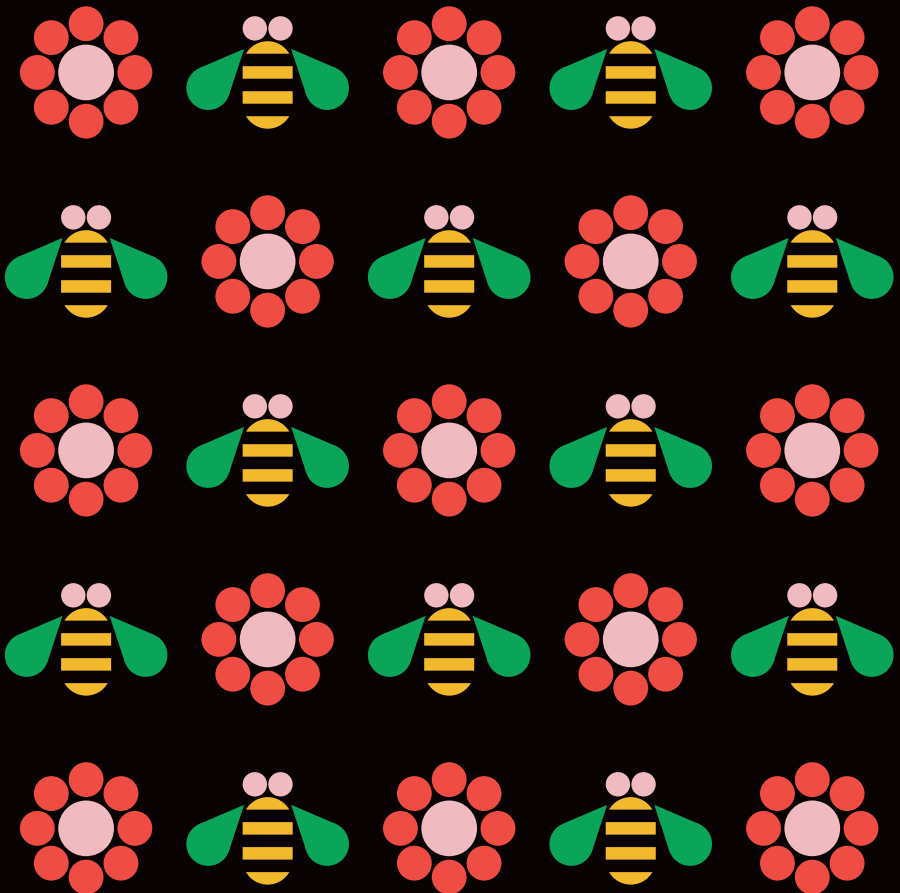


JORIS VAN ROSSUM

On Sexual Reproduction as a
New Critique of the Theory of
Natural Selection

*Sex as Creative Teleonomy and the
Implications for Darwinism*



ON SEXUAL REPRODUCTION AS A NEW CRITIQUE OF
THE THEORY OF NATURAL SELECTION

Joris van Rossum

On Sexual Reproduction
as a New Critique of the
Theory of Natural Selection

Sex as Creative Teleonomy and the Implications for Darwinism



Amsterdam 2014

Copyright © 2014 by Joris van Rossum

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording, or otherwise, without prior permission in writing of the author.

Second edition

Designed by Hans Stol

Cover image based on a design by Paul Rand

Printed in The Netherlands by Printforce

ISBN 978-90-9027200-9

NUR 738

Table of Contents

Preface

7

Introduction

11

I Background

25

II The Inability of the Theory of Natural Selection
to Explain Sexual Reproduction

45

III An Analysis of Darwinian Attempts to Explain
Sexual Reproduction and ‘The Queen of
Evolutionary Problems’

111

IV Discussion

133

References

171

Flower in the crannied wall,
I pluck you out of the crannies,
I hold you here, root and all, in my hand,
Little flower – but if I could understand
What you are, root and all, and all in all,
I should know what God and man is.

— *Alfred, Lord Tennyson*

I am convinced that, where men are
the most sure and arrogant, they are
commonly the most mistaken, and have
there given reins to passion, without that
proper deliberation and suspense, which
can alone secure them from the grossest
absurdities. — *David Hume*

Preface

My fascination with the theory of natural selection began during my early years at university, a fascination which had two different sides. On the one hand I was captured by the ingenuity of the theory. I was mesmerized by the way in which it seemed to solve many pressing problems around design and teleology in a unique and unprecedented way. At that time, I fully shared the admiration for the theory so frequently expressed by ardent Darwinists such as Richard Dawkins and Daniel C. Dennett. However, on the other hand, viewing living beings merely as whirlpools of meaningless matter in some corner of the dark universe had, at times, an overwhelming effect on me. As George Bernard Shaw wrote [1921], ‘[...] when its whole significance dawns on you, your heart sinks into a heap of sand within you. There is a hideous fatalism about it, a ghastly and damnable reduction of beauty and intelligence, of strength and purpose, of honour and aspiration [...]’. My fascination with Darwinism grew so strong that I eventually changed the field of my studies from law to biology.

In the course of time, however, two developments made me question the validity of Darwinism. First, reading philosophy, especially Arthur Schopenhauer, had a profound impact on me. Amongst many things, his works imparted to me the controversial position of naturalism, the paradigm in which the theory of natural selection operates. Second, I started to feel more and more that there was something within the theory of natural selection that was not quite right. Initially I could not quite grasp what this ‘something’ was, although I sensed that it related to the units of selection discussion as well as the philosophical problem of teleology.

Understanding what it was came as a sudden insight. I still recall the moment and the place when the pieces fell together, and I realized that the debate around the unit of selection essentially reveals the incapability to explain the end-directedness of living beings that exhibits itself in sexual reproduction. After my studies, this matter kept me occupied. I published two articles on the subject,¹ and in 2009 I commenced, alongside my daily job, working on a PhD dissertation at the vU University Amsterdam.

What is to be conveyed through this work is exactly this single insight I had more than 15 years ago, something that remained clear and strong during all these years. At the same time, experience has shown that this insight is not easy to communicate. I realize that this challenge will endure with this current work, and so I will be satisfied if it manages to persuade a few.

I would like to express my gratitude to several people. First, to Ton Derksen from the University of Nijmegen under whose supervision I published the afore-mentioned articles. For one day per week over last three years I have shared a room at the Department of Mathematics of the vU University Amsterdam, and I would like to thank my roommates and other members of the department for welcoming a stranger in their midst. Furthermore, I want to thank my colleagues at Elsevier who have tolerated me taking Fridays off, and have always shown interest in my work's progress. Through a twist of fate, I had the opportunity to ask the same person who edited my father's dissertation to edit mine as well: many thanks to Jules van Hagen for his valuable contribution to this manuscript. Naturally, I would like to thank my supervisors. First, René van Woudenberg for his guidance and kind support. I have enjoyed and valued the discussions we had during this project. I would like to especially thank Ronald Meester. I acknowledge that as a mathematician, taking up a biologist to write a philosophical dissertation

¹ Van Rossum [2003] and Van Rossum [2006].

PREFACE

was not a natural thing to do, but I think it worked out very well. His insistence for mathematical clarity has stimulated me to make my argument in much more precision. Moreover, his thorough understanding of the point I want to bring across was in many ways a great support and indispensable for the completion of this project. Finally, I would like to thank my wife Helga and my two sons Adam and Olivier. I realize that in recent years they have seen me behind my laptop much too frequently, but despite this, they have always remained supportive.

Preface to the second edition

The at times vehement reactions to my work when it appeared as a PhD thesis at the end of 2012 did not address the core of my argument. On the contrary, it confirmed my judgment of Darwinism as, in the words of Ludwig von Bertalanffy, ‘a theory so vague, so insufficiently verifiable and so far from the criteria otherwise applied in “hard science”’ [Bertalanffy 1978]. However, the reactions did reveal one aspect of the theory that I have not addresses sufficiently, namely that, besides many other biological terms and concepts, the term ‘unit of selection’ can be used with different meanings, and that this ambiguity can form an impediment to the understanding of my argument. For the sake of clarity, therefore, I have touched upon these possible other meanings, while stressing that also in these, they would not be able to solve the fundamental problem that I addressed in this work. Further, I have added a subtitle in order to give the term ‘creative teleonomy’, the kernel of my argument, a prominent place. And lastly, this edition contains some smaller textual adaptations.

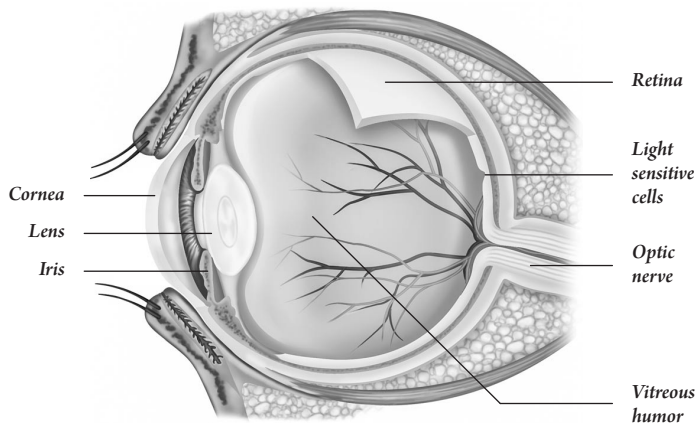


Figure 1. The human eye as an example of the mammalian eye.

Introduction

This work introduces a new critique of the theory of natural selection. In order to properly understand the critique, it is essential to understand the theory itself, but this understanding is not as widespread as often assumed. As Jacques Monod, a biologist who will play an important role in this work, remarked [1973], a curious aspect of the theory of evolution is that everybody thinks he understands it.

For a proper introduction to the theory, therefore, let us take a paradigm example of a complex biological feature, the mammalian eye, and see how the theory of natural selection would account for it. In a very simplified way, the mammalian eye functions as follows. Light passes first through the cornea and the lens. As the intensity of light falling on the eye can vary, the iris, located in front of the lens, can limit the light entry to the retina, thereby enhancing the resolution much like the lens diaphragm of a camera. In many types of mammalian eyes, the shape of the lens can be changed in order to focus the eye. When light has passed through the lens, it passes through the so-called vitreous humor and strikes the retina, on which an inverted image is displayed. In the retina, light is absorbed by light sensitive cells. These light sensitive cells transmit the information obtained via the optic nerve to the brain, where this information is processed (Figure 1).

Scientists, however, do not only deal with the question how things work, but also how these things come into existence. The mammalian eye, like all biological structures, is characterized by design, i.e. a high level of organization and complexity, and the existence of this structure therefore demands an explanation. It

was the explanation of this design that was one of Darwin's most important problems,² and the theory of natural selection was proposed as the solution.

Darwin's account of the existence of the eye roughly runs as follows. First, this eye did not appear overnight, but was formed in a long, gradual process. The current mammalian eye was formed from less complex forms of eyes, for example, the eyes of primitive fish, which in turn were formed from even simpler forms. This *evolutionary* process took place over periods of millions and millions of years, whereby the organ evolved step by step to its current form. Also, this evolutionary process was one of adaptation, that is to say that the evolution of the eye was characterized by it becoming more adapted to the needs of the organisms bearing it. In this specific case it means that in its evolutionary course the eye became more effective in providing vision, either in a constant or changing environment.

The mechanism driving this evolutionary process of the formation of the mammalian eye was natural selection. Darwin elucidates the working of this mechanism by considering some characteristics of biological entities. One is the existence of variation. As Darwin explains in *The Origin of Species* (1859), variation is the existence of 'slight differences which may be called individual differences, such as are known frequently to appear in the offspring from the same parents [...]' [Darwin 1968: p. 102]. Another important characteristic of the biological world is the struggle for existence. This struggle, as Darwin argues, 'inevitably follows from the high rate at which all organic beings tend to increase. [...] Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life' [Darwin 1968: pp.

² See Popper [1978]: p. 341.

INTRODUCTION

116–117]. The evolutionary process of adaptation through natural selection, then, follows as the inevitable and logical consequence of this set of characteristics. As Darwin argues:

Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection [...]. [Darwin 1968: p. 115]

When applied to the eye, this acts out as follows. Some animals in a population might have slightly smaller lenses or a thicker cornea. These varying characteristics are heritable – the offspring of the organism bearing that feature will tend to have the same characteristics. Moreover, some of these varying characteristics might provide the animals an advantage over others. For example, some eyes might have stronger muscles around the iris diaphragm which allow them to react faster and more effectively to light variations, or more light sensitive cells which make them better capable of capturing light. Through this enhanced eyesight thus obtained, the animal bearing it will have a greater chance to survive and reproduce – after all, the fitter an animal, the greater chance it has to survive and reproduce. And as due to competition not all individuals in a population are able to survive and reproduce, animals that have a better chance of doing so will replace the other animals, effectively leading to the evolution within the population of the old eye-type to one of the new eye-type with the stronger muscles around the

iris diaphragm or with the increased number of light sensitive cells. According to Darwin, this iterative process of variation and natural selection, then, is the major mechanism behind the evolutionary process of adaptation. Heritable variation that has an effect on the chance of animals to survive and reproduce will lead to the natural selection of those variations that increase the chances to survive and reproduce, iteratively leading to the development and further evolution of – sometimes very complex – features called adaptations.

This description of the mechanism, or principle, of natural selection as laid down in *The Origin of Species* more than 150 years ago, still forms the core of contemporary ideas about the workings of natural selection, although meanwhile biologists have proposed different interpretations of the mechanism. The well-known biologist Richard Dawkins, who together with George C. Williams and John Maynard Smith formed a school of highly influential evolutionary biologists in the 1960s and 1970s, developed an interpretation of natural selection that not only accounts for the evolution, but also for the origin of life. This description is most eloquently and accessibly laid down in his work *The Selfish Gene* (1976). Because of its crucial importance for this work, let us look at this description in detail.

Darwin's 'survival of the fittest' is really a special case of a more general law of *survival of the stable*. [...] Sometimes when atoms meet they link up together in chemical reaction to form molecules, which may be more or less stable. [...] If a group of atoms in the presence of energy falls into a stable pattern it will tend to stay that way. The earliest form of natural selection was simply a selection of stable forms and a rejection of unstable ones [...]. At some point a particularly remarkable molecule was formed by accident. We will call it the *Replicator*. It may not necessarily have been the biggest or the most complex molecule around,

INTRODUCTION

but it had the extraordinary property of being able to create copies of itself. [...]. Think of the replicator as a mold or template. Imagine it as a large molecule consisting of a complex chain of various sorts of building block molecules. The small building blocks were abundantly available in the soup surrounding the replicator. Now suppose that each building block had an affinity for its own kind. Then whenever a building block from out in the soup lands up next to a part of the replicator for which it has an affinity, it will tend to stick there. The building blocks which attach themselves in this way will automatically be arranged in a sequence which mimics that of the replicator itself [...]. This process could continue as a progressive stacking up, layer upon layer. This is how crystals are formed. On the other hand, the two chains might split apart, in which case we have two replicators, each of which can go on to make further copies. [Dawkins 1976: pp. 13–17]

Dawkins then proceeds to explain that the imperfection of the copying process leads to variation and that some of the varieties will be more stable than others (replicators are thus ‘active’, in the sense that they have an influence on their stability and that variation between replicators has an impact on that stability, i.e. some varieties are more stable than others). Replicators with high longevity will therefore tend to become more numerous, leading to a trend towards greater longevity in the population of molecules. Moreover, replicators that have a higher speed of replication, or fecundity, will also become more numerous.

As mis-copyings were made and propagated, the primeval soup became filled with a population not of identical replicas, but of several varieties of replicating molecules, all ‘descended’ from the same ancestor. Would some varieties have been more numerous than others? Almost certainly yes. Some varieties would

have been inherently more stable than others. Certain molecules, once formed, would be less likely than others to break up again. These types would become relatively numerous in the soup, not only as a direct logical consequence of their 'longevity', but also because they would have a long time available for making copies of themselves. Replicators of high longevity would therefore tend to become more numerous and, other things being equal, there would have been an 'evolutionary trend' towards greater longevity in the population of molecules.

But other things were probably not equal, and another property of a replicator variety which must have had even more importance in spreading it through the population was speed of replication or 'fecundity'. If replicator molecules of type *A* make copies of themselves on average once a week while those of type *B* make copies of themselves once an hour, it is not difficult to see that pretty soon type *A* molecules are going to be far outnumbered, even if they 'live' much longer than *B* molecules. There would therefore probably have been an 'evolutionary trend' towards higher 'fecundity' of molecules in the soup. A third characteristic of replicator molecules which would have been positively selected is accuracy of replication. If molecules of type *x* and *y* last the same length of time and replicate at the same rate, but *x* makes a mistake on average every tenth replication while *y* makes a mistake only every hundredth replication, *y* will obviously become more numerous. The *x* contingent in the population loses not only the errant 'children' themselves, but also all their descendants, actual or potential. [Dawkins 1976: pp. 18–19]

Given the fact that the primeval soup was not capable of supporting an infinite number of replicator molecules, competition for these limited resources ensured that replicators with a high degree of permanence, fecundity and copying fidelity became more

numerous. Competition also leads to the development of so-called vehicles, integrated and coherent instruments of replicator preservation.

The next important link in the argument, one which Darwin himself laid stress on (although he was talking about animals and plants, not molecules) is *competition*. The primeval soup was not capable of supporting an infinite number of replicator molecules. For one thing, the earth's size is finite, but other limiting factors must also have been important. In our picture of the replicator acting as a template or mould, we supposed it to be bathed in a soup rich in the small building block molecules necessary to make copies. But when the replicators became numerous, building blocks must have been used up at such a rate that they became a scarce and precious resource. Different varieties or strains of replicator must have competed for them. We have considered the factors which would have increased the numbers of favoured kinds of replicator. We can now see that less-favoured varieties must actually have become *less* numerous because of competition, and ultimately many of their lines must have gone extinct. There was a struggle for existence among replicator varieties. They did not know they were struggling, or worry about it; the struggle was conducted without any hard feelings, indeed without feelings of any kind. But they were struggling, in the sense that any mis-copying that resulted in a new higher level of stability, or a new way of reducing the stability of rivals, was automatically preserved and multiplied. The process of improvement was cumulative. Ways of increasing stability and of decreasing rivals' stability became more elaborate and more efficient. Some of them may even have 'discovered' how to break up molecules of rival varieties chemically, and to use the building blocks so released for making their own copies. These proto-carnivores simultaneously obtained

food and removed competing rivals. Other replicators perhaps discovered how to protect themselves, either chemically, or by building a physical wall of protein around themselves. This may have been how the first living cells appeared. Replicators began not merely to exist, but to construct for themselves containers, vehicles for their continued existence. The replicators that survived were the ones that built survival machines for themselves to live in. The first *survival machines* probably consisted of nothing more than a protective coat. But making a living got steadily harder as new rivals arose with better and more effective survival machines. Survival machines got bigger and more elaborate, and the process was cumulative and progressive. [Dawkins 1976: pp. 20–21]

Dawkins describes entities that evolve through the mechanism of natural selection as ‘active replicators with a sufficient amount of fecundity, longevity and copying fidelity’. The essential role of this process of replication can be shown by the following example. Let us, for the sake of the argument, assume a molecule that consists of 10 building blocks of two different sorts (A and B), and the sequence of these blocks is AAAAAABBBBB. Let us assume that the change of one building block will lead to an improved stability, for example, a change of the first one: BAAAAABBBBB. At the same time, all other changes will lead to a destabilization of that molecule (as we will see, this corresponds to the concrete situation whereby mutations, although being the source of evolutionary change, are in most cases harmful). Now if this molecule makes one copy of itself, the chances are that the combination BAAAAABBBBB will never see the light of day. Before this change occurs, other changes will have preceded it, and led to the annihilation of that molecule. But if this molecule makes 20 copies of itself, the chances are that BAAAAABBBBB will appear, and given the existence of competition, also that it will become dominant in the population. The fact that it makes sufficient

INTRODUCTION

copies of itself means that it can lose some bad copies, and consequently the right copy carrying the 'good' change can be filtered out, *naturally selected*. A condition for this process of replication is that this replicator's fecundity, longevity and copying fidelity is at the right level and proportion: its capacity to make copies should be sufficient, the replicator should be stable enough, and replication errors should not occur too frequently as this will make the replicator too unstable, nor too infrequently either as in such a case this process will not lead to evolutionary changes.

Both Darwin's and Dawkins' interpretations of the mechanism of natural selection share the notion that there is an entity that evolves by means of the evolutionary process of adaptation, an entity which is known in scientific literature as the 'unit of selection'. According to Darwin, this entity was the individual organism, while Dawkins provides a precise, theoretical description of this unit, namely, an active replicator with a sufficient amount of fecundity, copying fidelity and longevity. The evolutionary process of adaptation through natural selection takes place when random, heritable variation that has an effect on the success in survival and reproduction arises in a population of replicating units, in which case natural selection will act as a sieve filtering out variations that have positive effect on survival and reproduction. The features of living beings that evolved through this evolutionary process of adaptation are called adaptations, and exist due to their contribution to the survival and reproduction of the unit of selection (the replicator).

Dawkins' more precise explanation of the mechanism of natural selection and subsequent description of the unit of selection as a replicator is an important improvement on the theory of natural selection since its conception more than 150 years ago. Another crucial development, equally established by Dawkins' generation of biologists, is the application of this theoretical framework to the

revolutionized new insights in the underlying biochemistry of the biological world. Since Darwin's time, the knowledge of the biochemical basis of biological structures and processes has expanded enormously. In case of the eye, the biochemical processes underlying vision have been elucidated in detail (and, as most biochemical processes, have been shown to be of a breathtaking complexity). Take, for example, one aspect of the working of the eye, light reception on the retina. Light reception is established by two types of cells, the more sensitive rods, used in dim light, and cones, used mostly in brighter light and for color vision. Both of these cells contain photosensitive membranes, which are layers for catching photons. Within these cells, photons – light particles – are translated into electric signals, which are sent to the brain mediated through retinal ganglion cells, which serve as an interface between the photoreceptor cells and the brain and pre-process information. This translation – or transduction – of light into an electric signal is a complicated chemical pathway in itself, consisting of various stages. In total, an eye has been shown to consist of approximately three million retinal ganglion cells and 125 million photoreceptor cells.

Since Darwin, science has also shown us that all the structures of living beings – including that of the eye – are based on the information contained in a molecule called DNA. DNA is a large molecule that consists of a sequence of 4 different units called nucleotides that are organized in pairs. These helix-shaped strings – in human beings consisting of approximately 3 billion base pairs and packed inside every cell of the body in 46 different structures called chromosomes – carry all the instructions used in the development and functioning of organisms. Through a process called translation, the sequence of genetic fragments, called genes, are eventually translated into proteins, major and essential building blocks of the organism. It is the sequence of nucleotides of DNA that forms the basis of all structures of living beings, including the eye.

