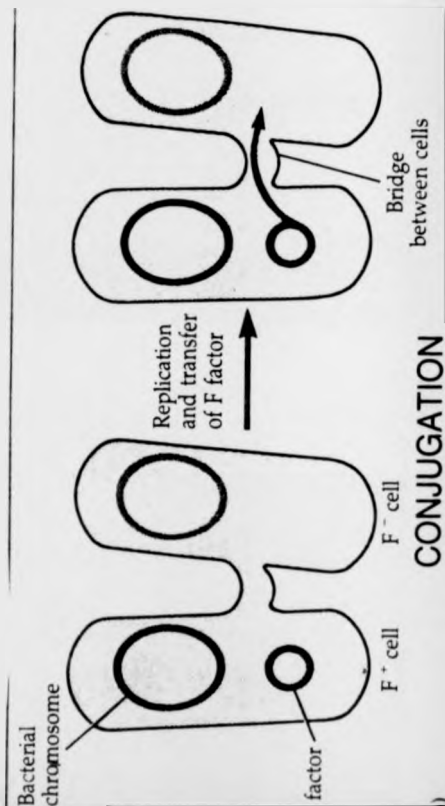
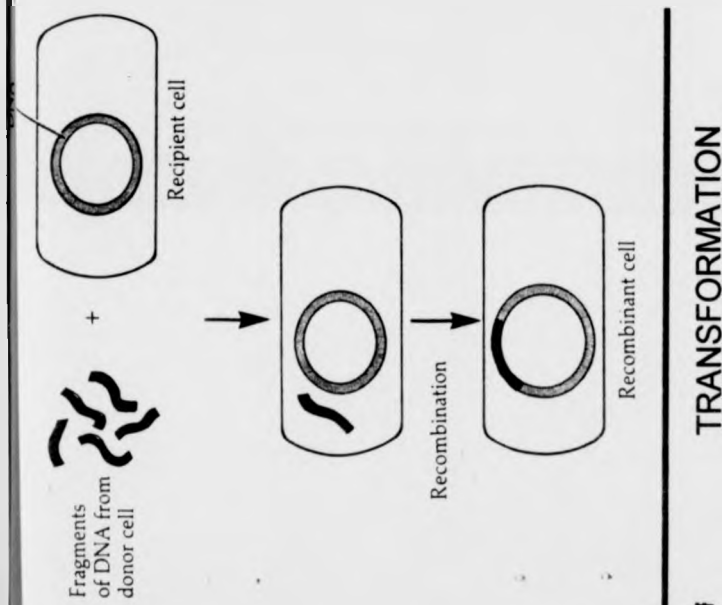
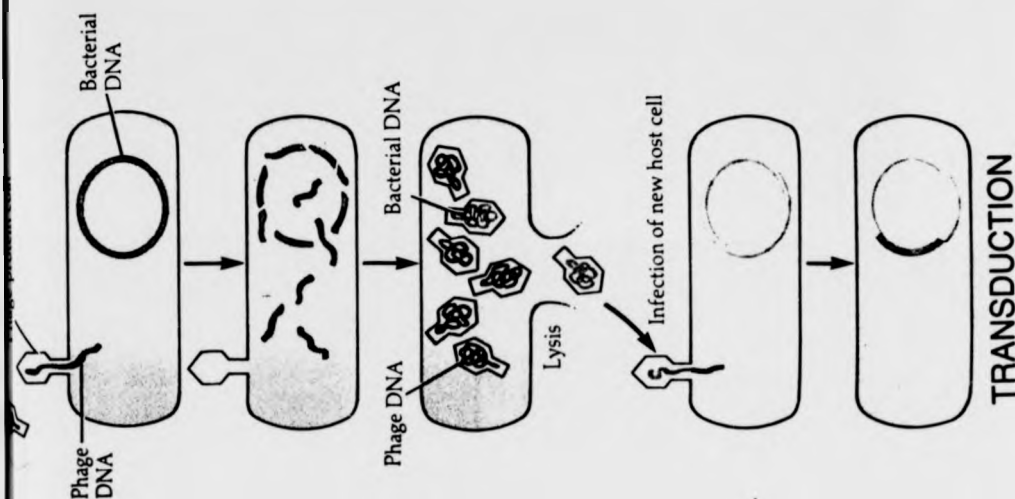