INTRODUCTION

Moreover, according to Dawkins, Williams and Maynard Smith, it is (fragments of) this DNA that acts as replicator in organisms, and subsequently is the unit of selection. DNA makes copies of itself – through replication, two copies are made of the same genetic code. Mistakes are made in that copying process, and also through other sudden and spontaneous changes in the cell – so-called mutations – changes in the genetic code of organisms occur. Most of these mutations are contrary to the needs of the organism (however many ways there may be of being alive, it is certain that there are vastly more ways of being dead, as Dawkins [1986] remarked) but as DNA makes copies of itself with a sufficient amount of fecundity, longevity and copying fidelity, those incidental changes that are beneficial to the needs of the organism, can accumulate.

The account of the existence of the mammalian eye would then run as follows. We saw that its current form originated from a more primitive form, such as the eye found in fish, and that its formation was a gradual one. Ultimately, evolutionary biologists claim, these changes are based on changes inflicted on the genetic code (mutations or copying mistakes). Most of these changes were harmful for the functionality of the eye (to paraphrase Dawkins, however many ways there may be of seeing, it is certain that there are vastly more ways of being blind!), but as the DNA carrying the genetic instructions of the eye was part of a replicator that replicated with a sufficient amount of fecundity, longevity and copying fidelity, the repetitive process of replication resulted in the gradual accumulation of beneficial mutations, leading eventually to the eye in its current form. It is in this way that natural selection is proposed as the mechanism behind the evolutionary process of adaptation, leading to the development of biological features such as the eye.

We have elaborately dealt with the principle, or mechanism, of natural selection, but when scientists talk about the *theory* of natural selection, they usually refer to more than just this mechanism. In

fact, the theory can be divided into two separate claims. The first one is the notion of evolution, the claim that organisms change over time. This notion includes the idea that different species can be traced back to common ancestors, the process of evolution thus leading to a diversification of living forms. The history of living beings is one of branching out into different forms, leading to the multitude of species that populate the world today which in the end can all be traced back to a universal common ancestor. This in itself formed a revolutionary element in the theory of natural selection, introduced at a time when the idea still prevailed that animal species are static and independently created. But Darwin did more. As we have seen, in *The Origin of Species* Darwin also proposed the *mechanisms* behind this evolutionary process. Darwin claimed that the most important evolutionary process is one of adaptation whereby organisms become better equipped for surviving in their environments, and that the most significant mechanism behind this evolutionary process of adaptation is the one we have elaborately dealt with, natural selection. Other less important mechanisms are sexual selection (already recognized by Darwin), and genetic drift (recognized around the 1930s). We will later deal with these mechanisms in greater detail. The theory of natural selection holds that through natural selection, sexual selection and genetic drift, organisms were designed in an evolutionary process of adaptation, and that this process furnishes an explanation for the design of all biological phenomena.

The goal of this study is to challenge the second element of the theory of natural selection. It does not call into question the first claim of the theory, evolution by common descent, and so the idea that organisms evolve, and different species can be traced back to common ancestors, is not challenged. What this study does challenge is the idea that the known versions of the theory of natural selection (versions, like those of Darwin and Dawkins, which can be distinguished on the basis of different interpretations of the

INTRODUCTION

mechanism of natural selection) can provide an account of all features of living beings, as it will be shown that these versions are fundamentally incapable of explaining a specific – albeit salient – feature of many organisms, namely sexual reproduction. Hence, this study does not call evolution by common descent into question, but denies the assertion that all biological features can be explained through the evolutionary process of adaptation.

Now it can be rightfully claimed that many scientists have already acknowledged that explaining sexual reproduction through the theory of natural selection is problematic, which led people to call sexual reproduction the ‘queen of evolutionary problems’ [Ridley 1993]. Many unsuccessful attempts can be found in scientific literature trying to explain sexual reproduction within the context of the theory of natural selection, attempts which will be listed in Chapter III of this work. The new critique in the current work is, however, of a different nature: the current work is intended to show that there is a *more principal and fundamental* problem in the explanation of sexual reproduction by means of current versions of the theory of natural selection.

The structure of this work is as follows. In the next chapter, more background is given to the reasons why the fundamental critique of the theory of natural selection, the subject of this study, has not been expressed earlier, which will bring us to reflect on the history of science and the role of the theory of natural selection therein.

In the second chapter the argument itself, why sexual reproduction cannot be explained by the known versions of the theory of natural selection, is provided. This incapability of the mechanisms recognized by the theory of natural selection – natural selection, sexual selection and genetic drift – to explain sex is established by analyzing the works of leading evolutionary biologists, including Charles Darwin and Richard Dawkins, representing different streams of biological thought. We will conclude that it is the

creative aspect of sexual reproduction (later in this study we will come to a description of sex as ‘creative teleonomy’) which the theory of natural selection, at least its existing versions, cannot account for.

The third chapter will provide an overview of Darwinian attempts to explain sexual reproduction, and analyze the problem that is commonly associated with these. We will determine the relation of this ‘queen of evolutionary problems’ with the conclusions of the second chapter.

In the fourth and final chapter, a wider context to the incapability of current versions of the theory of natural selection to account for sexual reproduction is provided through analyzing the works of the influential philosophers of science Karl Popper and Thomas Kuhn. As we will conclude that the inability to explain sexual reproduction poses a challenge for the naturalistic worldview at large, we will end this study by discussing theistic, vitalistic and finalistic doctrines as potential alternatives to account for biological phenomena.

I Background

Darwin provides a solution,
the only feasible one so far suggested,
to the deep problem of our existence.

— *Richard Dawkins*

Aut catechismus, aut materialismus
is their solution.

— *Arthur Schopenhauer*

§1. *The argument put forward in this study as to why sexual reproduction cannot be explained by current versions of the theory of natural selection has not been delivered before. In the following section, some facts and circumstances are discussed that could account for this.*

Sexual reproduction has been a persistent problem for the theory of natural selection, but as mentioned in the introduction, the conclusions of this study go a step further. Although evolutionary biologists have experienced problems accounting for sexual reproduction, the claim is new that, given their interpretations of the principle of natural selection, an explanation of sexual reproduction cannot be provided as a matter of principle. At the same time, the theory of natural selection has been attacked by its opponents from various angles but hardly from the angle of sex. What led to the situation in which scientists overlooked the fact that sexual reproduction is a phenomenon fundamentally alien to the theory? And why was sex never used as an argument against the theory of

natural selection by its opponents? These pressing questions demand an explanation in itself, but will also help to provide a wider context and more background to the issue, which is why we will discuss them here.

In fact, several factors that led to this situation can be identified:

- The fact that in many versions of the theory of natural selection, including Darwin's, sexual reproduction has served as a condition for the principle of natural selection, but was not subject to explanation itself;
- A certain vagueness that has surrounded biological terms and concepts, and a complacency among scientists which impeded a clear description of what can be accounted for by the theory of natural selection, and what cannot. This is closely connected to
- the fact that there are no scientific alternatives available to account for biological phenomena;
- With creationists as the most important opponents of the theory of natural selection, the discussion around the theory has focused on other aspects of living beings than sexual reproduction.

To start with the first one, the problematic aspects of sexual reproduction will only surface with those scientists that attempt to provide an explanation for sexual reproduction in the first place. This sounds like a self-evident thing to do, but when we look at Darwin's own explanation of the theory of natural selection as laid down in *The Origin of Species*, we see that this is not always the case. As we have already seen in the introduction, for Darwin the principle of natural selection is based on certain premises about the natural world, which can be seen as conditions leading, if fulfilled, automatically and necessarily to the evolutionary process

of adaptation. These conditions include the existence of heritable variation within a population causing differential reproductive success, and the struggle for survival among living beings. This struggle for survival itself rests on the tendency of organic beings to strive to increase their numbers to a maximum, and on the availability of limited resources that cannot support all offspring. What is thus assumed in his explanation of natural selection is the existence of living beings with their striving for survival and (sexual) reproduction. Because of this it is immediately clear why the problem of accounting for sexual reproduction never surfaced in Darwin's version. For Darwin, reproduction (including sexual reproduction) is not *explanandum*, something that needs to be explained through the principle, but *explanans*, something through which the evolutionary process of adaptation is to be explained. The problem of accounting for sexual reproduction will therefore only appear with those philosophers and biologists that work towards an explanation of the design of *all* biological features. And in this respect, the theory of natural selection had a bad start with Darwin.

An important question that follows from this omission is whether it is unintentional, or reflects Darwin's limited ambition in the explanation of biological phenomena. The above seems to suggest the latter, that is to say that Darwin simply wanted to explain the origin of species assuming living beings with their striving towards survival and reproduction, but other statements clearly indicate that Darwin's ambitions were to explain all biological features through the theory of natural selection. We see this, for example, when Darwin claims that, 'if it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down' [Darwin 1968: p. 219], which strongly suggests that his theory is intended to provide an explanation for all biological features. Independent of ambitions or intentions, however, it remains a fact that in the version of the theory of

natural selection as laid down in *The Origin of Species*, there is no room for the explanation of the origin of sexual reproduction.

The second factor contributing to the situation that the inability of the theory of natural selection to account for sexual reproduction has not received sufficient attention is the fact that the theory has suffered from a certain amount of woolliness. The biologist C.S. Pittendrigh went as far to refer to this vagueness as a 'common affliction of biological terms' [1958]. It is difficult to determine the boundaries of what the theory of natural selection can, and cannot, account for if these terms remain fuzzy and ill-defined. As also George C. Williams noted, often natural selection has done little more than to provide '[...] a vague aura of validity to conclusions on adaptive evolution and to enable a biologist to refer to goal-directed activities without descending into teleology' [Williams 1966: p. 20], and the theory has suffered from a lack of 'rigorous criteria for deciding whether a given character is adaptive, and if so, to precisely what is an adaptation' [Williams 1996: p. 4]. Despite the restrictions and limitations the theory of natural selection imposes on what kind of features of organisms can be explained, many evolutionary biologists and philosophers have often readily accepted these explanations. 'Natural selection' is often handled as an incantation that instantly eliminates the need for any accountability or clarification for the existence of these phenomena in living beings.

The ideas of the eminent biologists Jacques Monod, Richard Dawkins and George C. Williams can be seen as an attempt to overcome this vagueness (in case of Williams even explicitly). In groundbreaking books written in the 1960s and 70s, these biologists developed abstract and clear descriptions of living beings shaped by natural selection on the level of the biochemistry and molecular biology of organisms, and in this way more clearly defined what the theory of natural selection can explain. But although these biologists have made clear descriptions of what the theory of natural selection can account for [and what not], it will

be shown in this study that organisms that reproduce sexually do not fit these descriptions. In fact, we will observe that when these authors are trying to apply their conceptual descriptions of living beings shaped by natural selection to empirical reality, the above mentioned affliction of the theory of natural selection – vagueness through a lack of precision – rears its ugly head again, leading once more to vagueness, inconsistencies, and the incorrect conclusion that living beings fit these descriptions. As will be shown later in this study, the root of the problem of aligning living beings to their descriptions is sexual reproduction, a phenomenon that is alien to the existing interpretations of the working of natural selection provided by Monod, Williams and Dawkins.

This vagueness can, to a certain extent, be explained by a phenomenon Phillip E. Johnson refers to as ‘philosophical necessity’ [1991], i.e. the notion among scientists that the theory of natural selection somehow *must* be true, which is the third factor which we wish to discuss. This philosophical necessity lessens the need to find evidences or validations for it, or to clearly define its explanatory potential. To understand this phenomenon, we have to start by reflecting on the history of the theory of natural selection. The idea that species are static, an idea still prevalent before Darwin’s time, was more and more challenged by discoveries in paleontology, geology and biology throughout the 18th and 19th centuries. However, evolution, the notion that the existing forms of life are the descendants of pre-existing forms, only found a scientific explanation in Darwin’s ideas, whose theory of evolution by natural selection provided a compelling mechanism for evolution by common descent. But Darwin’s theory had not only biological, but also profound philosophical significance. Modern science commenced with the explanation of physical phenomena in the 16th and 17th centuries through the discoveries of Copernicus, Galileo and Newton. The advancement of science in fields other than the study of physical phenomena, however, was for a long time hindered by

the lack of success in accounting for biological phenomena. Their apparent goal-directedness, as well as their astonishingly complex design formed a fundamental problem and defied a scientific explanation. As such, it formed a problem for the naturalistic viewpoint which developed alongside modern science, the idea that the universe is essentially physical in nature. Living beings were left out of the Copernican revolution, whose existence until Darwin was still mainly accounted for as a special creation by an omniscient and omnipotent God. The inability to account for living beings through the scientific method led, in the words of Ayala [2010], to a 'split-personality state of affairs', whereby scientific explanations, derived from natural laws, dominated the sciences of the inanimate world, whereas natural theology, supernatural explanations, accounted for the origin of living beings. Darwin's theory of natural selection was so successful and of such great significance because it seemed to solve this split-personality state of affairs. The Copernican revolution was completed with Darwin's *Origin of Species*, which removed the last hurdle to a complete naturalistic interpretation of life and the universe. For the first time, living beings, their complex organization and adaptiveness, could be explained as a result of natural, mechanistic processes without having to resort to creationistic notions. The significance of this theory is illustrated by Dennett, when he says:

Let me lay my cards on the table. If I were to give an award for the single best idea anyone has ever had, I'd give it to Darwin, ahead of Newton and Einstein and everyone else. In a single stroke, the idea of evolution by natural selection unifies the realm of life, meaning, and purpose with the realm of space and time, cause and effect, mechanism and physical law. [Dennett 1995: p. 21]

Before Darwin's *Origin of Species*, living beings were mainly accounted for as a special creation by an omniscient and omnipotent

God, but creationist lines of thinking continue to form the most vocal opponents of Darwinism until this very day. In fact, they are almost the exclusive opponents. There have not been serious alternative scientific explanations, explanations that do not invoke supernatural entities such as an intelligent creator, to explain biological phenomena. There is simply no *scientific* theory other than the theory of natural selection to account for living beings, which contributed to the notion that it simply *must* be true. For many scientists, the theory of natural selection is, therefore, almost a necessity. This does not imply, of course, that biologists dogmatically accept Darwinism and do not feel the need to further analyze and find evidence for it, but there is an important difference between testing a theory against some plausible alternative, and looking for confirmation of the only theory that one is willing to accept.

The fact that the most vocal and almost exclusive alternative view to Darwinism is formed by the unscientific theories of creationists, could have added to a *fourth* circumstance that contributed to the situation that sexual reproduction has evaded scrutiny and has not been identified as a feature of living beings that cannot be accounted for by (existing versions of) the theory of natural selection. An important and grave consequence of the narrow scope of the Darwinian-creationist debate is that this debate focuses on issues peculiar to this discussion while neglecting others. This is exactly why we see that the contemporary discussion around Darwinism mainly focuses on a few, particular aspects. Evolution was the very subject of Darwin's *Origin*, and because the concept was generally conceived to be contrary to the Christian dogma of creation, it has played a dominant role in the debate up to now. As we will see later in this study, most of the scientific skepticism about Darwinism has centered on the notion that no *evolutionary* pathway is imaginable that could have led to the complex features of living beings. Sexual reproduction, however, is a phenomenon that does not play a role in this debate. We have seen that it is assumed

by Darwin to be a condition of evolution to take place, and it has never been a mystery for Christians either: its origin can be traced to the first pages of the Bible as one of the first commandments of God to living creatures, 'be fruitful and multiply'. The existence of sexual reproduction is simply assumed in both doctrines, and its existence can therefore not serve as a validation of the one, or falsification of the other, which explains why this phenomenon has not received sufficient attention.

In the third section, we will return to the narrow scope of the discussion, shedding more light on its origin. Before that, we will digress briefly and argue that the narrow scope of the debate about the theory of natural selection also has its effect when we look at the proposed validations of the theory of natural selection.

§ 2. In this section we will see that proposed validations of the theory of natural selection either concern validations of evolution by common descent, which is only one claim or element of the theory of natural selection, or concern at best limited validations of the mechanisms behind the evolutionary process of adaptation.

The effects of the discussed narrowness are also discernible when we analyze the alleged evidences for the validity of the theory of natural selection. As discussed, Darwin's theory of natural selection consists of two separate elements. The first is the notion of evolution by common descent, the second proposes the underlying mechanism for evolution, where, next to sexual selection and genetic drift, the most important role is played by the principle of natural selection. This study, as indicated, challenges the second element of the theory of natural selection, but does not call into question the existence of evolution by common descent.

Validations for evolution by common descent have convincingly been claimed. Into this category we must place evidences of evolution through the identification of homologies between organisms,

and data from the fossil record. The existence of certain kinds of similarities between organisms (homologies) do not seem to have a sound explanation unless we assume that these species sharing these similarities form a tree of life, and are not independently created. Moreover, there is the fossil record, which, through the order in which main groups of organisms appear, strongly suggests evolution by common descent. As even a well-known critic of Darwinism, Michael Behe, agrees, the evidence for common descent seems compelling [Behe 2007: loc. 93].³

The limited scope of the discussion surrounding the theory of natural selection explains why these partial validations, to be more precise, validations for evolution by common descent, are seen as complete validations of the theory of natural selection. The fact that only two paradigms dominate the debate suggests that these are the only available options. A validation of evolution by common descent therefore *de facto* implies a validation of the theory of natural selection. The notion that one aspect of the theory of natural selection – evolution by common descent – could be valid, while another – the proposed mechanism behind it – might not, is in this situation not something that can be easily placed.

When we search in scientific literature for validations for the proposed mechanisms behind the evolutionary process of adaptation, and focus on the most important one, natural selection, we find these to be surprisingly scarce. One class of these suggested

³ Although the evidence of common descent seems compelling, the particular pattern of evolution displayed in the fossil records does pose challenges for Darwinism, e.g. new forms of beings appear in a relatively short period of time, groups of animals often display stasis for long periods of time, and findings of transitional types between large groups of animals are rare. Reasoning from the theory of natural selection, however, one would expect a gradual evolution of forms and many transitional intermediates between species. The Darwinian theory of punctuated equilibrium, developed by Niles Eldredge and Stephen Jay Gould (1972), can be seen as an attempt to account for these seemingly contrasting phenomena.

validations concerns the presentation of actual occurrences, or examples, of the process of adaptation through natural selection. Although observation of the evolutionary process of adaptation is difficult as the process occurs over such long periods of time that they are mostly useless for science, some examples have been claimed. The evolution of the peppered moth (*Biston betularia*), which has been studied in detail for almost 200 years, is often referred to as a demonstration of evolution by natural selection:⁴ before the industrial revolution, the white-bodied form of the moth was most dominant (the so-called wild type, the typical form of a species as it occurs in nature), providing the moth with a camouflage color against the light colored trees which they rested upon. However, due to the wide-spread pollution during the industrial revolution, the tree barks became darker, causing the light-colored moth to die off from predation, and the black-bodied (melanic) moth to thrive. However, the evolution of the peppered moth provides only a partial demonstration of natural selection. If we divide Darwin's theory into (1) the idea of evolution through common descent and (2) its most important underlying mechanism, natural selection, this mechanism itself can be divided into two elements: (2a) random variation and (2b) selection working on that variation. As Ernst Mayr described, natural selection is a two-step process: the first step is the production of random variation; the second step is the actual process of non-random selection or elimination [Mayr 1978]. If the story of the peppered moth does not only demonstrate evolution (1), but also its mechanism (2), it only does so for one of its aspects, namely selection (2b), while lacking a reasoned account for the variation between the two forms (2a). The melanic moth prevailed in the population because of industrial pollution, so it was selected over the wild (white) type, but this does not account for of the origin of this variant. If the example were to be complete,

4 See for example Ridley [2004].

it should have shown that the melanic variant arose from the wild type by random mutations. This, however, is not provided.

The study of HIV (human immunodeficiency virus) provides a more comprehensive presentation of an actual occurrence of evolution through the principle of natural selection. Not only does it demonstrate evolution, natural selection as well as random variation, but these aspects are also analyzed and understood on the molecular level. Random variation is molecularly interpreted in the form of genetic accidents, or mutations, leading to changes in the survival rate of the viruses. HIV is a retrovirus that causes acquired immunodeficiency syndrome (AIDS), a disease of the human immune system. HIV uses RNA as its hereditary material, and reproduces by having a DNA copy made of its RNA inside a human cell. Most of the reproductive process is performed by enzymes supplied by the host cell, but the virus supplies the enzyme called reverse transcriptase that makes the virus's DNA version of the RNA version [Ridley 2004]. As the reverse transcriptase is normally not present in humans, it is frequently targeted by drugs, causing the virus to be stopped, but leaving the regular activities of the cell unharmed. A member of this class of drugs is lamivudine, or 3TC. Lamivudine is similar to the nitrogenous base cytosine, a component of DNA. When present, the reverse transcriptase will incorporate 3TC into the DNA chain instead of cytosine. This 3TC will then act as a chain terminator, causing the process of reproduction to halt. Now evolution by natural selection can be observed in the form of the acquisition and spread of resistance to this drug [Schuurman et al. 1995]. The first effect of administering the drug will be a dramatic decrease of the virus. However, after a few days, 3TC-resistant strains of HIV start to be detected, which subsequently start to increase in frequency, leading eventually to a 100% resistant population within weeks after the treatment. The resistance is achieved by a change in one codon in the gene that codes for reverse transcriptase, leading to the enzyme being

more discriminating between 3TC and cytosine. As a result, 3TC will be not incorporated, abolishing its effect. So we observe here an instance of evolution driven by natural selection acting on random variation in its full form. Random variation is developed in the form of random mutations. This mutation leads to different variants with different levels of fitness, causing one variant – in this case, the mutated form – to be naturally selected over the other, eventually leading to the change of a population – evolution – over time.

In some cases, evolution by natural selection is not only observed, such as in the case of the peppered moth and HIV, but deliberately stimulated by means of experimentation. Contrary to comparable theories in physics and chemistry, evolution does not easily lend itself for experimentation, but some scientists have successfully tested the theory of natural selection in laboratory settings. One of the best known examples is provided by Richard Lenski's *E. coli* long-term evolution experiment. The use of *E. coli*, an organism that is well understood on the genetic level (its entire genome has been sequenced), has allowed for many generations to be studied in a relatively short time. Lenski's experiment started in 1988, with 12 nearly identical populations of *E. coli*. The bacteria were grown in a stable environment, with glucose as the sole source of carbon and energy. In 2004, the population reached generation 20 000 (which in an annual plant would take 20 000 years; in humans 400 000 years assuming an average generation of 20 years). In 2004, Lenski published a comprehensive report of the findings on phenotypic as well as genomic level [Lenski 2004]. An increase in competitive fitness (calculated as the rate of cell doublings of the evolved population compared to the ancestor population) was established. Populations tended to become glucose specialists, not surprising as the bacteria were exclusively grown on glucose. Average cell size also increased. Also, all 12 populations

lost the ability to grow on D-ribose as a sole carbon source. Some genetic changes that could be located involved defects in DNA repair leading to hypermutability, although these mutator lines did not exhibit proportionally greater adaptation or specialization. Another genetic change involved a change in the regulatory gene *spot*, affecting many more genes, either increasing or decreasing their activity. These mutations led to a positive effect on the fitness of the bacteria and have been linked to the turning off the genes coding for a flagellum, which had no strong net effect on fitness in the laboratory environment, therefore saving energy [Cooper, Rozen and Lenski 2003].

Although HIV and Lenski's *E. coli* experiments have provided examples of evolution by common descent that showed all aspects of the theory – evolution, random variation, and natural selection – these examples or instances have an important limitation. The changes caused by mutations and retained by natural selection were never the creation, the design, of something substantial: a new protein, biochemical pathways, or morphological features. In fact, these changes were very small. Resistance to 3TC acquired by the HIV virus was caused by one codon in the gene which codes for reverse transcriptase, leading to the enzyme being more discriminating between 3TC and cytosine. Genetic changes that could be tracked in *E. coli* in Lenski's experiments concerned changes in a single regulatory gene. These changes were not only small, but also primarily a degeneration of existing functionalities instead of the creation and design of new ones. In other words, natural selection was not building something new, but breaking down something existing [Behe 2007]. The fitness enhancing effect in change in the *spot* gene is suggested to be the result of it being deactivated, resulting in bacterial flagella not being developed which in Lenski's artificial settings had no fitness enhancing effect, therefore saving the bacterium some energy. But in none of these cases, although

providing a demonstration of evolution through natural selection acting on random variation, did the observed process result in a design innovation.

§3. *In this section, we will look into the causes and origin of the narrowness of the debate surrounding the theory of natural selection ('God or Darwin'). This narrowness could be due to an erroneous conception of scientists, namely that their naturalistic paradigm is based on observation and reason alone, thereby ignoring the fact that philosophical assumptions are included in their Weltanschauung, which causes the neglect of alternative theories and paradigms that might explain organic phenomena.*

So far, the limited scope observed in the discussion surrounding the theory of natural selection, offering no scientific alternatives to account for living beings and only finding creationism as an adversary, has played an important role. It led to a neglect of sexual reproduction as a focus of criticism of the theory, and to a certain vagueness and woolliness of biological terms and concepts (or of the application of these terms to empirical reality). Moreover, it led to the situation whereby partial validations of the theory – the notion of evolution by common descent – were interpreted as validations of the complete theory including the mechanism behind evolution, while validation for the latter have, in fact, not been sufficiently provided.

This narrowness, however, is more an issue of choice than one of availability. Although there might be no alternatives available for the theory of natural selection which in the eyes of scientists are worth serious consideration, of course many alternatives *do* exist. A myriad of philosophical theories and doctrines have dealt with life, in fact, a study of the organic world has been a major theme in Western philosophy. But somehow these are kept outside of the discussion, and the debate is not taking place under the heading

of philosophy. What is the reason for this? Why are several philosophical doctrines and theories that provide an alternative explanatory framework for living beings mostly ignored in the contemporary discussion, and is the discussion narrowed to a simple ‘God or Darwin’?

To answer this, we have to return to the development of scientific thought, which commenced with the explanation of physical phenomena in the 16th and 17th centuries, but whose advancement outside physical phenomena was until Darwin hindered by the lack of success in explaining biological phenomena. Through his theory, living beings, their complex organization and adaptiveness, were believed to be explainable in a naturalistic way. An important characteristic of this naturalistic paradigm is the idea that it is built exclusively on empirical facts and observation. Scientists in general do not consider themselves metaphysicians, nor would they claim that their ideas and hypotheses are the fruit of philosophical activity (contrary to for example the Greek materialists, whose ideas show significant overlap with those of naturalists). Instead, their views are claimed to be entirely founded on the scientific method, the formulation and testing of hypotheses subject to specific principles of reasoning, and the collection of observable, empirical facts. We find this clearly with the eminent biologists G.G. Simpson, who contrasted science with the ‘Greek way of thinking’.

The actual origin of science in the modern sense involved a revolt against thinking in the Greek way. The Greek way, which became traditional in medieval Europe, was well expressed by Plato, for example, when he said in *The Republic*, ‘We shall let the heavenly bodies alone, if it is our design to become really acquainted with astronomy’. In other words the essence of things was believed to reside in a philosophical ideal, and observation of real phenomena was considered not only unnecessary but also positively wrong. Some five centuries after Plato, Ptolemy

again formalized the Greek way and helped to embed it in Western thought for another 1500 years when he said that the goal of astronomy was ‘to demonstrate that all heavenly phenomena are produced by uniform circular motion.’ Now, that is not physically true, and Ptolemy knew that it was not. He was explicit that his intention was not to explore physical reality. The early astronomers’ only gestures toward reality were attempts to ‘save the appearances’, that is, to try to eliminate obvious contradictions without abandoning their a priori philosophical ideals, such as that of uniform circular motion. ‘Saving the appearances’ was a euphemism for saving the philosophical postulates. Facts were not to be explained, but to be explained away. Science was born when a few thinkers decided that appearances were not something to be saved but to be respected. Those hardy souls – Copernicus, Galileo, and Kepler were among them – eventually abandoned the Greek way of deciding how things ought to be and gave us our way of observing how in fact things *are*. Definitions of science may differ in other respects, but to have any validity they must include this point: the basis of science is observation. [Simpson 1963: p. 81]

And for these scientists observing how in fact things are, and taking observation alone as the basis of science equals with the notion that ‘[...] there is nothing beyond the natural, physical world, no *supernatural* creative intelligence lurking behind the observable universe, no soul that outlasts the body and no miracles – except in the sense of natural phenomena that we don’t yet understand’ [Dawkins 2006: p. 14].

Thus, these scientists claim that there is nothing metaphysical about a naturalist’s approach. The naturalist does not assume anything *beyond* the natural, physical world. He or she takes what is immediately given and observable, and this is sufficient for him or her to come to an understanding of life and the universe. The

supernaturalists, on the other hand, invoke speculative entities and make metaphysical assumptions without any scientific proof, adding another, non-observable element to the immediately given, physical world.

But a serious objection against this notion could be made. Dawkins and Simpson, like the majority of naturalists, *do* make philosophical assumptions. A crucial one is that naturalists assume the objective existence of matter to be independent and ‘outside’ of consciousness. Naturalism starts with the assumption that matter is something objectively and unconditionally given, something that exists outside of the mind. After all, naturalists, and evolutionary biologists in particular, assume the existence of matter prior to consciousness (as in their view conscious life evolved out of non-conscious life, which in its turn evolved out of non-living matter) and consider consciousness (mind) as a function of the brain (matter). Now Dawkins or Simpson would perhaps claim that this notion is nothing but a matter of common sense, logical and self-evident without further need for argumentation or proof, but philosophers have argued that assuming matter outside of the mind is a *metaphysical* assumption that cannot be verified or falsified within the scientific framework. Materialism, as the doctrine is called that upholds this view, is a philosophical standpoint. The reason for this is that observable and empirical facts are always accompanied by another element – the observer. To assume that the former exists independently of the latter is an assumption that can never be scientifically proven, because – by definition – it can never be observed. In the words of philosopher Arthur Schopenhauer (1788–1860), objects are always accompanied by a subject, and to assume the former to exist independently of the latter, cannot in any way be proven or established, least of all by the scientific method. In his words, ‘materialism is the philosophy of the subject who forgets to take account of himself’ [Schopenhauer 1966: p. 13]. So against Dawkins’ claim that he does not assume anything beyond

the natural, physical world, we could claim that he *only* assumes the natural, physical world.

But materialism is not just a philosophical doctrine that transcends observation and scientific reasoning: it is also a controversial one. The German philosopher Immanuel Kant (1724–1804) presented a fundamental and influential criticism of materialism. In his philosophy, Kant makes a distinction between the objects of our experience, phenomena, and objects as they are in themselves, noumena. The former, including the naturalists' observations of the natural, physical world, are conditioned by the forms of our mind, most notably space, time and causality, forms that shape all our observations. The world that lies outside of our experience, the noumenon or the 'thing-in-itself', is unknown to humans. Thus, how things are for us is very different from how things are in themselves. As worded by the 19th century philosopher Friedrich Albert Lange, Kant essentially claims that:

[...] the objects of experience altogether are only *our* objects; that the whole objective world is, in a word, not absolute objectivity, but only objectivity for man and any similarly organized beings, while behind the phenomenal world, the absolute nature of things, the 'thing-in-itself', is veiled in impenetrable darkness. [Lange 2000: p. 156]

Whereas for Kant, space, time and causality are forms of our experience and do not belong to the 'thing-in-itself', materialism treats space, time and causality simply as objective, as something that belongs to the noumenon. While materialism claims that matter exists *outside* and *independent* of the mind, Kant would say that matter, together with its forms time, space and causality, only exists *within* the mind.

In any case, naturalism is more than science: it does not simply entail the rational and systematic analysis of facts and observations,

but is accompanied by implicit – and controversial – philosophical assumptions, such as the objective existence of matter. This assumption is implicit because naturalists seem to be mostly ignorant of them: they praise their method as being based solely on reason and empirical observations, and scorn others who are supposedly led by irrational speculations. But they do not realize that through their materialistic assumptions they have entered the realm of metaphysics, where such assumptions have been proven controversial and certainly not a matter of course. Dawkins *et al.* erroneously assume that the path of science, the method of empirical observations and reason, has culminated in naturalism, and that naturalism is the fruit of hard facts accompanied by reason, contrary to speculation, beliefs and superstition. Their mistake lies in the fact that science is not the same as naturalism, that the step from observing the natural, physical world to assuming that it exists outside of the observer is a philosophical, not a scientific, one. They are thus unaware that they have unconsciously entered the realm of philosophy, and thus overlooked that it is in this domain where the debate around the theory of natural selection should take place. Instead, the debate takes place on the level of ‘science vs. religion’, or ‘reason vs. faith’, with creationists as the most dominant representatives of the latter category.

Thus, our contemporary intellectual debate is dominated, on the one hand, by naturalists, often evolutionary biologists, who claim they recognize facts and nothing but facts, but have unconsciously entered the realm of philosophy, and on the other hand, by (Christian) supernaturalists, often inspired by dogmas that are unacceptable to the scientific mind. Or, as in Arthur Schopenhauer’s reflection (whose words still sound remarkably relevant after more than 150 years):

Aut catechismus, aut materialismus ist ihre Losung [...]. Daß es einen Plato und Aristoteles, einen Locke und zumal einen Kant

gegeben hat, haben sie vielleicht einmal auf der Schule gehört, jedoch diese Leute, da sie weder Tiegel und Retorte handhabten noch Affen ausstopften, keiner näheren Bekanntschaft wert gehalten; sondern, die Gedankenarbeit zweier Jahrtausende gelassen zum Fenster hinauswerfend, philosophieren sie aus eigenen reichen Geistesmitteln auf Grundlage des Katechismus einerseits und der Tiegel und Retorten oder der Affenregister, andererseits, dem Publikum etwas vor. Ihnen gehört die unumwundene Belehrung, daß sie Ignoranten sind, die noch Vieles zu lernen haben, ehe sie mitreden können. [Arthur Schopenhauer 1986: p. 302]⁵

Today's credo is *aut catechismus, aut materialismus* (either catechism or materialism), but this is a grave oversimplification of the discussion. Assuming naturalism as the fruit of observation and reason alone, and setting it off exclusively against the other dominant world-view in the Western world, creationism, leads to a distortion of the debate. As the conclusions of this study will indicate, the truth might very well be nearer to *nec catechismus, nec materialismus* (not catechism nor materialism), and it might be in the realm of philosophy where we have to explore alternatives to explain the design and idiosyncrasies of living beings.

5 Either catechism, or materialism is their solution. They may perhaps have heard at school of the existence of a Plato, Aristotle, Locke, and especially of a Kant; but as these people never handled crucibles and retorts or stuffed a monkey, they do not esteem them worthy of further acquaintance. Instead, they toss the intellectual labor of two thousand years out the window and treat the public to a philosophy concocted out of their own rich mental resources, on the basis of the catechism on the one hand, and of that of crucibles and retorts or the catalogue of monkeys on the other. They ought to be told in plain language that they are ignoramuses, who have much to learn before they can be allowed to have any voice in the matter [translation JVR].

II The Inability of the Theory of Natural Selection to Explain Sexual Reproduction

... vagueness,
that common affliction of biological terms.

— C.S. Pittendrigh

§1. *In this section we will see that Darwin's interpretation of the principle of natural selection as outlined in The Origin of Species cannot explain sexual reproduction since it assumes its existence. We will define Darwin's interpretation as insufficient in the sense that it assumes certain biological elements, viz. the existence of living beings with their striving for survival and reproduction.*

The theory of natural selection has been compared to Boyle's law, in the sense that it presupposes certain fundamental characteristics of living beings, rather than explaining them.⁶ Just as Boyle presupposes the existence and causal powers of the matter constituting gases, in the same way Darwin, in his explanation of the evolutionary process of adaptation, presupposes certain features of living beings. We can see this clearly by analyzing Darwin's most influential work, *The Origin of Species* (1859). As we have seen in the introduction, Darwin starts out with a description of a series of observations of the natural world. One such observation is the existence of variation in nature, another is the existence of a struggle for survival. The struggle for survival itself rests on the fact that there is a tendency of organic beings to strive to increase their numbers

6 See, for example, Barham [2002] and Walsh [2000].

to the maximum, and that limited resources cannot possibly support all offspring. These observations are presented as conditions which, if present, automatically lead to an evolutionary process of adaptation through natural selection. The evolutionary process of adaptation follows as the inevitable and logical consequence of this set of conditions or premises.

What is thus *assumed* in Darwinian explanations is that organisms tend to increase their numbers to the maximum, which implies the assumption of the existence of organisms that strive for survival and reproduction. What is *explained* is the evolutionary process of adaptation leading to design, but not living beings with their striving towards survival and reproduction themselves. The latter is presupposed. Modifications and adaptation of living beings are explained, but only *by presupposing* living beings striving for reproduction and survival. In essence, the theory proposes an explanation of the modification of organisms through the process of adaptation, but not the organisms themselves. It focuses on the differences between organic beings, and assumes, first, the organisms themselves, and, second, what they share, namely their striving towards survival and reproduction.⁷ The explanation of the evolutionary process of adaptation through natural selection as outlined in *The Origin of Species* is schematically shown in Figure 2.

The *explanans* refers to those elements that serve as conditions for the *explanandum*, the phenomenon to be explained. So central to Darwin's explanation of the evolutionary process of adaptation is that he takes one aspect of living beings, viz. individual organisms with their striving towards survival and reproduction, as a condition for what he aspires to explain, viz. the evolutionary

⁷ This conclusion relates to the ideas expressed in *The Origin of Species*. Both in earlier as well as in later works, however, Darwin did suggest some explanations for sexual reproduction which will be dealt with later. So the criticism of Darwin's explanatory framework in that he presupposes sexual reproduction relates to the ideas expressed in his most influential work, *The Origin of Species*.

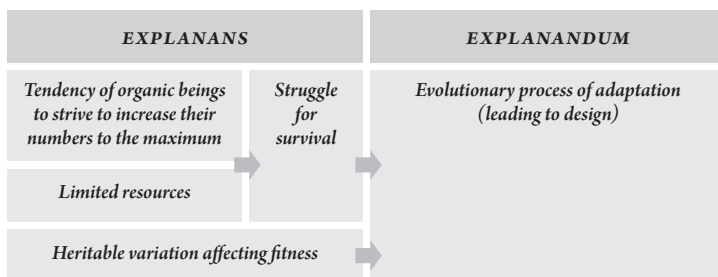


Figure 2. Darwin’s explanation of the evolutionary process of adaptation as described in *The Origin of Species*.

process of adaptation, a process which stands at the basis of the design of organisms.⁸

The use of the word ‘fitness’, a central concept within the theory of natural selection, reflects this theory’s nature. Although fitness is an ambiguous term (see Dawkins [1982] for a list of meanings attached to the term), it predominantly refers to the potential of

⁸ This explanation follows to an extent the so-called Deductive-Nomological model developed by Hempel and Oppenheim [Hempel and Oppenheim 1948; Hempel 1965]. This model states that scientific explanations consist of deductive arguments whereby the *explananda* always follow as a logical consequence of the one or more *explanantia*. Currently, this model is not widely supported amongst philosophers of science. Criticism targets the claim that this model states necessary conditions for successful explanations (as explanations can be put forward that do not follow this model), and the claim that the *explanans* must contain at least one law of nature (as there is no general consensus on the definition of ‘lawhood’, see Woodward [2011]). However, this model is not proposed as a model for Darwinian explanations but solely used to analyze Darwin’s explanation of the evolutionary process of adaptation, and for this reason this criticism does not concern us here. The explanatory framework for features or traits adhered to in this study (and which will be further outlined in the course of this work) is based on the notion that features or traits – as adaptations – can exclusively evolve for the stability or replication of a replicator of which it is part, and thus that these traits or features can be shown to benefit the stability or replication of that replicator.

living beings to survive and reproduce, and in that sense serves as explanatory ground for traits and features. For example, we find Darwin explaining that ‘an accidental deviation in the size and form of a body [...] might profit a bee or other insect so that an individual so characterised would be able to obtain its food more quickly, and so have a better chance of living and leaving descendants’ [Darwin 1968: p. 141]. So the deviation in size and form of the bee is explained by its fitness-increasing effect (it obtains its food more quickly, and thus has a better chance of living and leaving descendants). Thus traits (like longer legs, better eyesight or more colorful flowers) are explained through the already-assumed striving for survival and reproduction of living beings; the effect of such a trait is that the individual is better at surviving and reproducing than an individual without that trait, which consequently results in the fixation of this trait within the population.

In light of this analysis, it is also important to mark the difference between the preservation of traits and the survival of organisms within Darwin’s explanatory framework. Whereas preservation relates to traits or features, and thus to entities that are preserved over the generations and during the course of evolution, survival relates to organisms, and only concerns the survival within a lifespan. An organism has no evolutionary continuity. In the Darwinian context, an organism survives if it lives long enough to reproduce; destruction is in any case unavoidable (the use of the term survival in the context of organisms is therefore confusing and misleading). Traits, on the other hand, are potentially immortal, as they can spread through the population, and can endlessly be passed on from generation to generation. Moreover, traits or features are *explananda*, the very thing Darwin set out to explain. The survival of organisms, on the other hand, serves as *explanans*, as one of the conditions for evolution to take place. These two phenomena – survival of organisms and preservation of traits – are thus obviously different phenomena, with different places within the theory

of natural selection. In this light, it is remarkable that even Darwin did not clearly make this distinction, or at least did not consistently apply the terminology. In some passages of the *Origin of Species*, preservation and survival refer to modifications of qualities (traits), and in other passages to individuals, or even races. In some passages we find 'that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind' [Darwin 1968: pp. 130–131], and 'this preservation of favourable variations and the rejection of injurious variations, I call Natural selection' [Darwin 1968: p. 131]. But then a little further on we read, 'I can under such circumstances see no reason to doubt that the swiftest and slimmest wolves would have the best chance of surviving, and so be preserved or selected [...]' (p. 138) and, 'Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications, each profitable to the preserved being [...]' [Darwin 1968: p. 142]. Here, Darwin uses the term preservation for both organisms and modifications, despite their profoundly different role within the theory. Paradoxically enough, we find the most unusual subject of preservation within the subtitle of *The Origin of Species*, 'the preservation of favoured races in the struggle for life', a reference which does not reappear in the work. Thus, Darwin mixes up concepts and terms with distinct roles within the theory of natural selection. So we see that the earlier described frequently observed vagueness that accompanies biological terms has already affected the author of *The Origin of Species* himself.

We have seen that Darwin's interpretation of the principle of natural selection necessarily leaves sexual reproduction unexplained. We can describe this aspect of Darwin's theory in more general terms. Darwin's explanation of biological phenomena can be called *insufficient* in the sense that it explains the design through an evolutionary process of adaptation of certain biological features *by*

assuming the existence of other biological features, whose design can therefore not be accounted for. In that context, explanations through the theory of natural selection could be called *sufficient* when explanations through natural selection do not assume the existence of any biological features (after all, the theory has been specifically conceived to provide an explanation for these). In our search for an explanation for sexual reproduction through the theory of natural selection, we therefore first need to find an interpretation of the mechanism that provides such a sufficient explanation, and it is in that light that we will look at Dawkins' reading of natural selection.⁹ The focal point of this investigation will be the unit of selection, the unit adaptations exist for the benefit of. As we will establish in the next section, the potential sufficiency of explanations through the theory of natural selection in the sense as described above will depend on what is considered the unit of selection, namely to what extent this unit can be seen as something which is in its entirety shaped through (can be seen as the complete product of) the principle of natural selection.

§ 2. Interpretations of the mechanism of natural selection differ on what is considered to be the unit adaptations evolved for the benefit of, the so-called unit of selection. In this section, we distinguish between levels within the hierarchy of life that can be subject to the principle of natural selection, and investigate which of these can be seen as a (complete) product of the principle. Only units of selection that are of the latter

⁹ The definition 'sufficient explanation' should not be confused with 'complete' or 'ideal' explanations, as the definition does not imply that the conditions for the evolutionary process of adaptation to operate should be known a priori or in terms of some fundamental physical theory, a demand which is generally not considered necessary for a proper scientific explanation (see Woodward [2011] for a detailed treatment of this issue). 'Sufficient explanation' means that no *biological* aspects should be assumed in the explanation of the evolutionary process of adaptation.

category will render explanations through the principle of natural selection sufficient in the sense explained above.

In Darwin's interpretation of natural selection, organisms are considered the unit that adaptations evolve for the good of. Quoting Darwin again:

Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. [Darwin 1968: p. 115]¹⁰

The question on which level within the biological organization selection acts (which level is the unit of selection) is of pivotal importance. As adaptations are explained by reference to their selective advantage, it is crucial to clearly define *for whose* advantage adaptations are selected. There is no such thing as an adaptation without a unit for which this adaptation evolved. But throughout the history of Darwinism, the question regarding the level on which selection acts, a debate known as the unit of selection discussion, has been a

¹⁰ In this study we have focused on Darwin's idea, as expressed in the *Origin of Species*, that adaptations evolve for the benefit of the organism, but in some other works, Darwin incidentally proposed the notion of group selection to account for certain specific features (we will have more to say about group selection in a later section of this study). In *The Descent of Man, and Selection in Relation to Sex* (1871), Darwin proposed group selection to account for the existence of 'morally upright behavior', which does not have an obvious advantage for the people bearing it but does provide advantage for the group these individuals belong to [Wilson and Wilson 2008]. But apart from some exceptions concerning man, Darwin 'opted firmly for hypotheses supposing selection always to work at the level of the individual rather than the group' [Ruse 1980: p. 615].

subject of a fierce debate.¹¹ Ever since Darwin, various levels have been proposed: from organisms (Darwin himself), to groups and species, and all the way down to the gene.

The controversy around establishing the unit of selection arises from two circumstances: first, because various levels in the hierarchy of life can be subject to the principle of natural selection, and second, because the nature of adaptations found in living beings does not unambiguously point at one single unit.¹² To start with the first, Darwin identified heritable variation and the struggle for existence as conditions for natural selection. However, as has been claimed by Dennett [1995] and others, these conditions are not exclusively satisfied by biological entities. Any entity that finds itself in these conditions will be subject to natural selection, conditions which Dennett words as follows:

- Variation: there is a continuing abundance of different elements;
- Heredity or replication: the elements have the capacity to create copies or replicas of themselves;
- Differential ‘fitness’, the number of copies of an element that are created in a given time varies depending on interactions between the features of that element and features of the environment in which it persists. [Dennett 1995: p. 343]

All entities that have these characteristics will be subject to Darwinian selection leading to evolution. And within the hierarchical organization of the biological world, more levels exist that actually fulfill the conditions for natural selection to take place. Genes, cells, organism, they all (to some extent) reproduce and have differential fitness, which can make them subject to natural selection.