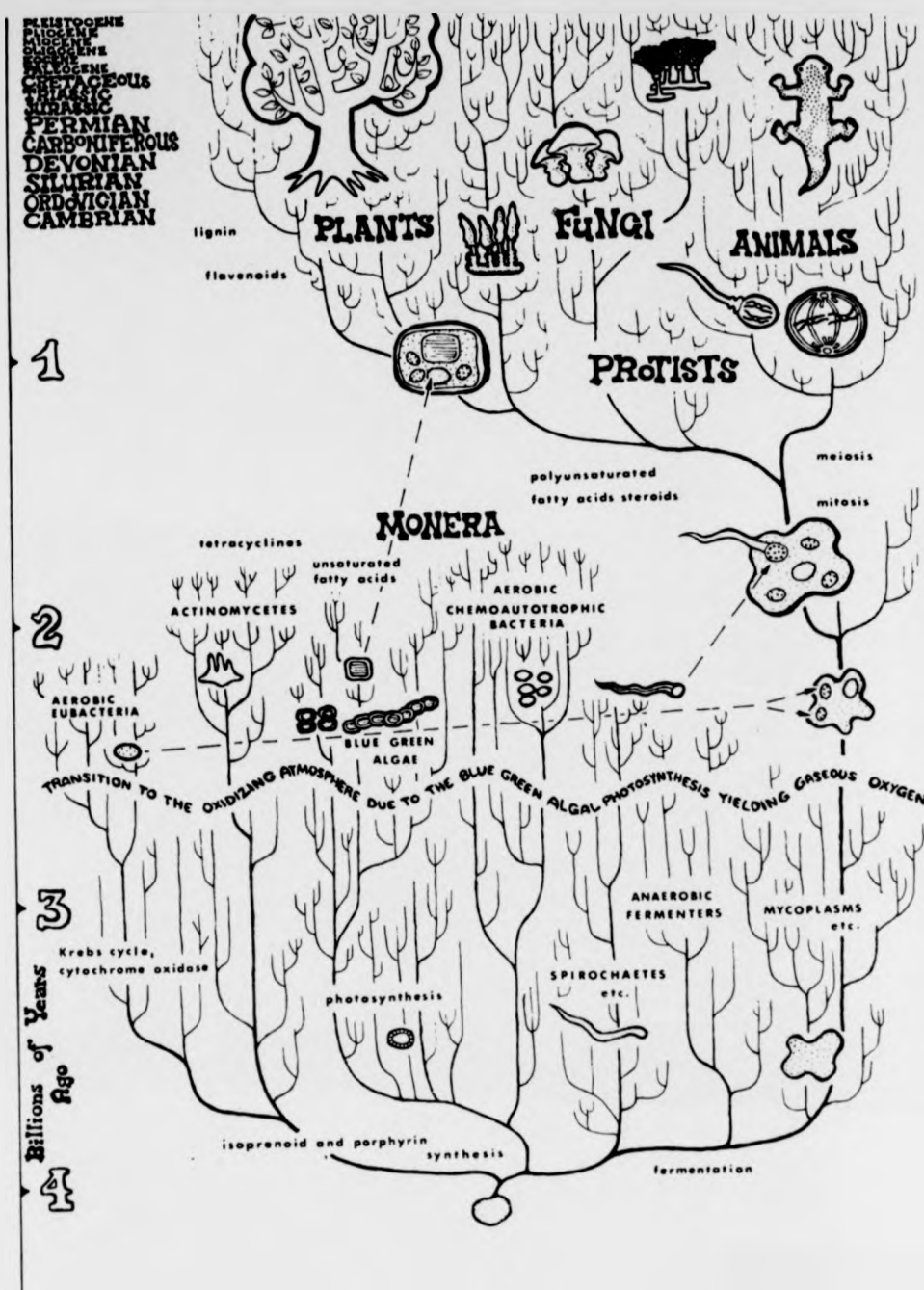
INFORMATION FLOWS FROM DNA THROUGH RNA TO PROTEIN



Appendix 5

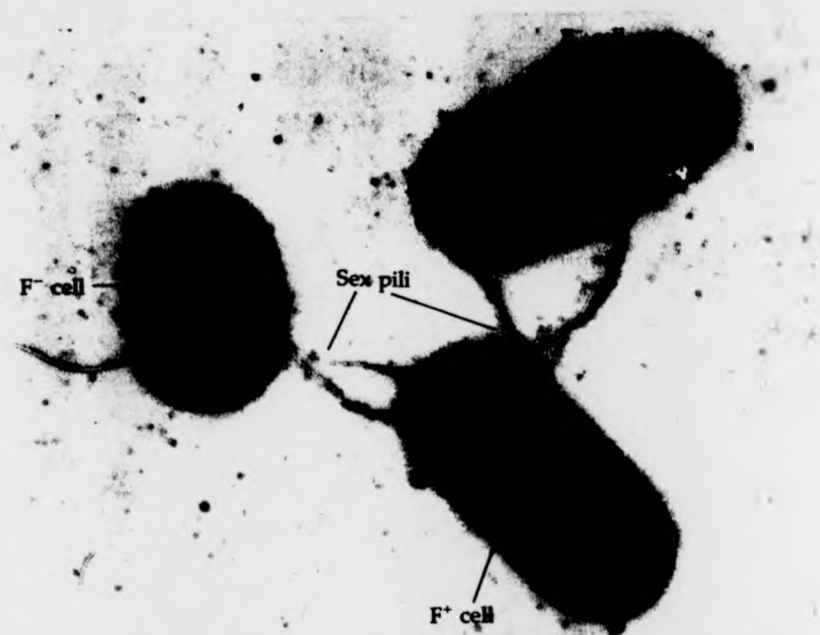
Appendix 5





Frontispiece: Theory of the origin and evolution of eukaryotic cells

¹ Margulis, Lynn. *Symbiosis in Cell Evolution: Microbial Communities in the Archean and Proterozoic Eras*. 2nd ed. (New York, London W.H. Freeman 1993)



Conjugation in *E. coli* ($\times 25,000$).

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