¹¹ See for example Hull and Ruse [1998]: pp. 149–152.

¹² See Okasha [2006] for an elaborate analysis.

The second factor that gives rise to the unit of selection discussion is that adaptations do not unambiguously point to a specific level. Natural selection leads to the evolution of traits – adaptations – that enhance the chance of survival and reproduction of entities. But not all traits point to the same level. Some adaptations appear to have evolved for the benefit of the organism, whereas some of them, such as altruistic behavior, seem to point at a group or population.

However, in light of the before-mentioned insufficient nature of Darwin's explanations through the principle of natural selection, an important additional element has to be introduced when considering the unit of selection. It is one thing to be *subject* to the principle of natural selection, but quite another to be a complete *product* of that mechanism. All entities that vary, reproduce differentially as a result of that variation and beget offspring that are similar to them, can be subject to natural selection, and organisms indeed fulfill those conditions (as also other levels in the hierarchy of life, and even non-biological entities). And if one defines the unit of selection as the level within the biological organization that can be *subject* to the principle of natural selection, then indeed the organism is a realistic candidate. But not all aspects of organisms, as was shown earlier, can be explained by that principle; the striving towards survival and reproduction of the organism serves as *explanans* for the principle of natural selection, and therefore cannot be explained by it. And thus, the organism cannot be seen as a complete product of the principle of natural selection, which amounts to saying that explanations through that principle are insufficient.

The difference between the potential of an entity being *subject* to the principle of natural selection and being the complete *product* of that principle is even more apparent with the non-biological entities that, according to the logic of Dennett, can be subject to natural selection. In *The Selfish Gene*, Dawkins lists a few potential

candidates: tunes, ideas, catch-phrases, clothes fashion, ways of making pots or building arches [Dawkins 1976: p. 206]. They all make copies of themselves and exhibit a sufficient degree of variation that affects fitness, and therefore will be subject to the principle of natural selection – ergo, evolve. Let us take making pots as an example. Knowledge of making pots gets transferred from master to apprentice, but in some cases an apprentice will misunderstand his teacher, or perhaps he is forced to use different materials than his master. So there will be variation in the way of making pots. Let us assume one apprentice changes the temperature of the oven, or uses clay of a different type. These changes may lead to an improvement – more solid pots, for example. If so, this way of making pots will then have a better fitness, what is to say that, *ceteris paribus*, this method will be picked up by more people than the older method which led to less solid pots. And this process will continue, as this new method will be transferred with variation, etc. etc. Here, it is indeed legitimate to claim that ways of making pots are subject to the principle of natural selection, which means that through a process of accidental change, inheritance and differential fitness, the art of making pots will change over time, and branch out into different ways of making pots. Ways of making pots is *subject* to the principle of natural selection, but it is another thing to say that ways of making pots in itself and as a phenomenon is the *product* of natural selection. Ways of making pots primarily exists in the minds of human beings, and their existence does not make sense as independent entities (human beings in themselves might also be subject to the principle of natural selection, but on a completely different level). The art of making pots is a human activity, and originated and gets propagated in human beings only. It can be *changed* by the principle of natural selection, where alterations of the methods, materials used, etc. can occur, but the origin of pot making has to be sought somewhere else.

§3. *Dawkins' concept of the replicator can be interpreted as an attempt to arrive at a unit of selection that can be seen as a complete product of the principle of natural selection.*

In Darwin's interpretation of the principle of natural selection, the organism was denoted the unit of selection. We concluded that this unit might be subject of the principle of natural selection, but cannot be seen – in its entirety – as its product. The striving towards survival and reproduction of organisms is assumed, and therefore it is not explained. Being at the wrong side of the explanatory equation, the organism as unit of selection leaves a non-explained residue. A question that follows from this, therefore, is whether we can identify a unit of selection that *can* be seen as a unit that is subject to the principle of natural selection, as well as seen as a product of that principle. That would secure a sufficient explanation of living beings through the principle of natural selection, instead of an insufficient one in the sense that biological features are assumed. It is in this light that we will explore Dawkins' concept of the replicator.

In Darwin we find the organism as the unit of selection, whereas Richard Dawkins proposes a fundamentally different unit. Dawkins belongs to a group of scientists (consisting among others of George C. Williams and John Maynard Smith) that objects to notions that adaptations exist for the benefit of the organism, groups or even species. These biologists maintain that natural selection cannot or rarely leads to adaptations that exist for the benefit of these levels. Building on the ideas of George C. Williams, Dawkins claims that adaptations can only exist for a chemical entity with specific features and characteristics, an entity which he summarizes as an active replicator with sufficient amount of fecundity, copying fidelity and longevity. We have elaborately analyzed this concept in the introduction of this study.

Now Dawkins' definition of the unit that is subject to the principle of natural selection – an active replicator with a sufficient degree of longevity, fecundity and copying fidelity – falls within the general categories of Dennett's abstract definition of replication, heredity and differential fitness, but with an important distinction. With Dawkins, the mechanism of natural selection solely rests on chemical and physical principles, as the *origin*, *permanence* and *replication* of the unit of selection are explainable by elementary chemical and physical processes. Dawkins' fundamentally different approach from that of Darwin in determining the unit of selection can be discerned when we again take a look at his reasoning in *The Selfish Gene*.

Darwin's 'survival of the fittest' is really a special case of a more general law of *survival of the stable*. [...] Sometimes when atoms meet they link up together in chemical reaction to form molecules, which may be more or less stable. [...] If a group of atoms in the presence of energy falls into a stable pattern it will tend to stay that way. The earliest form of natural selection was simply a selection of stable forms and a rejection of unstable ones [...]. At some point a particularly remarkable molecule was formed by accident. We will call it *the Replicator*. It may not necessarily have been the biggest or the most complex molecule around, but it had the extraordinary property of being able to create copies of itself. [...]. Think of the replicator as a mold or template. Imagine it as a large molecule consisting of a complex chain of various sorts of building block molecules. The small building blocks were abundantly available in the soup surrounding the replicator. Now suppose that each building block had an affinity for its own kind. Then whenever a building block from out in the soup lands up next to a part of the replicator for which it has an affinity, it will tend to stick there. The building blocks which attach themselves in this way will automatically be arranged in

a sequence which mimics that of the replicator itself [...]. This process could continue as a progressive stacking up, layer upon layer. This is how crystals are formed. On the other hand, the two chains might split apart, in which case we have two replicators, each of which can go on to make further copies. [Dawkins 1976: pp. 13–17]

The unit of selection in Darwin's version of the theory, as we have seen, was the organism with its striving for survival and reproduction, and is as such something which *itself* requires an explanation as biological phenomenon. Biological features are characterized by design, and the theory of natural selection is specifically invoked to account for this design. And if some biological features serve as the condition for the explanation of other biological features, the explanation through the theory is insufficient. Dawkins' replicators, on the other hand, are built up from stable molecules whose origin (e.g. under the influence of an undirected energy source such as ultraviolet light or lightning occurring in the primeval soup) as well as its permanence (through chemical bonds) can be physically and chemically accounted for. Moreover, the process of replication is based on the *chemical* – not biological – phenomenon of affinity among different groups of chemical compounds.¹³ Dawkins' analysis of the unit of selection and his objection to the organism as unit can be seen as an implicit attempt to overcome the previously described gap in Darwin's account of the principle of natural selection. It is implicit because Dawkins never explicitly mentions the nature of the gaps in Darwin's explanatory framework, but through the build-up of his argument he clearly describes the origin, permanence and replication of the unit of selection as a physical and chemical phenomenon.

Dawkins ensures that the unit of selection can itself be seen as something which is completely built up through the principle of natural selection, something which in all its aspects can be regarded

as the *product* of that principle. The unit of selection, by definition, plays an essential role in the Darwinian explanatory scheme, and if this unit cannot be seen as a product of natural selection, the entire

13 This study will focus on the problems to associate sexual reproduction with the concept of the replicator, but there are more fundamental difficulties with this interpretation of the principle of natural selection that fall outside the scope of this work. An example of such a problem is the presentation of the iterative process of replication as a purely chemical phenomenon. The process of replication is presented by Dawkins as a purely chemical and physical phenomenon. As replication precedes the possibility for biological features (adaptations) to evolve, it cannot depend on these biological features themselves. It therefore must have a chemical or physical, as opposed to a biological basis. But at the same time, it is hard to imagine how this repetitive process could have this physical or chemical basis. Creating copies depends on the repetitive process of the binding of elements, and subsequently on their splitting apart. But natural laws will direct processes in either one direction – either binding based on affinity, or splitting based on repulsion. So it's either way, which makes it difficult to imagine how the process of replication can occur in a systematic, repetitive way. In this context, Dawkins' claim in *The Selfish Gene* that 'two chains might split apart' [Dawkins 1976: p. 17] is a rather poor explanation. This problem also surfaces in the attempt to trace the origin of life. In organisms we find an interdependency between DNA and proteins, as DNA does not replicate and translate (via RNA) into proteins without proteins themselves, and proteins do not come into existence without DNA. As replication is accomplished in modern cells through the cooperative action of proteins and nucleic acids, this poses challenges when one wants to reconstruct the origin of life, and determine what the first self-replicating molecule was, a molecule that served as both information and function, both genotype and phenotype. According to scientific literature, several lines of evidence suggest that a primordial form of RNA preceded DNA, as it is simpler (single stranded instead of double stranded in case of DNA), and RNA can be read and replicated directly, contrary to DNA that needs to unzip the two strands in order to read or replicate the nucleotide information. Moreover, RNA can take up many structural forms, and in some of those forms can act as an enzyme, and some RNA molecules are known that act as RNA polymerases, catalyzing the replication of RNA. However, no RNA has been found yet that could catalyze its own replication [Ridley 2004: p. 530].

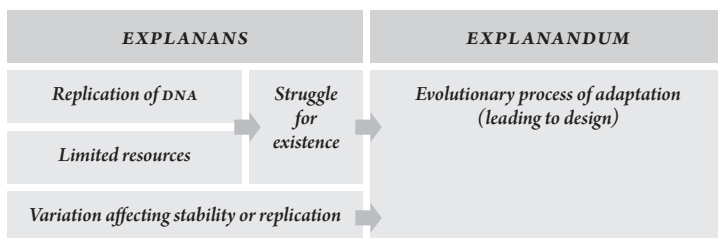


Figure 3. Dawkins' explanation of the evolutionary process of adaptation.

Darwinian explanation is insufficient. By transferring the unit of selection to a level that can be purely accounted for as a physical or chemical (vs. biological) phenomenon, Dawkins' unit can be seen as something that is not only subject to the principle of natural selection, but also as a complete product of it (see also Figure 3).

This greatly enhances the value of the theory of natural selection, and is a crucial step in arriving at a sufficient explanation through natural selection, accounting for sexual reproduction as well. Dawkins' description of the replicator as unit of selection is a correct theoretical model of an evolutionary process of adaptation – in fact the only one proposed – when one aims to arrive at sufficient explanations of design through an evolutionary process of adaptation. But the aim of this study is to show that the problem with this interpretation is that this model cannot be successfully applied to empirical reality due to the existence of sexual reproduction. The problem with Dawkins' interpretation of the principle of natural selection is therefore not of theoretical nature, but resides in the impossibility to fit actual living beings within this theoretical framework. Living beings do not behave according to Dawkins' model.

We will establish this conclusion in several ways. First, we will analyze how Dawkins, *et al.*, apply this model to empirical reality, which led to the idea that the gene is the unit for which adaptations evolved (the so-called gene-centered view of evolution, also

referred to as genic selectionism). We will see that this view is wrong, as it is based on an erroneous assumption about the relation between the evolutionary process of adaptation, adaptations and the unit of selection. Next, we will analyze the ideas of Jacques Monod, whose version of the theory of natural selection shows great overlap with that of Dawkins, but who is also incapable of giving a satisfactory translation of this model to empirical reality. Third, having established that it is sexual reproduction that causes these problems, we will attempt to explain sexual reproduction as an adaptation using our renewed insights into the relation between the evolutionary process of adaptation, adaptations and the unit of selection. We will conclude that it fails since sexual reproduction exhibits what we will denote by the term 'creative teleonomy'. We will end with analyzing alternatives for the unit of selection, – groups or species – and conclude that they, controversial as they are in themselves, are equally inadequate in providing an explanation for sexual reproduction.

§ 4. In this section we see that the gene-centered view of evolution, the idea that the gene is the unit of selection, is wrong, as it rests on an erroneous assumption about the relation between the evolutionary process of adaptation, adaptations and the unit of selection.

Dawkins' abstract description of the unit of selection as replicator was called 'an act of metaphysics' by the philosopher of science David Hull, in the sense that Dawkins 'provides a general analysis of replicators and leaves it a separate issue which entities in the empirical world happened to have the required characteristics' [Hull 1984: p. 150]. However, Dawkins follows his theoretical analysis by an empirical investigation. He turns his eye to the empirical world to determine which levels correspond to his theoretical description. The method he follows here is one of elimination. Various levels within the organism are considered, and those eliminated that

do not sufficiently conform to his description of the active replicator with a sufficient amount of fecundity, longevity and copying fidelity.

To start with, Dawkins argues that in sexually reproducing species, *individual organisms* are unlikely candidates to serve as units of selection. Individuals are temporary aggregations or federations of genes and are not stable through evolutionary time. In every generation, the genetic content of organisms is reshuffled, which make them not conform to the requirement of longevity. Neither does Dawkins consider *groups* (groups of organisms) unitary enough to be 'selected' in preference to another population. They may last a long while, but they are constantly blending with other populations and so losing their identity [Dawkins 1982: p. 100]. Thus, groups as well as individual organisms are not adhering to the 'sufficient amount of longevity' requirement.

In sexually reproducing species, the individual is too large and too temporary a genetic unit to qualify as a significant unit of natural selection. The group of individuals is an even larger unit. Genetically speaking, individuals and groups are like clouds in the sky or dust-storms in the desert. They are temporary aggregations or federations. They are not stable through evolutionary time. [Dawkins 1976: p. 36]

What about *species* as unit of selection? Whereas Dawkins claims that species do exhibit greater longevity, they lack another essential characteristic, namely replication with a sufficient frequency. As Dawkins explains:

[...] the putting together of a certain quantity of evolutionary change demands a certain minimum of selective replicator-eliminations. Whether the replicators that are selectively eliminated are genes or species, a simple evolutionary change requires only

a few replicator substitutions. A large number of replicator substitutions, however, are needed for the evolution of a complex adaptation. [Dawkins 1982: p. 106]

And Dawkins claims that the frequency of replication in species, or more specifically, the gene pool of a reproductively isolated group, is simply too low.

[...] there may be a case for regarding the gene-pool of a reproductively isolated group, such as a species, as a replicator. If we provisionally accept the logic of this case, we can visualize evolution directed by selection among such replicators, but I have [...] concluded that this kind of selection is unlikely to explain a complex adaptation. [Dawkins 1982: p. 109]

So if not sexually reproducing organisms, groups or species, what unit corresponds with the description of a replicator with a sufficient amount of fecundity, copying fidelity and longevity? Here, a fundamental distinction becomes evident between asexual and sexual reproduction. Following Dawkins' analysis, if there is no sex, we may treat the entire genome of an asexual organism as a replicator. In asexually reproducing organisms, the entire genome may qualify as a replicator that makes copies of itself with a sufficient amount of permanence, copying fidelity and fecundity, and therefore serves as the unit adaptations exist for the good of. In those cases in which sex but no chromosomal crossover (the shuffling of genetic material between chromosomes through homologous recombination) occurs, entire chromosomes might serve as units of selection, and adaptations could be seen as being for the good of the preservation of the chromosome. However, as Dawkins maintains, in sexually reproducing organisms the only candidate that can serve as a unit of selection is the gene. It is neither the

organism, nor any other candidate except the small genetic fragment that qualifies as a replicator, hence, as unit of selection.¹⁴

The genes are the immortals, or rather, they are defined as genetic entities which come close to deserving the title. We, the individual survival machines in the world, can expect to live a few more decades. But the genes in the world have an expectation of life which must be measured not in decades but in thousands and millions of years. [Dawkins 1976: p. 36]

The level within sexually reproducing organisms that sufficiently adheres to the description of active replicators with a sufficient amount of fecundity, copying fidelity and longevity and can therefore be seen as the unit of selection, is the small genetic fragment called the gene. It is not the individual, groups nor species because these lack elementary features required to serve as replicators, such

14 In the description of the unit of selection as 'active replicator with a sufficient amount of fecundity, copying fidelity and longevity', we have until now ignored one other characteristic Dawkins referred to, namely 'germ-line' (the complete description being 'an active, germ-line replicator with a sufficient amount of fecundity, copying fidelity and longevity'). Germ-line means that the replicator must be one that is potentially the ancestor of an indefinitely long line of descendant replicators, as opposed to dead-end replicators, those which do not have this potential. This distinction is clearly inspired by the empirical fact that most of the genes in organisms are dead-end: genes in somatic cells cannot be transferred to the next generation, and therefore cannot undergo an evolutionary process of adaptation. Their fate is sealed, so to say, within the organism. Only genes in gametic cells (reproductive cells that fuse during fertilization, and thus form the basis of the new organism in sexual reproduction) can potentially be transferred to the next generation, and thus undergo this evolutionary process of adaptation, i.e. are germ-line. As this aspect of the replicator has no bearing on the point that will be made in this study, we will continue to use the definition 'active replicator with a sufficient amount of fecundity, copying fidelity and longevity'.

as the frequency of replication and longevity. It is only the gene that must be seen as an active replicator with a sufficient amount of fecundity, copying fidelity and longevity, and therefore the unit which adaptations evolved for the benefit of.¹⁵

George C. Williams, in his groundbreaking work *Adaptation and Natural Selection* (1966), reaches the same conclusion in a more technical way:

The essence of the genetical theory of natural selection is a statistical bias in the relative rates of survival of alternatives (genes, individuals, etc.). The effectiveness of such bias in producing adaptation is contingent on the maintenance of certain quantitative relationships among the operative factors. One necessary condition is that the selected entity must have a high degree of permanence and a low rate of endogenous change, relative to the degree of bias [...]. Acceptance of this theory necessitates the immediate rejection of the importance of certain kinds of selection. The natural selection of phenotypes cannot in itself produce cumulative change, because phenotypes are extremely temporary manifestations. [...]. The same argument also holds

¹⁵ While some biologists unambiguously point to the gene as unit of selection, they still sometimes refer to 'individual selection'. We see this, for example, with Maynard Smith, an ardent supporter of the gene-centered view on evolution, when he writes, 'A [...] way of classifying selective forces is in terms of "group" and "individual" selection. Thus, natural selection will operate on any set of entities with the properties of multiplication, heredity, and variation. If the entities in question are individuals, we can speak of "individual selection"; it is this type of selection with which the vast majority of evolution theory is concerned' [Maynard Smith 1978: pp. 1–2]. This terminology is confusing as it can be associated with Darwin's interpretation of the principle of natural selection whereby adaptations evolve for the good of individual organisms proper. For this reason, the terminology 'individual selection' will be avoided in this study, and the terms 'genetic selectionism' or 'the gene-centered view of evolution' are used instead.

for genotypes. [...] Only in species that can maintain unlimited clonal reproduction it is theoretically possible for the selection of genotypes to be an important evolutionary factor. [...] It is only the meiotically dissociated fragments of the genotype that are transmitted in sexual reproduction, and these fragments are further fragmented by meiosis in the next generation. If there is an ultimate indivisible fragment it is, by definition, 'the gene' [...]. [Williams 1966: pp. 22–24]

Translated into less technical terms, some entities have a greater chance to survive than others. For the existence of these different survival rates to permit the evolutionary process of adaptation, some conditions have to be met. One of them is that these entities must have a sufficient amount of permanence over time. After all, the entity cannot undergo the process of adaptation if this entity is ephemeral. This condition implies that selection cannot work on certain entities, including phenotypes (a term used to denote the morphology of an organism) and genotypes (a term meaning the genetic make-up of an individual organism), as these are temporary manifestations. At best, only the genotypes in asexually reproducing species can be seen as units of selection. Meiosis is an elementary process in sexual reproduction whereby gametes are produced (sperm cells in males, and egg cells in females that will form the zygote after fertilization), and in this process the genetic make-up of an organism is sampled and recombined. Therefore only the genetic entities that are transmitted in the process of meiosis can be seen as units of selection, as these are the only ones that are indivisible, and therefore have enough permanence. These genetic entities are called the genes.

A few things can be said about the choice for the gene. First, Dawkins and Williams do not categorically exclude all alternatives. Groups or species selection, for example, is considered unlikely,

not theoretically impossible. We will deal with these alternatives in more detail later, but at this stage we will first analyze the level that was seen as the most logical unit of selection in their view, the gene.

Next, it must be noted that a closer look at this concept of the gene reveals some conceptual problems. In the process of replication, a gene made out of specific molecules is serving as mold or template for the creation of a gene made out of other molecules, which must therefore in that sense be seen as *another* gene. Thus, Dawkins' gene that shows continuity over time is not defined by its substance, or material make-up. One could possibly define this gene in terms of a structure, or form, but questions can be raised how a 'structure' or 'form' can be an entity that plays such an essential role within the theory of natural selection, and how for such an entity adaptations can evolve for the benefit of. Thus although deeper philosophical problems lie behind the concept of 'the gene', in this study we will continue with its intuitive notion as used by evolutionary biologists.

However, the main comment that must be made about the gene-centered model of evolution is that it is – to put in bluntly – wrong. More specifically, while Dawkins might rightfully claim that genes are the most appropriate units within sexually reproducing organisms that can be seen as active replicators with a sufficient amount of fecundity, longevity and copying fidelity, this does not imply that genes can subsequently be appointed as the units of selection of sexually reproducing organisms in the sense that the design of organisms can be explained through the principle of natural selection acting on genes.

In a way, this conclusion is already implicit in Dawkins' definition of the replicator. The replicator is the unit that undergoes the evolutionary process of adaptation, it is the replicator therefore that is designed through natural selection. The fact that the sexually reproducing organism is not a replicator therefore already

implies that its design cannot be accounted for by natural selection. But we can illustrate it more clearly by again looking at the process of adaptation, adaptations and the replicator, and precisely map the relationship between them. Adaptation can refer to the *process* whereby an entity becomes better suited to its habitat, or to particular *features* that evolved as a consequence of that process. Dawkins' concept of the replicator allows us to describe this process, and the features evolving as a consequence of it, more precisely. Let us imagine a replicator with a number of base pairs, where some sequences of base pairs lead, through their phenotypic expression, to an increased frequency of this particular replicator.¹⁶ For example, the phenotypic expression of a sequence leads to more efficient replication, or results in a better stability of that sequence in relation to other replicators through the creation of a protective wall of proteins [Dawkins 1976: p. 21]. Although these sequences only form a very small subset of the total number of possible sequences, natural selection explains how, to use Dawkins' phrase [1996], 'Mount Improbable' can be climbed, i.e. how eventually these highly specific sequences will evolve through the evolutionary process of adaptation. Through the iterative process of replication with a sufficient amount of fecundity, longevity and copying fidelity, new varieties will continuously emerge and natural selection will eliminate those varieties that are detrimental, and retain those varieties that are beneficial to the survival (stability or replication) of the replicator, leading to the evolutionary process of adaptation. The principle of natural selection explains design through the evolutionary process of adaptation, but it is crucial to note that this adaptation refers to adaptation *of the replicator*.

¹⁶ The phenotypic expression is the translation of a sequence of base pairs into the building blocks of the organism's phenotype, or morphology. In organisms this is the translation of the DNA sequence into proteins, see also the introduction of this work.

It is the replicator that adapts, and therefore it is *on the level of this replicator* that we can account for design through the principle of natural selection.

Within the phenotype, certain features can be distinguished that perform certain functions. These phenotypic traits are the expression of certain regions, or parts of the replicator's DNA. Features that evolved through natural selection we call adaptations. Thus, adaptations are the expression of parts of the replicator's DNA, and are selected due to their contribution, via their phenotypic expression, to the stability or replication of the replicator. This means that adaptations are always directed at the stability or replication (survival) of the replicator, which constitutes their selective value.

Dawkins' principle of natural selection also implies that the design exhibited by replicators is ultimately shaped by random mutations. The source of the specific sequence of DNA molecules are undirected changes (such as mistakes in the copying process, point mutations, inversions, deletions, insertions), which through their phenotypic effects can be either preserved or discarded. Natural selection, then, works as a non-random sieve, filtering out those varieties (that are constantly offered through the process of replication) which are beneficial to the stability or replication of the replicator. Random mutations in the DNA sequence shape the replicator, but non-random selection filters out the 'fittest' sequences. Mayr accordingly described natural selection as a two-step process: the first step is the production of random variation; the second step is the actual process of non-random selection or elimination [Mayr 1978].

When we conclude that the gene is unit of selection, this means that the process of adaptation always takes place *on the level of the gene*, and that adaptations are expressions of DNA which are always *part of the gene* and evolve for its benefit. It is on the level of the gene that we can account for design though the evolutionary process of adaptation. But the fundamental implication of this is

that the gene as the unit of selection cannot explain the sexually reproducing organism. With genes as the unit of selection, natural selection can exclusively account for the specific constitution of these genes themselves, and can only account for adaptations that are phenotypic expression of *part* of those genes. Consequently, with genes as unit of selection, no account can be given for the design of anything that is the expression of DNA that exceeds the level of the gene – cells, organs, macroscopic structures, let alone the organism itself – all these fall outside of the explanatory potential of natural selection.

An important objection against this idea (that the gene-centered model of natural selection renders the explanation of design of anything that is the expression of DNA which exceeds the level of the gene impossible) could be made as follows. It is true that the principle of natural selection can only account for design on the level of the gene, but the extent to which this gene is adapted, will depend on the environment in which this gene finds itself. Ultimately, the selective value of adaptations lies in their contribution to the stability or replication of the gene, which we can call their end-direction, or ultimate goal [Ayala 1970], but a variety of forms and processes can fulfill this ultimate goal. And what these forms and processes are, will depend on the environment in which they operate. Thus, organisms living on land will evolve different adaptations than organisms at sea, and organisms living in warm climates will evolve different adaptations from those in the arctic. But this environment also consists of the other genes within the genome. The dependency between gene and genome is comparable to the dependency between adaptations and the ecological environment in which the phenotype operates. So, just as the process of adaptation will lead to the adaptation of organisms to that specific environment (fish adapted to water, plants living in arid conditions adapted to arid circumstances), so will the process of adaptation working on genes among other genes lead to a process

of co-adaptation between these genes, leading to well-integrated, co-adapted gene complexes, and thus in this way to design above the level of the gene.

We see this argument expressed by G.C. Williams, who claims that the existence of a well-integrated genetic complex that exhibits unity and design does not invalidate the gene-centered model of natural selection.

Obviously it is unrealistic to believe that a gene actually exists in its own world with no complications other than abstract selection coefficients and mutation rates. The unity of the genotype and the functional subordination of the individual genes to each other and to their surroundings would seem, at first sight, to invalidate the one locus model of natural selection. Actually these considerations do not bear on the basic postulates of the theory. [Williams 1966: p. 57]

Williams claims that the environment in which a gene operates is not just the ecological environment, but also the genetic and somatic environment. The most intimate environment in which a gene operates is the other genes at the same locus (a specific location of a gene on a chromosome). As human cells are diploid (containing two copies of the same chromosome),¹⁷ two different forms of genes might exist on the same locus, which are called alleles. For example, gene *a* may be favorably selected in a population in which the normal allele at the *a*-locus is *A*, but unfavorably in a population in which it is mainly *A'*. The selective value also depends on genes at other loci. Thus, gene *a* may be favorably selected in genotypes *BB* and *Bb*, but unfavorably in genotype *bb*. So the selective value depends on the genetic environment in which the gene

¹⁷ Except for the sex chromosomes. In humans, females have two of the same kind of sex chromosome (*xx*), while males have two distinct sex chromosomes (*xy*).

operates, and this genetic environment can be considered to be all the other genes in the population, at the same and other loci. The other environment in which a gene operates is the somatic environment. The interpretation of the genetic message, the expression of DNA, depends on its somatic environment, without which genes cannot not be translated into proteins. Moreover, the same genetic messages can be interpreted by different somata in different ways. A certain gene might give effect A in soma x, but the same gene might give effect B in soma y. The third environment is what is usually meant by 'environment' such as climate, predators, parasites, food resources, etc., which are generally well understood as evolutionary factors.

This argument, however, does not illustrate that the gene-centered view on evolution can explain the design of anything that exceeds the level of the gene. What Williams shows instead, is that, *assuming* the existence of well-integrated gene complexes called genotypes, natural selection acting on individual genes can lead to adaptation of these genes to this genetic environment. Thus, changes will be valued against the genetic – as well as the somatic and ecological – environment in which these appear. The effect of natural selection acting on individual genes will consequently be the co-adaptation of a collection of genes in well-integrated gene complexes. But this is not the issue that needs to be resolved, nor an answer to our question. What needs to be answered is how these well-integrated gene complexes can arise, how these gene complexes are created in the first place. Earlier on we have seen what kind of integrated (i.e. designed) gene complexes the principle of natural selection can account for: those of a replicating string of DNA. Changes to a string of DNA consist of the replacement, deletion, inversion or addition of nucleotides, altering the genetic content of the string of DNA, and therefore its phenotypic expression. These changes are retained through the chemical bonds between these nucleotides, forming a chemically locked string

of nucleotides. Through these chemical bonds, these replicators show permanence over time, another condition for the principle of natural selection to operate. As these strands of DNA replicate with the right amount of fecundity, copying fidelity and longevity, changes will be naturally selected, which means that those with phenotypic effects which increase the stability or replication of the replicator are retained, and those that decrease that stability are discarded. Moreover, through this replication with the right amount of fecundity, copying fidelity and longevity, these beneficial changes can accumulate, leading to highly complex, well-integrated gene complexes. But again, the reason why the genomes of sexually reproducing organisms *cannot* be seen as gene complexes that are shaped by the principle of natural selection is that the genomes of these organisms do not behave as replicators. The only levels in sexually reproducing organisms that do behave as replicators are the genes, but sexually reproducing organisms cannot be accounted for through the principle of natural selection. The design displayed in the integration and cooperation of genes cannot be accounted for by the selective accumulation of beneficial changes in the sequence of DNA, powered by replication with the right amount of fecundity, copying fidelity and longevity.

In a way, the validity of this conclusion is independent of Williams' rightful conclusion that the existence of a well-integrated genetic complex in which a gene operates, does not invalidate the gene-centered model of natural selection. Williams is right in saying that natural selection acting on individual genes can lead to adaptation of the genes to this genetic environment when we *assume* the existence of integrated gene complexes. But the issue is that natural selection acting on individual genes cannot lead to the *formation* of the integrated gene complexes of sexually reproducing organisms in the first place.

In line with the analysis of Williams, Richard Dawkins refers to two different ways in which harmonious cooperation can come about.

One way is for harmonious complexes to be favoured by selection over dis-harmonious complexes. The other is for the separate *parts* of complexes to be favoured in the presence, in the population, of other parts with which they happen to harmonize. [Dawkins 1982: p. 242]

This second way in which harmonious complexes can come about is the selection of genes in the genetic, somatic, and ecological environment, where the genetic environment can mean the genome as well as the population at large. Again, this might be true, but it does not alter the fact that the genetic environment of the genome of sexually reproducing organism *itself* cannot be accounted for by the principle of natural selection.

In fact, Dawkins was not unaware of the problems associated with sexually reproducing organisms.

Given that life can be viewed as consisting of replicators with their extended phenotypic tools of survival, why in practice have replicators chosen to group themselves together by the hundreds of thousands in cells, and why have they influenced those cells to clone themselves by the millions of billions in organisms? [Dawkins 1982: p. 251]

Dawkins admits that by transferring the Darwinian explanatory scheme to the level of the gene, the organism is a hard thing to account for. Having reduced the workings of the principle of natural selection to the level of the gene, explaining organisms then becomes indicating why replicators have 'chosen to group themselves together'. In *The Extended Phenotype* (1982), Dawkins lists some possibilities, for example that alternative life forms would be less stable, or would provide fewer opportunities for evolution. But these explanations are not the sort of explanations that the principle of natural selection can provide. The explanatory potential of the principle of natural selection exclusively consists of the

explanation through the evolutionary process of adaptation, and this process of adaptation, as we have seen, can exclusively take place on the level of the replicator. The options he proposes of why 'replicators have chosen to group themselves together' are not part of the explanatory repertoire of natural selection.

In fact, this conclusion seems to have dawned on Dawkins himself when he says:

I have not aspired [...] to give a completely satisfying answer to the question of why there are large multicellular organisms. I will be content if I can arouse new curiosity about the question. [Dawkins 1982: p. 263]

Thus we must conclude that appointing the gene as unit of selection does not provide a successful application of Dawkins' theoretical model, the only model that would yield sufficient explanations (including one for sexual reproduction) through the principle of natural selection. Dawkins' *concept* of replicator-selection does not contain the gaps of the traditional Darwinian explanation. The explanatory scheme is self-contained: the gaps are filled in the sense that it does not rely on another, unexplained – biological – element such as the organisms' striving towards survival and sexual reproduction. In the traditional Darwinian explanation, the phenotypic trait or adaptation was the *explanandum* and the organism with its behavior toward survival and reproduction the *explanans*. For Dawkins, the *explanans* for adaptations is the process of replication undergone by replicators, which can be accounted for as a physical and chemical phenomenon. But the translation of that model to reality in the form of genic selectionism is not viable. With genes as unit of selection, we are not able to account for design on any level higher than that of the gene, which leaves this interpretation unable to account for the design displayed in cellular structures, cells, tissues, organs, as well as the organism itself.

At the end of this section, a cautionary remark has to be made. Earlier in this chapter, the unit of selection was defined as that unit on which selection acts, which was defined further as the unit adaptations evolve for the good of. It must be noted, however, that the definition ‘the unit on which selection acts’ allows it to be applied to an entirely different entity: it could also refer to *what units* are selected. Here, the gene, as the unit of selection, would be the unit that is selected for the good of reproducing organisms, such that those genes (or alleles) are selected over other genes that allow the organism to survive and reproduce more successfully.

It is a separate question whether the unit of selection is indeed used in that different meaning by biologists.¹⁸ At this place, it is more important to conclude that the gene as unit of selection in that meaning would not bring us further to the solution of our problem. In this model, the working of natural selection rests upon the existence of reproducing organisms, and therefore cannot account for sexually reproducing organisms. In fact, this model is

¹⁸ The idea that biologists conflate and use the same term for a variety of meanings, and that this ambiguity leads to more confusion (a confusion explicitly admitted by biologists, see for example Mayr [1997]), seems obvious by looking at the literature. In just a handful of sources (Mayr [1997], Lloyd [2012], Dennett [1995]), the unit (also called objects, levels and targets) of selection is described as the entity ‘that is being selected’, the units that are the ‘beneficiaries of selection’, the ‘unit which survives or not, which reproduces or not, and which reproduces successfully or not’, and ‘the level adaptations exist for the good of’, not directly suggesting descriptions of one and the same thing. Earlier we have made the distinction between at least two possible different things: the unit adaptations exist for the good of the replicator (let’s call it unit #1), and those units that are selected in the context of reproducing organisms (let’s call it unit #2). These are two entirely different concepts: in the latter meaning, the gene as the unit of selection is selected *for the good of the organism*, and thus here it is the organism that fulfills the role of the unit of selection #1. Moreover, different meanings, or at least an insufficient demarcation between them, seem to surface when we analyze the arguments of some biologists that refute the notion that the gene is the unit of selection. These scientists, such

essentially a genetic form of Darwin's interpretation of the working of natural selection, whereby the reproducing organism is the unit of selection in the meaning of 'the unit adaptations evolve for the good of'.

In this study we have focused on the unit of selection in Dawkins' definition as the unit adaptations evolve for the good of, and for good reasons. The only way in which we could come up with a sufficient explanation by means of natural selection was to adopt Dawkins' replicator model. But appointing the gene as that replicator has been proven unsuccessful and flawed.

§ 5. The difficulty to apply the concept of replicator-selection to empirical reality is additionally shown through the works of Jacques Monod, whose interpretation of natural selection shows great overlap with that of Dawkins. We will also see that problems arise when he attempts to match his conceptual analysis with empirical data, leaping into vague, unclear descriptions and even incorrect conclusions.

as Gould and Sober, claim that genes cannot be the unit of selection because genes are *not directly visible* to natural selection (for example Sober [1984]; see also Reeve and Keller [1999]). The notion of 'visibility', however, applies more to the unit of selection in meaning # 2, not to the unit in meaning # 1. Vice versa, a gene as unit # 2 does not necessary have to be a replicator with permanence, fecundity and copying fidelity in order for it to be selected by natural selection – it just has to be present in a reproducing organism and provide an advantage to its carrier. Thus, the replicator-description clearly relates to the unit of selection as that unit adaptations evolve for the benefit of (unit # 1). Additionally, the difference between these two different meanings, relating to two entirely different concepts, becomes clear when we try to conceptually match the 'unit that is selected' with 'the unit adaptations evolve for the good of'. How could a gene that is selected because provides its carrier an advantage be the same gene that adaptations evolve for the good of? These are clearly entirely different things. In fact, this mixing up of different concepts under identical terms is strongly reminiscent to the confusion we observed earlier with Darwin around the term 'survival', being used inconsistently in relation to organisms as well as traits.

The problem of accounting for sexually reproducing organisms through natural selection can also be demonstrated through the works of Jacques Monod. Contrary to Dawkins, who first analyzed what a unit of selection should foremost look like before determining which levels in the organism correspond to these requirements, Monod in his work *Chance and Necessity* [1971] focuses directly on accounting for organisms themselves. In this renowned work, the French Nobel Prize laureate attempts to provide a general theory of organisms based on the molecular theory of proteins and the genetic code. The analysis Monod provides is interesting as it reveals the same problems as encountered with Dawkins. Although starting from different points, Monod also concludes that replication is the *vis a tergo* of design through the principle of natural selection, but he is equally unable to properly apply the concept of replication to the sexually reproducing organism.

Chance and Necessity starts with an attempt to objectively describe the essential differences between living beings and inanimate objects. Monod identifies three major characteristics. The first one is the *teleonomic character* of living beings, which he describes as exhibiting 'oriented, coherent and constructive activity', by which he means that they display end-directed processes and behavior. The second essential feature of living beings is that they are 'self-constructing machines', by which he means that the structure of a living being, its phenotype, is the result of morphogenetic interactions within the living beings itself, and that it owes nothing to the action of outside forces. From fertilization to adulthood, living beings are not being built by an outside agent, but through processes within the organism itself. It is the characteristic of *autonomous morphogenesis*. The third characteristic is that living beings are self-reproducing machines. Living beings reproduce *ne varietur* (unaltered) the information corresponding to their own structure. Monod refers to this feature as 'invariant reproduction', which is in fact identical to *replication*. Of these three characteristics, Monod

claims that teleonomy is the most challenging, and at the same time the most pressing to address. As teleonomy will turn out to be an essential concept within this study, we will first describe in more detail what we mean with the term.

The term teleonomy was coined by C.S. Pittendrigh [1958] to describe end-directed phenomena without implying non-naturalistic notions. Living beings, Pittendrigh claims, are end-directed, or rather, end-directedness is an essential characteristic of them. The problem, however, is that terms like goals, end-directedness and purpose are stained through an implicit association with Aristotelian final causes, Aristotle who is often claimed to have assumed that goals are true causes for processes and functions in living beings.

Biologists for a while were prepared to say a turtle came ashore *and* lay its eggs, but they refused to say it came ashore *to* lay its eggs. These verbal scruples were intended as a rejection of teleology but were based on the mistaken view that the efficiency of final causes is necessarily implied by the simple *description* of an end-directed mechanism. [Pittendrigh 1958: p. 393]

Teleonomy, then, is introduced to *describe* end-directed mechanisms, while at the same time stressing ‘that the recognition and description of end-directedness does not carry a commitment to Aristotelian teleology as an efficient causal principle’ [Pittendrigh 1958: p. 394]. End-directedness is an essential feature of organisms, Pittendrigh claims. The term ‘organism’ is derived from the term organization, and organization is always relative to some end.

There is no such thing as organization in any absolute sense, pure and simple. Organization is always relative, and relative to an end; it differs from mere order in this respect. [Pittendrigh 1958: p. 394]

The term ‘teleonomy’ does not only apply to human or animal behavior, but also to plants growing towards the light, or to the coagulation of blood, or to the metabolism in cells, in other words, to all end-directed processes and activities in the organic world. Other terms coined for this feature of organisms is ‘projective’ [Monod 1971], ‘purposeful organization’ [Lifson 1987] and ‘purposeful character’ [Pross 2005].

At the same time, Monod claims that these teleonomic processes in living beings still call for an explanation. The claim that the existence of end-directed mechanisms does not imply that ends, purposes or goals are true causes and are therefore not ‘metaphysically charged’ [Pross 2005] does not alter the fact that these mechanisms require a scientific explanation, as the teleonomic properties of living beings challenge one of the basic postulates of modern science. This is that the laws of nature are *objective*, in the sense that no purpose is ascribed to them, a notion which constitutes the cornerstone of the scientific method. Yet all living systems are teleonomic or projective, and this projective character of living beings calls for an explanation, as accurately worded by Pross:

On the one hand the laws of nature are *objective* – no purpose is ascribed to them. That realization was at the heart of the scientific revolution of the 17th century. Yet on the other hand biological systems are, as Monod put it, *projective*. All living systems are involved in carrying out a *project*, be it to hunt for food, find a mate, or carry out research into the origin of life, or whatever. Enveloped as we are within a biotic world, we tend to take this projective character of living systems very much for granted. However, from a strictly chemical perspective this behavior of matter is quite remarkable. How is it at all possible for a chemical system to act purposefully [...]. How could *projective* systems have emerged from an *objective* universe? Clearly troubled from this dilemma, Monod went so far as to state that

this apparent contradiction constituted ‘the central problem of biology’. [Pross 2005: p. 384]

As we have seen, Monod summarized the three essential characteristics of living beings as teleonomy, autonomous morphogenesis, and replication. He then continues to claim that although in principle these characteristics do not necessarily have to go alongside each other (for example, crystalline structures are capable of replication but are devoid of a teleonomic apparatus), in living beings they do. Moreover, it is in the *relation* between these characteristics, especially teleonomy and replication, that we can find the solution to the problem of teleonomy, the paradox of the existence of teleonomic systems in a mechanistic universe. Monod elaborates this relation further on the level of the molecular theory of proteins on the one hand, and the genetic code on the other.

Proteins, explains Monod, are the essential, although not exclusive, molecular agents of teleonomic mechanisms. Living beings are chemical machines, and primarily proteins channel the activity of that machine. More specifically, teleonomic performances rest upon the proteins’ stereospecific properties, i.e. their ability to recognize other molecules by their shape. Proteins channel, through their stereospecific properties, the activities of living beings in two ways:

1. They act as enzymes, catalyzing reactions between specific molecules;
2. Through regulatory processes as feedback inhibition and feedback activation, often performed by allosteric proteins (proteins that change shape when they bind particular molecules), proteins regulate the chemical machinery of living beings so that it forms a coherent system.

In the latter case (the second way), certain molecules (effectors)

regulate the enzymatic workings of the proteins. For example, regulator α inhibits the production of molecule A, or regulator β enhances the production of B.

An elementary aspect of the regulatory workings of proteins is that, although they are physiologically rational (that is, are useful in that they contribute to the coherence of the living being), they are chemically arbitrary. To use the earlier example, there is no *chemical* necessity (i.e. it is not defined by chemical laws) that substance α inhibits the production of molecule A, or that an increase of the concentration of β stimulates the production of substance B. There is no chemical necessity between α and A or β and B, nor in the inducing or inhibiting character of that relation. These relations are purely the result of the stereospecific properties of the allosteric proteins.

[...] so far as regulation through allosteric interaction is concerned, *everything is possible*. An allosteric protein should be seen as a specialized product of molecular 'engineering', enabling an interaction, positive or negative, to take place between compounds without chemical affinity, and thereby eventually subordinating any reaction to the intervention of compounds that are chemically foreign and indifferent to this reaction. The way in which allosteric interactions work hence permits a complete freedom in the 'choice' of controls. [Monod 1971: p. 78]

These stereospecific properties, the proteins' three-dimensional form which determines their specific functions, are based on the sequence of their amino acid residues. Within the cellular environment, a protein strand with a specific sequence of amino acids folds spontaneously and autonomously into its three-dimensional, (pseudo-globular) functional shape. The protein strand itself, on the other hand, is based on the sequence of nucleic acids in DNA. The sequence of the nucleic acids in DNA is translated into amino

acids, whose sequence within the polypeptide will subsequently determine its three-dimensional form, which in turn will determine its enzymatic and regulatory properties. In that sense, 'one must regard the total organism as the ultimate epigenetic expression of the genetic message itself' [Monod 1971: p. 102]. In other words, the development of phenotype finds its ultimate basis in the genetic code.¹⁹

The sequence of DNA, the sequence of the four nucleic acids determining the sequence of amino acids, and ultimately determining the three dimensional structure of proteins, is 'free' in the sense that no restriction is imposed upon it by the overall structure. There is no chemical necessity or even preference for any combination of nucleic acids, so that the code is 'chemically arbitrary'. So the ultimate source for the teleonomic properties of living beings is free from a chemical point of view. Monod continues to claim that the proteins also form the molecular basis of the second characteristic of living beings, autonomous morphogenesis. The process of spontaneous and autonomous morphogenesis is based on the stereospecific recognition properties of proteins and so primarily a microscopic process before manifesting itself in macroscopic structures [Monod 1971: p. 82].

This aspect of the teleonomic properties and structures of living beings is of fundamental importance, and provides one element in the solution to the problem of teleonomy. The astonishing abundance of biological teleonomic systems, systems moreover sharing some elementary characteristics – such as, using our earlier terminology, their striving towards survival and reproduction – might lead to the idea that these features have some chemical or

¹⁹ The term 'genetic code' can be used in two meanings. It can refer to the way in which information encoded in genetic material is translated into proteins (i.e. which sequences of three nucleotides, called codons, correspond to what amino acids), or it can be used to mean the complete nucleotide sequence of an organism. When we will speak of genetic code, we will mean the latter.

physical basis, that these processes or activities are inherent to the forces of physics or chemistry. A notion, of course, which is fundamentally contrary to the concept of causality, which categorically denies that natural phenomena immanently exhibit any specific direction towards certain specific directions, goals or end-states, or to the creation of systems that exhibit those particular properties. Monod, by analyzing these teleonomic features, clearly eliminates any suggestion towards that direction. The teleonomic properties of living beings as well as their macroscopic, morphological structures do have a chemical basis, in the sense that these properties are founded on the possibility of complex molecules to form stereospecific complexes. At the same time, from a chemical point of view, there is absolutely no necessity for the existence of *these specific* molecules. The stereospecific characteristics of proteins find their ground in the sequence of amino acids in the proteins, which in turn are based on the sequence of nucleic acids on the strands of DNA. But at none of these levels does chemistry dictate the precise characteristics of those features – neither on the sequence of DNA, nor on the sequence of proteins strands, nor on the three-dimensional form of proteins do we find chemistry to dictate specific sequences or forms. Again, from a chemical point of view, much is possible. Chemically, any combination of nucleic acids on a string of DNA is as likely to occur as any other, and is totally unrelated to the potential teleonomical consequences these sequences, through the translation into amino acids and the subsequent folding of strings of amino acids into proteins, might have.

As said, this notion accounts for one aspect of the problem of teleonomy: living beings do exhibit end-directed mechanisms, but these mechanisms are shown not to be inherent to the forces of chemistry or physics. More concretely, teleonomic processes ultimately find their basis in the (micro)structure of organisms (most dominantly in those of proteins), and this (micro)structure finds its basis in the sequence of nucleic acids in DNA. And this sequence

is in no way dictated by the laws of chemistry, from which perspective all sequences can exist with an equal probability.

But this conclusion immediately raises another question. If there is no chemical basis for the specific sequence of DNA molecules leading to the teleonomic processes and morphological structures of living beings, what is the ground of their existence? Why do we see an abundance of *those specific* sequences – an infinitesimal subset of the total of possible sequences – that do stand at the basis of teleonomic mechanisms, and not many other configurations that are, physically, equally probable? If there is no chemical basis for the specific DNA sequences that lead to the highly coherent, oriented and constructive activities of proteins, then what is the basis of their existence? It is here, of course, where the principle of natural selection comes in, and this principle provides the second aspect of the solution to the problem of teleonomy. And as with Dawkins, an elementary role is played by the other important feature of DNA, namely, the possibility of replication, the third characteristic of living beings as described by Monod.

Contrary to the freedom that exists in the sequence of nucleic acids, the process of replication *does* impose a necessity. Where there is complete freedom on the level of the sequence of nucleic acids, on the level of replication no freedom exists. Each of the four elements of DNA is individually pairable with *only one* other element. Through – here again – the stereospecific characteristic of DNA, the process of replication will necessarily lead to an exact copy of the DNA. So whereas on the level of the sequence of DNA forming the basis of the teleonomic and morphogenetic features of proteins there is from the chemical point of view a complete freedom, on the level of replication there is necessity, in that the process of replication will necessarily result in an exact copy of the string of DNA.

The second aspect of DNA crucial for the explanation of the existence of teleonomy is that, despite the essentially conservative

nature of the process, errors, or mutations, can occur. And these mutations, Monod claims, form the creative source of innovation in the biosphere. And it is this process of replication ensures that deleterious mutations are discarded, and beneficial mutations can spread through the population.

The initial elementary events which open the way to evolution in the intensely conservative systems called living beings are microscopic, fortuitous, and totally unrelated to whatever may be its effects upon teleonomic functioning. But once incorporated in the DNA structure, the accident – essentially unpredictable because always singular – will be mechanically and faithfully replicated and translated: that is to say, both multiplied and transposed into millions or thousands of copies. Drawn from the realm of pure chance, the accident enters that of necessity, of the most implacable certainties. [Monod 1971: p. 114]

And from a source of noise, as Monod puts it, natural selection draws all the music in the biosphere.

Indeed natural selection operates *upon* the products of chance and knows no other nourishment; but it operates in a domain of very demanding conditions, from which chance is banned. It is not to chance but to these conditions that evolution owes its generally progressive course, its successive conquests, and the steady development which it seems to suggest. [...] Hence the only acceptable mutations are those which, at the very least, do not lessen the coherence of the teleonomic apparatus, but rather strengthen it in the orientation already assumed or (much more rarely) open up new possibilities for it. [Monod 1971: pp. 113–114]

As with Dawkins, Monod identifies the replication of DNA as the

vis a tergo of natural selection. Through this process, DNA evolves by offering new varieties to the filter of natural selection, whereby *only those changes are retained that are beneficial to the organism*. Therefore, Monod claims, the solution of the problem of teleonomy is provided through the relation between two essential characteristics of living beings, namely teleonomy and invariant reproduction (also referred to by Monod as ‘invariance’, and which we concluded earlier to be a synonym for replication). In fact, the only hypothesis that modern science deems acceptable is that:

[...] invariance necessarily precedes teleonomy. Or, to be more explicit, the Darwinian idea that the initial appearance, evolution, and continuous refining of ever more intensely teleonomic structures are due to disturbances occurring in a structure *which already possesses the property of invariance* – and hence is capable of preserving the effects of chance and thereby submitting them to the play of natural selection. [Monod 1971: p. 32]

The replication of DNA is the underlying mechanism that opens the possibility of the existence of those specific sequences of DNA that give rise to the teleonomic processes and activities through the principle of natural selection. It is due to the process of replication that from the noise of random mutations, the music of the biosphere can be created. Monod shows that the design displayed in the organism’s micro and macrostructure (morphology), which in turn stands at the basis of its teleonomy, is based on the design in the form of the specific sequence of nucleotides of DNA. This design is shaped by the evolutionary process of adaptation through the principle of natural selection, which exclusively takes place with replicating entities. Therefore, replication precedes teleonomy. Natural selection operates upon the products of chance, for example in the form of mutations, and this creation is always blind and purposeless. Natural selection, on the other hand, works as a sieve

through which only those changes are retained that contribute to the survival (stability or replication) of the replicator of which it is part. Adaptations and teleonomic processes are therefore always directed to the conservative process of the replication or stability of the replicating entity of which they are part. The similarities with Dawkins' analysis are obvious.

So far so good. But also here problems arise when we try to match this conceptual description with empirical data. Monod starts directly with explaining the organism itself, contrary to Dawkins who starts with a general analysis and description of the *unit of selection*, after which he tries to find a unit which corresponds to that description. Since Monod makes it his explicit goal to account for organisms through the principle of natural selection, he cannot stop short at the gene as the replicating unit that is shaped by natural selection. But the fundamental problem Monod is faced with is that the sexually reproducing organism *cannot* be seen as something that replicates. The sexually reproducing organism, as Dawkins rightly shows, is simply not a replicator. And so while Dawkins thought he had found a way out of this difficulty by appointing another level as unit of selection, Monod with his explicit ambition and focus to explain design on the level of the organism, cannot. But instead of realizing the incongruent nature of organisms in light of his conceptual analysis of natural selection, Monod leaps into vague, unclear descriptions and even incorrect conclusions while attempting to match his conceptual analysis with empirical data. For example, we find Monod claiming that:

[...] the source of the information expressed in the structure of a living being is *always* another, structurally identical, object.
[Monod 1971: p. 22]

But this is simply not the case with sexually reproducing organisms. Here, the source of the information expressed is *never* another,

structurally identical object (identical defined as the source being derived via a process of replication from another object). If this were the case, indeed organisms would be replicators. But no structurally identical object of sexually reproducing organisms exists, as they are all unique, the one-of-a-kind and once-in-a-lifetime combination of the genetic material of two other – equally – unique organisms. So here Monod confuses sexual reproduction with asexual reproduction.

Likewise, we see Monod erroneously claiming that the organism:

[...] is entirely logical, wonderfully rational, and perfectly adapted to its purpose: to preserve and reproduce the structural norm. [Monod 1971: p. 30]

In sexually reproducing organisms, however, the norm, the sequence standing at the basis of their teleonomy, is not preserved, and not reproduced. It is newly and uniquely created in every generation. Elsewhere in *Chance and Necessity* we read:

All the functional adaptations in living beings, like all the artifacts they produce, fulfill particular projects which may be seen as so many aspects or fragments of a unique primary project, which is the preservation and multiplication of the species. [Monod 1971: p. 14]

Here, Monod suddenly claims something fundamentally different from the earlier mentioned descriptions. The end-direction of teleonomic processes and behavior is described as the preservation and multiplication of the species. Monod seems to suggest that species are like giant units of selection, being the units that are multiplied and preserved through the teleonomic processes and behavior and whose content contains the genetic program giving

rise to teleonomic processes and behavior and is transmitted *ne varietur* from generation to generation. Here Monod, out of the blue, suggests the existence of species selection. We will deal with the possibility of group and species selection later, but now we already announce that this form of selection cannot be made in line with his theoretical model.

The analyses of Dawkins and Monod show us the following. Dawkins is right when he claims that only replicators with a sufficient degree of longevity, fecundity and copying fidelity can be units of selection, that is, entities that can be seen as a product of the process of adaptation and the entity adaptations evolved for the benefit of. He is also right when he concludes that genes are the only entities within sexually reproducing organisms that adhere to that description. He is wrong however, when he subsequently concludes that genes are the units of selection of sexually reproducing organisms. The process of adaptation can only account for adaptation *on the level* of the replicator, and the only adaptations that can be explained, are adaptations that are (the expression of) *part* of the replicator. This means that by assuming the gene as unit of selection, the sexually reproducing organism cannot be accounted for.

The analysis of Monod, starting straight from the organism, shows something similar. One of the essential characteristics of living beings is their oriented, coherent and constructive activity (teleonomy), and their morphology (phenotype). These are based on design, more specifically, the design of DNA sequences, and design can only be accounted for as a result of the process of adaptation, which, assuming adaptation takes place through the principle of natural selection, exclusively takes place with replicating entities. However, the structural norm of sexually reproducing organisms, the highly specific sequence of DNA that stands at the basis of teleonomy, is not replicating, and therefore the sexually reproducing

organism cannot be accounted for as shaped by the process of adaptation through the principle of natural selection.

§ 6. *The inability to explain sexually reproducing organisms within Dawkins', Williams' and Monod's conceptual framework is additionally analyzed by considering an attempt to explain sexual reproduction as an adaptation. We will define the teleonomy exhibited in sexual reproduction as creative – as it is directed to the creation of new genetic codes – and place it against conservative teleonomy, directed to the stability or replication of a genetic code that in itself is shaped by the process of adaptation, which alone can be accounted for by the principle of natural selection.*

It is exclusively with sexually reproducing organisms that the problems addressed in this study are encountered. As Dawkins indicated, in case of asexual reproduction, the entire genome, the DNA sequence standing at the basis of the entire organism, can be seen as a replicator. Therefore, the DNA sequence underlying the asexually reproducing organism can be accounted for as being designed by the process of adaptation through the principle of natural selection. Moreover, parts of the organism can be seen as adaptations because the DNA coding for these features is part of the replicator. But sexual reproduction breaks the unity of the DNA sequence that comprises the organism. The consequence of this is that the genotype of the organism is disqualified as the unit of selection, and its design can therefore not be accounted for through the principle of natural selection (the idea of the gene as unit of selection, as we have concluded, is not able to provide an account for the design of the organism). So without sex, we would not have the problems analyzed in this study.

So while Dawkins reasoned from the point of view of the *replicator*, and Monod did so from the *organism*, we can in our turn analyze the inability to apply the concept of replicator-selection to

sexually reproducing organisms from the point of view of *sexual reproduction* itself, by attempting to explain this feature through the principle of natural selection. Adding this third point of view (which will equally establish the inability of natural selection to cope with sexual reproduction) will hopefully enhance the understanding of this problem, but it will also enable us to come to a more precise description of the problem of sex.

First, let us start with the theory. Let us assume that sexual reproduction is a feature that – in animals – is constituted by the primary and secondary genitalia, glands, and certain sections of the brain. For features to be explained by the principle of natural selection, they are to be accounted for as adaptations. Based on the earlier exposition of the relation between the process of adaptation, adaptations and the replicator, sexual reproduction should then be seen as the expression of a *subset* of the DNA sequence of a replicator, and should have been selected due to its contribution to the stability or replication (survival) of the replicator of which it is a part. In other words, the sequence of DNA standing at the basis of sexual reproduction, the sequence coding for the genitals, hormone system, and relevant parts of the brain, should be part of a replicator for whose benefit it evolved, and this feature should be directed to its stability or replication. But this is clearly not the case with sexual reproduction. Sex is not directed to the stability or replication of a replicator of which the sequence of DNA standing at the base of this feature is a subset. The only replicating string of DNA that can be possibly identified in sexually reproducing organisms is the gene, but by no means does this string encompass the DNA coding for sexual reproduction. Hence, sexual reproduction cannot be explained as an adaptation, and, therefore, not accounted for by the principle of natural selection.

The incongruity of sex can be seen more clearly when we consider that sexual reproduction is not directed to a 'stability or preservation' at all, something which we can better understand when

we analyze sex by means of the concepts *conservative* and *creative* processes. The process of replication – the chemical process through which the principle of natural selection can operate – is conservative in nature. It will faithfully – although not too faithfully as to allow for changes which form the source for evolution – replicate the sequence of DNA into multiple copies. As Monod mentioned:

The initial elementary events which open the way to evolution in the intensely conservative systems called living beings are microscopic, fortuitous, and totally unrelated to whatever may be their effects upon teleonomic functioning. But once incorporated in the DNA structure, the accident – essentially unpredictable because always singular – will be mechanically and faithfully replicated and translated: that is to say, both multiplied and transposed into millions or thousands of copies. Drawn from the realm of pure chance, the accident enters that of necessity, of the most implacable certainties. [Monod 1971: p. 114]

The fact that replicators replicate, and that they faithfully replicate the changes brought about in the linear sequence of nucleotides, opens the possibility for natural selection to operate. Any adaptation finds its possibility in this conservative process of replication. Evolution, innovation, always consists of a change in the linear structure of nucleotides, and it is in the background of this replication of the linear structure that natural selection can do its work. Any adaptation finds its possibility in this conservative process of replication, but also its limitation. The fruit of the evolutionary process of adaptation through the principle of natural selection is always a specific linear sequence of nucleotides. The principle of natural selection can account for the accumulation of specific sequences of DNA, naturally selected due to the selective value of the structures and processes that these sequences code for, consisting

in the contribution to the stability or replication of that replicator. The fact that this sequence is faithfully replicated (based on chemical processes independent of any structures that would need an account for their design themselves), and that this sequence exhibits permanence and stability over time (through the chemical bonds between the nucleotides), forms the very basis of the process of adaptation.

But this *a priori* rules out the possibility of an *adaptation* that *alters* the DNA sequence (please note the stress on *adaptation*. It is true that the process of replication must allow for changes in the DNA sequence through mutations, changes that are always random, but this is something fundamentally different from adaptations that create these alterations). Monod correctly argued that invariant reproduction, replication, is primary to design, a specific sequence of nucleotides on DNA. Replication is a chemical process that happens autonomously. Replication cannot be based on complex structures or processes – if it was, these structures or processes would need an explanation of their own design, and therefore render explanations by the theory of natural selection insufficient. So as adaptations can only have evolved in the background of DNA faithfully replicating its nucleotide sequence, and the selective value of adaptations subsequently lies in the contributions these adaptations have in the stability or replication of these replicators, how could adaptations have possibly evolved that *alter* the DNA structure or create new varieties of DNA sequences?

They could not, although this is exactly what happens in sexual reproduction. In sexual reproduction, through meiosis and fertilization, individuals mix their genomes, combine parts of their DNA to form a new genome. But this, as seen above, can never be interpreted as an adaptation. If we adapt the language of Monod and describe sexual reproduction as a teleonomic process, we observe that it is directed to a certain end, namely the creation of new individuals with a new and unique DNA sequence. At the same time,

the principle of natural selection forces us to interpret this direction in a certain way, namely as the conservative direction of preservation or replication of the replicator of which the DNA coding for sexual reproduction is part. It is only through that association that sexual reproduction could be accounted for as an adaptation evolved through the principle of natural selection. But the *creation* of new individuals containing a new DNA sequence through sexual reproduction cannot be interpreted as the *conservative* preservation or replication of a replicator of which it is part.

The teleonomy exhibited in sexual reproduction is not directed to the preservation or replication of a replicator in which these features find their genetic ground, but it is directed to the *creation* on a new individual with a unique genetic code. Where Monod clearly showed that teleonomy, evolved in the background of the replication of DNA and selected as a consequence of it enhancing the stability or replication rate of this DNA, should essentially be a *conservative* process, in sexual reproduction we see teleonomic processes directed towards *creation*. And as these processes are not directed to the conservation of a level corresponding to Dawkins' description of a replicator that incorporates the genetic program standing at the basis of these processes, they cannot be seen as features evolved through the principle of natural selection, in other words, as adaptations.

In this context, it is important to recall the *vis a tergo* of natural selection: the replication of DNA. It is the replication of DNA – not an adaptation, but a *condition* for the process of adaptation – which leads to design, the making up and differential survival of the most convenient combinations of DNA nucleotides leading to the best adapted functions and structures, where 'the best' relates to the potential of that combination of genes to survive, i.e. be stable and replicate. But in sexual reproduction, we see something *fundamentally* different happening. Here, the replication of DNA is *not primary* in relation to teleonomy. The DNA is not replicated,

but combined and rearranged into a new organism through complex teleonomic processes. While the theory of natural selection is built on the assumption that the replication of DNA is the condition for natural selection to take place, in sexual reproduction it is the teleonomic processes that create new combinations of DNA sequences. For Monod, creation, the shaping of organisms through random mutations, was always blind and purposeless, and natural selection was the sieve through which nature ends up with convenient combinations of genes. But in sexual reproduction, teleonomic processes *themselves* create new and unique combination of genes, combinations that therefore do not find their source in random changes after which natural selection can do its work, but find their background in teleonomic processes – more concretely, sexual reproduction – themselves. Monod claims that the selective theory is the only theory so far proposed that can give a scientific explanation of teleonomy by interpreting replication as the primary phenomenon in which background design can evolve. Other philosophical systems and religious ideologies, as Monod claims, assume the reverse hypothesis, namely that ‘invariance is safeguarded, ontogeny guided, and evolution oriented by an initial teleonomic principle’ [Monod 1971: p. 33]. But the problem is that the level of replication that *does* manifest itself in living beings, cannot account for the teleonomy exhibited in sexually reproducing organisms. Dawkins showed that the only level that adheres to the requirements of an active replicator with a sufficient degree of longevity, fecundity and copying fidelity is the gene, but this gene, as we have seen, cannot account for design on a level higher than the gene itself. Replication, therefore, is not the basis of teleonomy exhibited in living beings. Sexual reproduction is directed at the *creation* of a specific, new and unique organism, not directed at the Darwinian direction of preserving or replicating something existing which is ultimately shaped by random changes, such as mutations. And it is this creation, the fact that the activities pursued

by an organism are directed at the creation of something new, not at preserving something that can be labeled as a replicator, which leads to the conclusion that sexual reproduction cannot be something that has evolved as an adaptation through the principle of natural selection.

We can also formulate the problem of accounting for sexual reproduction through the principle of natural selection in the following way. The version of the theory of natural selection that would render a sufficient explanation of biological phenomena through the principle of natural selection revolves around certain concepts, such as replicators, the evolutionary process of adaptation, design, adaptations, phenotype, teleonomy, mutations and natural selection. Moreover, these concepts stand in a specific hierarchical relation to each other. The principle of natural selection can account for design through the evolutionary process of adaptation. This process of adaptation can exclusively, as Dawkins has shown, take place on the level of replicators. Within the phenotype (or morphology, or micro- and macrostructure) of organisms, features can be distinguished that perform certain distinct functions. These features are accounted for through the principle of natural selection as adaptations. Adaptations are the expression of a part of the replicator. The ultimate source of adaptations is always random through mutations, but these adaptations are non-randomly sieved by natural selection. The selective value of these adaptations lies in their contribution to the stability or replication of the replicator of which they are part. When adaptations exhibit teleonomic processes and behavior, this means that these processes and behavior are directed to the stability or replication of this replicator.

In asexually reproducing organisms, we find these elements present in the right hierarchy and relation. Here, empirical data fit the theory quite well. The entire genome in asexually reproducing organisms can be seen as a replicator. This means that its design, in the form of the sequence of DNA in the genome, can be accounted

for through the principle of natural selection, which means that it is shaped by random mutations, and subsequent non-random, natural selection. Teleonomic processes are directed to the stability or replication of the replicator of which the DNA coding for the features that exhibit these features is part, namely, the genome of the asexually reproducing organism, and can therefore be fully accounted for as adaptations. In *sexually* reproducing organisms, we also find all of the concepts of natural selection. Genes replicate and thus serve as replicators. Genes are preserved (as well as species). Design exists in the form of a linear sequence of DNA nucleotides, which leads to morphological structures of organisms which exhibit teleonomic processes and behavior. Random mutations occur on the level of DNA, and these mutations are naturally selected. At the same time, while we see all of the elements of the principle of natural selection present in sexually reproducing organisms, they do not stand in the right relation and hierarchy. For one, as we have seen, the design leading to morphological structures does not exist on the level of the replicator, which necessarily means that they cannot be accounted for through the principle of natural selection. The sexually reproducing organism, as Dawkins rightly showed, does not replicate. The gene replicates, but this cannot be seen as a replicator accounting for the design of the sexually reproducing organism, as this gene *does not encompass* the DNA exhibiting design. The replicator should encompass design, not be part of it! Equally, the design on the level of the sexually reproducing organism is *not* the fruit of random mutations, which are subsequently non-randomly naturally selected, but the product of non-random teleonomic processes, namely, sexual reproduction. But teleonomic processes, as seen above, should always be conservative. This means that they should be directed to the stability or replication of the replicator of which these features' DNA is part. Or, even more succinct and phrased in the terminology of Richard Dawkins: the unit of selection should be an active replicator with a

sufficient amount of fecundity, copying fidelity and longevity, and additionally *incorporate* the design standing at the basis of the phenotype, or structure, that exhibits teleonomic processes.

§ 7. In the previous sections we have seen that individual strands of DNA cannot serve as unit of selection of sexually reproducing organisms; in this section we will exclude the possibility that groups or species could serve as units of selection and would be able to provide an explanation for sexual reproduction.

We can summarize our analyses so far as attempts to place sexually reproducing organisms within the theoretical frameworks of Dawkins, Williams and Monod by considering individual, linear strands of DNA as units of selection, objects that in their eyes come closest to the ideal of active replicators with a sufficient amount of fecundity, longevity and copying fidelity. All these attempts failed. The gene is not a viable unit of selection. Monod gets into problems when he is faced with the fact that the DNA that stands at the basis of the design of living beings does not behave as a replicating string of DNA. And sexual reproduction, the culprit of the inability to place living beings in Dawkins' framework, is a creative, not a conservative process.

But although Dawkins considered individual, linear strands of DNA as the most likely candidates (leading in his view to the appointment of the gene as unit), he, as well as other evolutionary biologists, left other options open. As we have seen, natural selection working on groups of organisms or species is considered unlikely, but not impossible.²⁰ So while the attempts earlier dealt-with seem to suggest that sexual reproduction cannot be explained as an adaptation, there is still the option to consider that sexual reproduction evolved for groups or species. Can the evolutionary process of adaptation working on groups have led to sexual reproduction? If this were the case, we could already describe how the process

would have had taken place. Natural selection started to operate on the level of replicating DNA, as this is the only level where the principle can operate on purely physical and chemical grounds without having to assume biological features in the first place (which would render this explanation insufficient). These organisms, shaped by the principle of natural selection operating on the replicating genome (which would thus be asexually reproducing organisms), would organize themselves into groups, and these groups would behave as replicators themselves. Through this, the principle of natural selection would operate on the level of these groups, which

20 The notion that natural selection can act on the level of the group or species, as well as on the individual, was common before the emergence of the gene-centered view on evolution in the mid-1960s which challenged the likeliness of group selection. A major focal point of this critique was a work by the biologist Wynne-Edwards called *Animal Dispersion in Relation to Social Behaviour* [1962], where the idea was proposed that there are adaptations that exist for the good of the species. More concretely, group selection was proposed to explain why animals exploit resources sustainably [Leigh 2010]. We have already dealt with some objections against the likeliness of group or species selections by Dawkins, but the proponents of the gene-centered view of evolution, most notably Maynard Smith [1964], Williams [1966] and Dawkins [1976, 1982], claimed in more detail that some elementary conditions requisite for natural selection to take place are absent in groups. For example, there is the lack of stability of groups. For natural selection to be effective, the ‘selection coefficient’, a measure for the rates of survival of alternative entities, must be high in relation to the rates of change within that entity [Williams 1966: p. 23]. If the selective force working on entities is low but the entities have a high level of endogenous change (that is, are not enough stable), selection works too slowly to accumulate changes in that entity. And while Williams claims that *genic* selection coefficients are high relative to mutation rates, this does not apply to *groups* of genotypes. If populations are evolving rapidly and have a low rate of extinction and replacement, the rate of endogenous change might be too great for group selection to have any cumulative effect. Dawkins argues similarly, as we have succinctly seen before. Another problematic aspect of group selection concerns their replication. As Williams rightfully claims, group selection must be based on the differential

led to the evolution of adaptations for that level. Group-selection came thus into play when the lower-level units, themselves formed by the principle of natural selection working on the level of replicating DNA, engage in fitness-affecting interactions with each other. In that way, sexual reproduction would have evolved as fitness-enhancing interaction for such a group.

This, however, is impossible, and the impossibility to explain sexual reproduction as adaptation for the good of a group or species can be established by considering a premise for group selection to take place, namely the occurrence of variation. Variation is the source of all design that is produced through the evolutionary

survival and reproduction of whole groups; a process he considered most unlikely [Leigh 2010]. Whole groups must behave as replicators, replicators, moreover, that replicate with the right amount of longevity, fecundity and copying fidelity. But how do groups 'replicate'? How do they undergo a process of continuously making copies of themselves, allowing for beneficial changes – changes that increase the likelihood of groups to survive and replicate themselves – in the group to accumulate, and changes that are diametrical to the interest of the group, to perish? A subcategory of group selection is species selection, the notion that adaptations evolve for the good of the species. For species, the problem of 'stability', or 'longevity' is less prominent. Species show relative stability and longevity over time. But for species, replication is also a serious issue. While species do exhibit greater stability and longevity, they lack another essential characteristic, namely replication with a sufficient frequency [Dawkins 1982: p. 106]. And the frequency of replication in species, or more specifically, the gene pool of a reproductively isolated group, is simply too low (Dawkins [1982]: p.109). Thus, the chance of successfully explaining sexual reproduction as adaptation for a group, including species, is unlikely as groups can hardly be seen as fulfilling the premises for the principle of natural selection to be operative. Maynard Smith, Dawkins and Williams also claimed that there is in fact no need to invoke group selection. Altruistic behavior that was often interpreted and seen as proof of group adaptation could be explained as an example of *kin-selection*. Kin selection, a concept developed by Haldane [1955] and Hamilton [1963], refers to the mechanism whereby genes are selected that cause individuals to favor close kin, owing to the high

process of adaptation, so likewise this variation must occur within groups for group selection to lead to the evolution of adaptations. And while the occurrence of variation is another – problematic – condition for group selection to take place in general, it will be an insurmountable problem when we try to explain sexual reproduction specifically through group selection.

All heritable characteristics of organisms ultimately find their basis in DNA. The origin of these characteristics are, as we have seen, random mutations, such as point mutations, inversions, deletions, and insertions. Variation between groups implies that all individuals belonging to a group will share these characteristics.

probability that kin shares those genes. This form of selection was suggested to account for seemingly unselfish behavior, for example towards the offspring of siblings, and unlike group selection, this form of selection is in agreement with the gene-centered view on evolution, as these adaptations essentially exist for the benefit of the gene. The criticism of the notion of group selection by these authors led to a consensus amongst biologists that natural selection almost never operates on the level of groups [Wilson 1997]. Group-level adaptations can evolve in theory, but not at all or rarely in practice. The notion of group selection, however, experienced a modest re-emergence in the seventies in the form of the theory of multilevel selection. This theory claims that selection can, and does, take place at multiple levels, including at that of the group. These ‘neo-group selectionists’, with David Sloan Wilson and Elliot Sober as prominent representatives, regard the wholesale rejection of group selection as a mistake. Not advocating a return to the naive ‘good for the group’ tradition of which Wynne Edwards has become the symbol, they claim the pendulum has swung too far in the opposite direction [Okasha 2006: p. 177]. As David S. Wilson and Edward O. Wilson claim, ‘In hindsight, it has become clear that both claims were too extreme. The balance between levels of selection can tilt in either direction. Between-group selection is sometimes a weak evolutionary force, as Williams supposed, but it can also be very strong, enabling groups to evolve into veritable superorganisms. There is no single formula; answers must be worked out on a case-by-case basis’ [Wilson and Wilson 2008: p. 382]. A more recent advocacy for group selection is accompanied by an attack on the notion of kin-selection [Nowak, Tarnita and Wilson 2010].

So mutations occurring in one individual must spread through the population so that all individuals will share this characteristic in contrast to members of another group. How can these characteristics spread through the population? Here, we cannot rely on the principle of natural selection. If natural selection would be responsible for the spread of characteristics within a group, natural selection would be working on individuals, not on groups (and natural selection working on individuals cannot explain sexual reproduction, as was already concluded).

As Maynard Smith [1964] argued, the only way in which all the members of the group could receive this characteristic is through genetic drift. Genetic drift is defined as the change of gene frequencies over generations resulting from chance rather than from selection. Let us imagine a population of 10 individuals, three of them have genotype AA , four have Aa , and three aa . There are then 10 A alleles and 10 a alleles. Moreover, if we assume that the genotypes produced by AA , Aa and aa have the same fitness, natural selection will not be operating. The most likely outcome is that in the next generation, the gene frequencies will be 0.5 A and 0.5 a , but this is not a certainty. This can happen as the genes, through homologous recombination, are a random sample from the parental generation, and thus some genes can appear more frequently in gametes than others. It can also happen that some individuals, for reasons that do not relate to their fitness (in other words, by chance), manage to reproduce more successfully than others. For example, an individual with a certain genotype might find an early death by being at the wrong spot at the wrong time without having the chance to reproduce. So genetic drift will occur in the sense that the distribution of genes in the gene pool will randomly change over time.

Genetic drift is the only mechanism besides natural selection by which these characteristics could have spread through the population. But for genetic drift to cause these characteristics to spread through the population, some specific conditions have to be met. For example, it can exclusively take place in small populations: the

smaller the population, the larger will be the role of genetic drift [Ridley 2004: p. 138; Williams 1966]. But in the end, the reason why it is impossible that sexual reproduction evolved through group selection is that the mechanism of genetic drift, an essential condition for group selection to be operative, *rests on the existence of sexual reproduction itself*. The change of gene frequencies over generations which results from mutations occurring in one individual spreading through the population by genetic drift so that all individuals will share this characteristic in contrast with members of another group, the premise for group selection to take place, can only take place when organisms reproduce sexually.²¹ But this means that we cannot explain sexual reproduction through group

21 One could argue that genetic drift can also occur with asexually reproducing organisms. The earlier mentioned form of genetic drift takes place as genes, through homologous recombination, are random samples from the parental generation, which thus does not concern asexually reproducing organisms. But genetic drift, defined as the change of gene frequencies over generations resulting from chance rather than from selection, takes also place as some individuals for reasons that do not relate to their fitness (in other words, through chance) manage to reproduce more or less successfully than others. And this latter form of genetic drift occurs with asexually reproducing organisms as well. Let us imagine a population of 30 asexually reproducing individuals, 10 of genotype AA, 10 of Aa, and another 10 of aa, and all these genotypes have the same fitness. Also here, frequencies of genotypes within the population will not remain constant over time. For example, some individuals of genotype AA can die before they manage to reproduce, and some of genotype Aa might by chance find more food resources which allows them to reproduce more effectively. The gene frequencies therefore change due to genetic drift instead of natural selection. Thus this leaves one possible scenario that we have to explore. Sexual reproduction cannot have evolved through the mechanism of natural selection working on a replicating string of DNA nor on a group, but can sexual reproduction have emerged through the mechanism of genetic drift occurring with asexually reproducing organisms? In other words, is there a possibility that organisms that initially reproduced asexually, developed sexual reproduction through this form of genetic drift? No, this cannot, and for two reasons. First of all, there is a fundamental difference in the occurrence of genetic drift in sexually reproducing populations,

selection. A premise for group selection to be operative is genetic drift, and genetic drift both assumes and requires sexual reproduction. If we attempt to explain sexual reproduction through group selection, we mix the condition for the explanation (variation assuming genetic drift assuming sexual reproduction) with the explanation itself (sexual reproduction). So while it is unlikely that group selection results in the evolution of complex adaptations in general, group selection resulting in the evolution of sexual reproduction is impossible, as group selection already assumes the existence of sexual reproduction.

and genetic drift occurring in asexually reproducing organisms. In the former, genetic drift can cause changes *within* organisms, as sexual reproduction recombines the genetic content inside organisms. So the genetic constitution in sexually reproducing organisms can be changed through genetic drift, but this genetic constitution remains unchanged in asexual reproducing organisms. Genetic drift occurring with asexually reproducing organisms cannot change the distribution of genes within organisms, but only change the distributions *of* asexual organisms. So it cannot account for the emergence of new features within organisms at all, which leaves it unable to account for sexual reproduction. Second, while genetic drift can explain the change of distribution of designed entities (either genes or organisms), it cannot account for design itself. Natural selection is therefore crucial as it is a mechanism that offers the possibility to account for design, how, in the words of Monod, from the noise of random mutations and disturbances of genetic material, the music of the biosphere can be created. Through the iterative process of mutations, replication and natural selection, natural selection can lead to the accumulation of organisms with a specific make-up. Operating as a sieve through which only those changes are retained that contribute to the stability or replication of the replicator, only natural selection can lead to design. Genetic drift, on the other hand, leads to the random distribution of genes or organisms, but never to design. Sexual reproduction is a complex biological feature constituted by organs like the primary and secondary genitals, gland system, and some sections of the brain, a feature in other words, characterized by design. It can thus never be explained through genetic drift. Genetic drift can lead to evolution, but never to design.

§ 8. *The mechanism of sexual selection is equally unable to account for sexual reproduction. This means that the theory of natural selection in the versions we have investigated cannot account for an elementary characteristic of living beings, sexual reproduction.*

Until now, we have concluded that sexual reproduction cannot be accounted for by the *principle* of natural selection, as sexual reproduction cannot be explained as a trait (adaptation) that evolved through that mechanism, at least in the known versions of the theory of natural selection. But the theory of natural selection consists of more mechanisms. The principle of natural selection might be the theory's most important principle or mechanism, but it is not the only one.

One of the other mechanisms is genetic drift, which was defined as the change of gene frequencies over generations resulting from chance rather than from selection. We have dealt with this mechanism as a source of variation between groups. We have concluded, however, that genetic drift assumes sexual reproduction, so this mechanism cannot explain sexual reproduction either.

Another mechanism or principle of the theory of natural selection is sexual selection. As Darwin himself also realized, some forms of design cannot be explained by natural selection, such as the peacock's tail and its behavior of displaying it. To account for these features, Darwin introduced the mechanism *sexual selection*. Sexual selection was dealt with by Darwin in the *Origin of Species*, and more extensively in *The Descent of Man and Selection in Relation to Sex* (1871). In *The Origin of Species* we read:

Sexual Selection [...] depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring. [Darwin 1968: p. 136]

Success in reproduction depends on the success in the struggle over the females. Thus, those males that are best equipped for that struggle will reproduce and transfer their characteristics to the next generation. Victory can depend on several factors, such as vigor as well as the possession of special weapons, but the contest can also take place with more peaceful weapons, such as beauty or by singing in the case of birds. These features, which are not directly connected with the act of reproduction but enhance the bearers' chance to perform that act, Darwin called secondary sexual characteristics [Darwin 1922: p. 319]. Thus, sexual selection can explain how features that do not provide a direct advantage in terms of survival, can evolve, namely due to their contribution to reproductive success. In fact, this form of selection could explain why certain organisms have developed features that may even diminish an individual's chance of survival, such as the peacock's tail. The existence of these features would bring an advantage to organisms, not in terms of survival, but in relation to reproduction, so that the reduced survival rate of peacocks with long, colorful tails is compensated by their increased advantage in reproduction.

In fact, Darwin's sexual selection combines two distinct mechanisms.

Sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species; whilst natural selection depends on the success of both sexes, at all ages, in relation to the general condition of life. The sexual struggle is of two kinds; in the one it is between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remain impassive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners. [Darwin 1922: p. 939]

The first class of secondary sexual characteristics – like pugnacity, weapons of offence and the means of defense, increase the chance of reproduction as they increase the chance of success in obtaining a mating partner in the struggle amongst the other males. The second class of secondary sexual characteristics like singing, plumage or antics, form an advantage in sexual reproduction not because it allows males to fight with other males more effectively, but only because *females select* based upon these features. So this advantage depends on the fact that females select males for this feature, not because it allows males to struggle more effectively with other males. So we have sexual selection (1), resulting in things like increased pugnacity and means of defense in light of the struggle between males for females, and sexual selection (2), resulting in things like increased beauty or complexity in songs or plumage in light of females selecting males for these features.

This can be true, but sexual selection, of course, can never explain sexual reproduction. The latter assumes the former. In fact, as we have seen with genetic drift that occurs in sexually reproducing organisms, sexual selection should rather be seen as a mechanism that takes place when conditions for the principle of natural selection to be operative are present. In case the conditions of evolution by the principle of natural selection (struggle for survival, heritable variation effecting fitness, etc.) are present, other mechanisms will take effect as well. Genetic drift within organisms will occur in the sense that the distribution of genes in the gene pool will randomly change over time, especially in small populations. If there is a struggle between males for the possession of females, sexual selection will take place on the basis of characteristics like strength, pugnacity and weapons of offence, as well as on characteristics like song, plumage or antics in case females choose males based on these.

For all these mechanisms, sexual reproduction is an elementary assumption. Genetic drift and sexual selection exist because of sexual reproduction, and therefore can never explain it. Sexual

ON SEXUAL REPRODUCTION

| EXPLANANS | | EXPLANANDUM |
|---|--|---|
| Tendency of organic beings to strive to increase their numbers to the maximum | Struggle for survival | Evolution by genetic drift (not leading to design) |
| Limited resources | | Evolutionary process of adaptation (leading to design) |
| Heritable variation affecting fitness | | |
| Struggle between males for the possession of females | | Evolutionary process of adaptation by sexual selection of secondary characteristics like pugnacity, weapons of offence and the means of defence (leading to design) |
| Struggle between males for the possession of females | Females choosing most attractive males | Evolutionary process of adaptation by sexual selection of secondary characteristics like singing, plumage or antics (leading to design) |

Figure 4. The explanation of evolution by natural selection (as in Darwin's version of the theory of natural selection), genetic drift and sexual selection. Note that only evolution by natural selection and sexual selection can lead to design through the evolutionary process of adaptation.

reproduction is *explanans* not only for the evolutionary process of adaptation through natural selection, but also for evolution by genetic drift and evolution by sexual selection (see Figure 4). None of these mechanisms can account for sexual reproduction. The problem, the elementary gap of the theory of natural selection, is therefore the fundamental incapability to account for one aspect of living beings that serves as the very condition of all of these mechanisms – sexual reproduction.

In conclusion, sexual reproduction cannot be explained by the existing versions of the theory of natural selection. Sexual reproduction is exhibited by creative teleonomy – directed to the creation of new genetic codes, and not conservative – directed to the stability or preservation of a genetic code of which the DNA coding

for sexual reproduction is part. And this creative aspect of this teleonomic process makes it impossible to have it accounted for by the principle of natural selection as an adaptation for the good of a string of DNA. Nor can it be accounted for by the principle of natural selection working on groups. The other mechanisms or principles of the theory of natural selection, genetic drift and sexual selection, are equally unable to account for sexual reproduction as they both assume and require its existence.

III An Analysis of Darwinian Attempts to Explain Sexual Reproduction and 'The Queen of Evolutionary Problems'

Problems cannot be solved
by thinking within the framework
in which they were created.
— Albert Einstein

§1. *This chapter provides a historical overview of attempts of evolutionary biologists to explain sexual reproduction. Additionally, it will analyze the 'queen of evolutionary problems', the problem most commonly associated with the explanation of sexual reproduction through the theory of natural selection, and determine the relation of this problem with the conclusions of the previous chapter.*

In the previous chapter we have analyzed the conceptual framework of living beings that Dawkins, Monod and Williams use when they aim to provide an explanation of living beings through the principle of natural selection. The essence of the framework is that adaptations exist for the good of a replicating string of DNA of which the DNA coding for these adaptations is a part, and that these adaptations evolve due to their contribution to the stability or replication of these replicators. We have concluded that sexually reproducing living beings do not fit into this framework. This revealed itself after our scrutinizing Dawkins' choice of the gene as the unit of selection – a choice which became the dominant view among evolutionary biologists. Dawkins was compelled to settle on the gene as the unit of selection, i.e. the unit that adaptations

exist for the benefit of, as this is the only unit within sexually reproducing organisms that behaves as a replicator. We, however, have come to the conclusion that this gene cannot serve as unit of selection and that this appointment rests on an erroneous understanding of the relation between the evolutionary process of adaptation, adaptations, and the replicator.

At this stage of our analysis, we make two important observations. First, we must remember that the conclusions presented in the previous chapter are novel. Despite the fundamental objections against the gene-centered view on evolution which have been outlined in this work, the view that adaptations – including sex – exist for the good of the gene, became, and still is, the dominant idea amongst evolutionary biologists. Second, Darwinian explanations require more than a mere indication of the unit for the good of which adaptations exists. A Darwinian explanation for a feature as an adaptation should also provide its function, an account as to *how* it benefits that unit, how it contributes to the stability or replication of the unit. We can call the ability of succulent plants to store water in their leaves and roots an adaptation *because* this feature increases the success of survival in arid environments in which these plants are found.²²

However, when we analyzed the possibility to explain sexual

22 Thus a Darwinian explanation for a feature consists of indicating (1) the replicator of which the DNA coding for this feature is part and (2) how this feature benefits this replicator, i.e. its function. This explanation in itself, however, rests on the assumption that if a feature evolved for the benefit (stability or replication) of a replicator, this feature continues to benefit this replicator over time. It is on account of this assumption that the *current* characteristics of features are used to determine the possibility of a *historical* process, i.e. the evolution of a feature by means of the mechanisms of the theory of natural selection. As with many biological concepts, ‘function’ has been a source of biological-philosophical debate, see for example Amundson and Lauder [1998], Kitcher [1998], Godfrey-Smith [1998] and Wouters [2003].

reproduction as an adaptation in the previous chapter, we never arrived at this aspect of the explanation for sex as we got stuck in the attempt to find a unit of selection. Yet contemporary evolutionary biologists do assume this unit to exist in the form of the gene, and also made attempts to indicate how sex benefits the gene. In this chapter we will analyze how they addressed this second aspect of the explanation of sex, how this feature – sexual reproduction – is assumed to benefit the stability or replication of the gene.

The question can be raised why we are doing this. As can be rightfully argued, this analysis is unnecessary because we have already concluded that an explanation of sexual reproduction within the framework of Dawkins, Williams and Monod is impossible. Sex cannot be explained as an adaptation because no replicator can be identified of which the sequence of DNA standing at the base of this feature is a subset – full stop. An important reason, however, why we will still make this analysis is that by doing so the so-called ‘queen of evolutionary problems’ will surface. In the introduction of this work, we have already stated that many scientists acknowledge that explaining sexual reproduction through the theory of natural selection is problematic, which led people to call sexual reproduction the queen of evolutionary problems. At the same time, we have stated that the critique in the current work is of a more fundamental nature. In this chapter we will delve into this ‘queen of evolutionary problems’, so as to describe its relation to the conclusions of Chapter 11.

The structure of this chapter is as follows. We will first deal with those explanations for sexual reproduction that predate the emergence of the gene-centered view on evolution, as these had an influence on later explanations as well. Having arrived at the explanations for sex within the gene-centered model of evolution, we will list the most important ones, as well as analyze their reception amongst evolutionary biologists. After that, we will determine exactly where these explanations conflict with the conclusions of the

previous chapter, and analyze in detail the problem known as the queen of evolutionary problems.

§2. *In this section we analyze Darwinian explanations for sexual reproduction in versions that hold that adaptations are for the good of groups or species, which were dominant before the 1960s and 1970s.*

Earlier in this study, we have analyzed Darwin's explanation of the evolutionary process of adaptation as described in *The Origin of Species*. This explanation was shown to be insufficient in nature, as it assumes the struggle for existence (survival and reproduction) as a fact and prerequisite for natural selection. In some of his other works, however, Darwin did suggest explanations for sexual reproduction. Prior to his ideas about natural selection, Darwin had suggested that sex generates differences between parent and offspring, and that this is an adaptation that enables species to evolve. Later Darwin suggested that sex exists as it keeps the amount of variation within certain limits [Gishelin 1988]. These suggestions, however, in no way amount to a solid explanation of sexual reproduction.

One of the first detailed Darwinian accounts of sexual reproduction was provided by August Weismann (1834–1914). Despite the fact that his account must be dismissed beforehand as he erroneously adheres to the notion of group selection, we will still deal with his explanation as it formed the basis of explanations within the gene-centered view on evolution. Weismann is mostly known for his germ plasm theory according to which, in multicellular organisms, heredity only takes place through the germ cells. The somatic cells, on the other hand, do not function as agents of heredity because genetic information cannot be transferred from soma to germ cells. Although expressed in terms that pre-date the genetic and molecular revolutions of evolutionary biology, this notion is still central to modern evolutionary biology. Only changes in the DNA that are part of the germ cells will be transferred to the

next generation. Changes occurring to DNA that are part of the somatic cells will not be transferred.

Weismann provided an account of sexual reproduction in his essay *The Significance of Sexual Reproduction in the Theory of Natural Selection* [1889]. This account finds its origin on the one hand in the above mentioned germ plasm theory, and on the other on an erroneous understanding of heredity and variation.

Let us look in more detail at the latter. Weismann's ideas as well as Darwin's on heredity and variation are very different from current ideas. Current ideas find their basis in the modern (or new) synthesis, which emerged around the 1940s. This synthesis unified evolutionary biology and Mendelian genetics. George Mendel (1822–1884) showed that traits are linked to distinct genes, rather than to constitute a continuous blend of characteristics inherited from two parents. In the modern synthesis, this conception of heredity was fused with the theory of natural selection, as it was allegedly shown that natural selection is consistent with Mendelian concept of inheritance. In the decades thereafter, the molecular basis of genetics was revealed which culminated in the discovery of DNA in 1953. Darwin, however, adhered to the idea of blended heredity, i.e. that the characteristics of an individual are a blend of those of its parents.²³ Moreover, Darwin believed that environmental changes were necessary to generate variation [Winther 2000]. For Darwin, all variability was due to changes in the conditions of life. Also, Weismann adhered to the idea that variation among individuals was caused by external, not internal circumstances.

But this conception of the cause of variation leads to problems when considering Weismann's germ plasm theory. As we have

23 This concept does not mean that the characteristics of an individual are based on a blend (in the sense of a mix) of the genes of its parents (this being in line with the modern synthesis): it means that, for example, the height of a person is always some interim value between his or her parents' height, or the hair color a value between his or her parents' colors.

seen, this theory states that in a multicellular organism, heredity only takes place by means of the germ cells. So changes occurring within somatic cells, and variation henceforth created, are not heritable. On the other hand, the environment has very little effect on the germ cells. So how can variation, the essential condition for the principle of natural selection to do its work, arise? Or, as Weismann wrote:

Individual variability forms the most important foundation of the theory of natural selection: without it the latter could not exist, for this alone can furnish the minute differences by the accumulation of which new forms are said to arise in the course of generations. But how can such hereditary individual characters exist if the changes wrought by the action of external influences, during the life of an individual, cannot be transmitted? [Weismann 1886: pp. 267–268]

It is here where sexual reproduction comes in. Weismann claims that the secret of the existence of sexual reproduction lies in providing variability among individuals. The ‘object’ of sexual reproduction is to create those differences that form the material out of which natural selection produces new forms, characteristics and species.²⁴

I believe that such a source is to be looked for in the form of reproduction by which the great majority of existing organisms are propagated: viz. in sexual, or as Hackel calls it, amphigonic reproduction [...] The object of this process is to create those individual differences which form the material out of which natural selection produced new species. [Weismann 1886: p. 272]

To conclude, Weismann proposes that the theory of natural selection is by no means incompatible with the theory of germ plasm,

adding that through this theory, sexual reproduction appears in an entirely new light; it has received a function as the engine behind individual variety, that necessary condition for natural selection to operate.

As we have seen, Weismann's assumption concerning the origin of heritable variation is erroneous as he was ignorant of genes and DNA. According to current biological knowledge, DNA carries the heritable genetic information of organisms, and the heritable variation between individuals is constituted by the linear sequences of nucleotides which constitutes DNA. Moreover, changes within this DNA are caused by mutations in the form of point mutations, inversions, deletions, or insertions of strings of DNA. These random changes, however, can have external as well as internal causes, and more importantly, can also occur within the DNA of germ cells.

But despite the fact that heritable variation can still originate in the genetic information residing in the germ cells, a fact which removes the very reason that gave rise to Weismann's account for sexual reproduction, it still remains true that sexual reproduction *increases* the genetic variability between organisms. Contrary to

24 Asexual reproduction ('monogonic processes'), Weismann argues, can never produce this variation. Natural selection is impossible in a species propagated by asexual reproduction. But, as one might remark, what does this individual variation originate from? Sexual reproduction creates variety by combining individual differences in ever new combinations in every generation, but what do these individual differences come from in the first place? The influences of the environment, the sole source of variability according to Weismann, on the germ cells is not strong enough to account for this variation. External influences can only produce changes in the molecular structure of germ cells over very long – too long – periods of time. This origin of hereditary individual variability, then, has to be sought for in the lowest, unicellular organisms. In these, the distinction between body-cell and germ-cell does not exist, and therefore, external influences can cause variety. Various external influences that act upon the individuals of unicellular species will lead to hereditary individual differences.

Weismann's notion, variation *can* originate in sexually reproducing organisms through mutations occurring in the DNA of germ cells. But at the same time, sexual reproduction will *enhance* this variation through combining the genetic content in ever changing combinations. Sex is not necessary to create variation but will enhance its occurrence. For this reason, supplying variation, benefiting the species by making it more adaptive, has been proposed by scientists after Weismann as the function of sex. In fact, Weismann's ideas prevailed for nearly 80 years [Ghiselin 1988]. We see his views reflected in Fischer [1930] and Muller [1932], who also claimed that 'mixis', the generation of new combinations of genes by mixing genomes through sexual reproduction, benefit species by increasing their rate of evolution, making them more adaptive.²⁵

§3. Several theories have been developed from the mid-1960s onwards attempting to explain sex as adaptation that is in line with the gene-centered model of evolution. These theories struggle to account for the cost of meiosis.

In this study we have concluded that the gene-centered model on evolution is based on an erroneous understanding of the relation between the evolutionary process of adaptation, adaptations, and the replicator. Adaptations can only be accounted for as features that benefit the stability or replication of a replicator of which the DNA coding for these adaptations is part, which disqualifies anything above the level of gene – including sexual reproduction – as an adaptation that evolved through the principle of natural selection.

It is therefore no surprise that when, building on this flawed assumption, scientists attempted to explain sexual reproduction for the good of the gene, they ran into problems. When you start with erroneous premises, chances are that you will run into problems somewhere along the way. One of these problems, one that

explicitly entered the consciousness of evolutionary biologists, is the following. During the process of meiosis, when gametes are produced (germ cells in males, and egg cells in females that will form the zygote after fertilization), only half of the genes make it to these individual cells. Thus, only half of the genes of a genome will be transferred to the next generation. So if sexual reproduction

25 Weismann's ideas are outdated and controversial not only because of the earlier mentioned fact that Weismann adhered to the notion of group selection, but also because Weismann's notion seems to assume that evolution is a goal in itself. Sexual populations would outcompete asexual populations as they evolve more rapidly in response to environmental change. The biologist Graham Bell called Weismann's theory the Vicar of Bray hypothesis, after a fictional sixteenth-century cleric who quickly switched between Protestant and Catholic rites as the ruling monarch changed [Ridley 1993]. But this idea is profoundly flawed, a 'teleology trap', the argument being that evolution is a goal in itself. Bell argued, 'Only gradually did it dawn on modern biologists that the Weismann logic was profoundly flawed. It seems to treat evolution as some kind of imperative, as if evolving were what species exist to do – as if evolving were a goal imposed on existence' [Ridley 1993: p. 31]. However, as Ridley himself argued, this teleology trap can be avoided. Stating that sex has an advantage for species as it allows them to better evolve indeed would be a flawed argument. Evolution, indeed, is never a goal in itself, so no adaptation can exist only for the benefit 'to evolve'. So Weismann's reasoning is indeed flawed when he says, 'I do not know what meaning can be attributed to sexual reproduction other than the creation of hereditary individual characters to form the material upon which natural selection may work' [Weismann 1886: p. 281]. Or, 'The object of [sexual reproduction] is to create those individual differences which form the material out of which natural selection produces new species' [Weismann 1886: p. 272]. Not evolution, nor natural selection, nor the creation of new species can be seen as a goal adaptations exist for the benefit of. But survival can be. And if sexual reproduction increases the survival rate of a species by allowing them to better adapt to new circumstances, then sexual reproduction can be seen as a means towards this goal of survival, just as any other adaptation can be seen in this light. Evolution is not a goal in itself, but the evolutionary process of adaptation is a means towards survival assuming the ever changing conditions of life in which species must operate.

is an adaptation for the gene, why are half of those genes discarded during that process? What can be the benefit of sex so that it compensates for 50% of the genes being discarded during sexual reproduction? Therefore, as Williams argued, the primary task for anyone wishing to show that sex is evolutionarily advantageous is to find a 50% advantage to balance the 50% cost of meiosis [Williams 1975: 11].²⁶ Attempts to explain sexual reproduction therefore consist of describing what conditions could have led to the evolution of this seemingly maladaptive feature.²⁷ Several theories have been proposed to account for sex, and in this section the most important ones will be listed, including an overview of the reception of these theories amongst evolutionary biologists. In this overview, we will largely follow a well-known work on sexual reproduction, Matt Ridley's *The Red Queen* [1993]. An analysis of these theories based on the lessons from the previous chapter will be provided

26 The conclusion of this study is that current versions of the theory of natural selection cannot explain the existence of sexual reproduction, no matter whether such a quantitative advantage can be given over asexual reproduction. Williams, however, is clearly not willing to consider this option when he says, 'The impossibility of sex being an immediate reproductive adaptation in higher organisms would seem to be as firmly established a conclusion as can be found in current evolutionary thought. Yet this conclusion must surely be wrong. All around us are plant and animal populations with both asexual and sexual reproduction. Can we seriously consider that the quantitative appointment of resources to these two processes is not subject to Darwinian selection? Do aphids, coelenterates, and various higher plants seem to be evolving a reduced frequency of sexual reproduction? Only consistently negative answers are possible for these questions [...]. The observed incidence of asexual and sexual reproduction must represent for these forms the currently adaptive optimum maintained by selection. In these populations there can be no net disadvantage to sexual reproduction' [Williams 1975: p. 11]. In other words, Darwinism, more specifically the gene-centered view of evolution, must be right, and therefore sexual reproduction must have a selective value. The goal is to find it. The first premise possibly being wrong is not considered an option.

in the section after this one, so all the criticism that is listed in this section concerns criticism from evolutionary biologists that adhere to the gene-centered model on evolution.

One group of theories to explain the function of sex revolves around the idea that the selective value of sexual reproduction lies in the creation of variation, identical to Weismann's theory but applied to the gene. We have seen that for Weismann, it was an elementary procedure to suggest a mechanism for variety in light of his germ plasm theory on the one hand, and his erroneous understanding of heredity and variation on the other. According to the current understanding of heredity and variation, heritable variation between entities consists of changes within DNA caused by mutations in the form of point mutations, inversions, deletions, or insertions of strings of DNA, and these random changes can also occur within the DNA of germ cells. But although sexual reproduction is not essential to supply variation, it does add to it, which

27 Maynard Smith [1978] wrote about the cost of males. About half of the offspring that a female produces are males, but in a way these males form a dead end as they cannot produce offspring themselves. If females would reproduce asexually by means of parthenogenesis and these females would in turn produce asexually reproducing females, not just half of their offspring would be able to reproduce itself, but all. So what is the advantage of sex that could compensate for its cost in light of the above? Two things must be noted here. First, Maynard Smith's cost of males only applies to those species where there are separate male and female sexes, so it excludes hermaphroditic species. Second, for those species it applies to, the cost of males is a problem that is not particularly related to the gene-centered view of evolution. The cost of males is a problem that applies to any interpretation of the theory of natural selection that sees the selective value of traits in producing offspring *in a quantitative way* (the more, the better). There is also a 'cost of males' according to interpretations of the theory of natural selection that assume adaptations for the good of individuals, or groups of species as long as it sees the selective value of traits quantitatively. Why does sex exist as it produces N offspring (genes, individuals), while it could produce $2N$ offspring if males would not exist?

caused biologists to continue to see sexual reproduction as an adaptation for the good of the group by enhancing variation even after Weismann's ideas about heredity and variation became outdated. Next, group selection became controversial, but the same reasoning can be applied to genes as well. With equal right, sexual reproduction can be seen as an adaptation for the good of the gene by providing variation. George C. Williams and John Maynard Smith assumed that sexual reproduction should be seen in this light, because through creating genetic variation it increases the likelihood of the survival of offspring when facing changed or uncertain conditions. In his work *Sex and Evolution* [1975], Williams proposed several models in which variety could give an adaptive advantage. The *Aphid-Rotifer* model applies to organisms that live in isolated confined spaces for longer periods of time, but periodically will establish new colonies. Sexually reproduced colonists in such a new habitat are more likely to include the winning genotype, giving sexual reproduction an advantage. The *Strawberry-Coral* model deals with sessile organisms that multiply vegetatively in continuous habitats, but produce seeds or spores that are widely dispersed. The *Elm-Oyster* model deals with organisms whereby large numbers of the young of a sessile form compete for space fully utilizable by one adult, and one of the very few fittest is likely to win all or most of the space. Here, genetically diverse progenies are more likely than uniform ones to include the fittest few. The analogy for these models is a lottery, on the assumption that the best chance to win a lottery is to buy many different tickets instead of buying many tickets with all the same number.

Another theory developed in the 1970s to explain the advantage of sex by providing variety is the *tangled bank* theory, proposed by Michael Ghiselin. The idea here is that in an overcrowded space with many competitors, it pays to diversify. Here, the analogy is an economic one. As Ghiselin explains:

Briefly summarized, it asserts that in a saturated environment, it pays to diversify. When it's a seller's market for, say, automobiles, manufacturers should produce just one kind of good. But in a buyer's market, the manufacturers should produce a variety of automobiles of different sizes and costs. When they do, the market for such goods will actually increase; for example, some people will do without a car if only expensive ones are available. Translated into ecological jargon, diversity raises environmental carrying capacity by increasing the number of niches. [Ghiselin 1974: p. 16]

In other words, in an overcrowded space, it pays off to diversify, as each sibling uses a slightly different niche. Clones, on the other hand, are forced to occupy the same – overcrowded – one.

Another group of theories revolve around the idea that sexual reproduction is an adaptation countering the negative effects of mutations. Mutations are the changes the principle of natural selection can act upon. But mutations are not necessarily beneficial to the organism. In fact, the great majority of them are neutral or deleterious to the needs of the organism. Eventually, the accumulation of these mutations, called their mutational load, will be harmful to organisms. The theory called *Muller's ratchet* proposes that sexual reproduction evolved as an adaptation to ease that mutational load. The theory is named after the biologist H.J. Muller, who we have encountered as a supporter of Weismann's idea that sexual reproduction benefits species by increasing variety [Muller 1932]. At a later stage, Muller also suggested that sex prevents genetic deterioration through mutational load. A species without recombination, Muller argued, would not only be hampered in its evolutionary advancement but actually subject to genetic deterioration [Muller 1964]. In asexually reproducing organisms, genetic defects would inevitably accumulate. However, sexual

reproduction allows defect-free genes to spread through a population thereby replacing the deleterious ones. Sexual reproduction is proposed as an efficient process to remove mutations. As Ridley in *The Red Queen* [1993] explains:

There are ten water fleas in a tank, only one of which is entirely free of mutations; the others all have one or several minor defects. On average only five of the water fleas in each generation manage to breed before they are eaten by a fish. The defect-free flea has a one-in-two chance of not breeding. So does the flea with the most defects, of course, but there is a difference: Once the defect-free flea is dead, the only way for it to be re-created is for another mutation to correct the mutation in a flea with a defect – a very unlikely possibility. The one with two defects can be re-created easily by a single mutation in a water flea with one defect anywhere among its genes. In other words, the random loss of certain lines of descent will mean that the average number of defects gradually increases. Just as a ratchet turns easily one way but cannot turn back, so genetic defects inevitably accumulate. The only way to prevent the ratchet from turning is for the perfect flea to have sex and pass its defect-free genes to other fleas before it dies. [Ridley 1993: pp. 47–48]

According to another theory, sexual reproduction is an adaptation to get rid of deleterious mutations at an even earlier stage. According to the *repair hypothesis*, sexual reproduction is not primarily an adaptation for purging deleterious mutations out of a population, but an adaptation for repairing them. An important process within meiosis is homologous recombination, whereby parts of chromosomes are exchanged, leading to chromosomes having a unique mixture of maternal and paternal DNA. Homologous recombination is, however, a type of genetic recombination that does not only occur during meiosis, it is also a process used for repairing

harmful breaks that occur on strands of DNA called double strand breaks. DNA can be damaged through endogenous processes, such as replication errors, as well as exogenous factors such as radiation and UV light. Organisms have an elaborate system for DNA repair and protection. When only one of the two strands of a double helix has a defect, the other strand can be used as a template to guide the correction of the damaged strand. Various such mechanisms exist, for example base excision repair, nucleotide excision repair, and mismatch repair. However, in case of so-called double-strand breaks, the other strand cannot be used as a template. In this case, other mechanisms get into action, one of them being homologous recombination.

Proponents of the repair hypothesis claim that sexual reproduction arose, and is maintained, because of the direct advantage of recombinational repair of genetic damage [Michod and Levin 1988]. Genetic variation is produced as a by-product of recombinational repair, but it may not be the primary function of sexual reproduction.

Yet another theory, the *Red Queen theory* (no relation to the queen of evolutionary problems) was introduced by Leigh van Valen in 1973. The term is taken from the character in Lewis Carroll's *Through the Looking Glass*, who said that it takes all the running you can do to keep in the same place. The observation that stands at the basis of this theory is that in the biological world, survival never gets easier. Organisms might well adapt to their environments, but they can never become static as competitors and enemies are also adapting to their niches. For the Red Queen hypothesis, sex has nothing to do with adapting to the inanimate world, but has to do with competing with other species. Or, as Ridley calls it, with the enemy that fights back [Ridley 1993]. The great struggle does not consist in fighting the physical environment, but the biological one, such as in the form of parasites, predators and competitors. Organisms are therefore involved in a constant

‘genetic arms race’, whereby every organism must constantly run to stay at the same place: continuous adaptation is needed in order for organisms to maintain their relative fitness amongst the organisms they co-evolved with. In *The Red Queen*, Ridley explains why the interaction between host and parasite is an intense one. Parasites have a deadlier effect than predators. There are many of them, and are usually smaller than their hosts, which means that parasites live shorter lives and pass through more generations in a given time than their hosts, providing an advantage in rate of evolution. Parasites provide exactly the incentive to change genes every generation that sexual reproduction provides, ‘the success of the genes that defended you so well in the last generation may be the best of reasons to abandon these same gene combinations in the next’ [Ridley 1993: p. 67].

In summary, we have four groups of theories to account for sexual reproduction that are compatible with the gene-centered model on evolution (see also Cartwright [2001]: p. 99):

1. Sex as a producer of variable offspring to thrive as environments change through time (Williams’ lottery models);
2. Sex as a producer of variation to thrive in an overcrowded space with many competitors (the tangled bank theory);
3. Sex keeping at bay the effects of damaged DNA, by weeding out deleterious mutations (Muller’s ratchet) or repairing them (the DNA repair theory);
4. Sex as an enabler of organisms to remain competitive in a world where other organisms are poised to take advantage of any weakness (the Red Queen).

As Matt Ridley documents in *The Red Queen*, the first three groups of explanations for sexual reproduction have received substantial criticism. The lottery model, sex as a creator of genetic variation thereby increasing the likelihood of offspring surviving under

changed or uncertain conditions, is assumed to work only under specific circumstances, namely when the reward of the lottery is very high. Only if a few of the offspring survive and do spectacularly well, does sex pay off. Moreover, it only works with species whereby young are produced that migrate elsewhere. Sex, on the other hand, is ubiquitous. Moreover, empirical data seem to contradict the model: assuming that sex would indeed be an adaptation for facing uncertain conditions, a correlation must be found between ecological uncertainty and sexuality, a correlation which is not found (see Ridley [1993]: p. 59).

The case for the tangled bank theory is also not considered too strong by evolutionary biologists. This theory would predict a greater occurrence of sexual reproduction in those animals and plants that have small offspring than among the plants and animals that have few large young. This correlation, however, cannot be established, nor does the level of recombination among mammals show the correlation with size, age, fecundity that would be expected with the tangled bank theory. As Ridley writes, 'it is hard to find dedicated enthusiasts of tangled banks these days' [Ridley 1993: p. 61].

For a variety of reasons, theories that consider sexual reproduction as an adaptation for the repair of DNA or the removal of deleterious mutations do not attract wide support either (see Ridley [1993]: pp. 44–51). The repair theory gives an advantage for recombination, but is silent on outcrossing. From a repair point of view, there is no reason that DNA from different individuals should mix during fertilization. Moreover, polyploidy, the fact that organisms contain more than two paired sets of chromosomes, provides the same advantage for organisms as recombination does in terms of repair, but is more economical. Also, the question is why the process of recombination only takes place during meiosis, and not every time the cell divides during mitosis. Further, Muller's ratchet theory is considered to work too slowly, and is also cumbersome

and ‘expensive’ compared to alternatives to get rid of deleterious mutations.

Although the Red Queen theory, the idea that sexual reproduction occurs because it allows hosts to change genotypes each generation and thereby evade their co-evolving parasites, has been popular for many years, here science is not unequivocal either. Some scientists doubt that parasites alone can provide a complete explanation for sex [Agrawal 2006], others claim that increasing variation does make natural selection more effective, at least in some organisms [Hoekstra 2005], suggesting support for the lottery model, while others again simply claim that, ‘despite many years of theoretical and experimental work, the explanation of why sex is so common as a reproductive strategy continues to resist understanding’ [De Visser and Elena 2007: p. 139].

§ 4. The proposed explanations listed in the previous section are analyzed in context of the conclusions we drew in the previous chapter.

Let us analyze the attempts to explain sex within the framework of the gene-centered model detailed in the previous section.

- The first thing we have to conclude – as we have done earlier – is that all these explanations are necessarily false, as by assuming sex to be for the good for the gene, the proponents of these theories violate the lessons of the previous chapter.
- But even disregarding this fundamental flaw, we have seen that none of these proposed explanations have led to a scientific consensus within the gene-centered model of evolution. In the eyes of evolutionary biologists, the queen of evolutionary problems still exists. The cost of meiosis has turned out to be too high to allow for a solution to be satisfactory to the scientific community.
- We see these explanations as an attempt to accomplish what

Williams saw as their major task, namely to find a 50% advantage of meiosis to balance the 50% cost. In doing this, they are comparing sexual reproduction to asexual reproduction (a form of reproduction whereby none of the genes are discarded) and try to come up with circumstances or environments whereby the advantages of sexual reproduction over asexual reproduction are so vast that they compensate for the 50% loss of genes compared to asexual reproduction. Thus, things like the change of environments, the harmful effects of the accumulation of harmful mutations, or the existence of parasites are proposed as circumstances that could allow for this advantage.

- In the previous chapter, we have discussed the conceptual problems connected with the term ‘gene’, concluding that in any case it cannot be defined in terms of its substance or material make-up. But in the explanations for sexual reproduction discussed in this chapter, this concept gets even more abstract. When scientists talk about the ‘good of the gene’ they are not even talking about *specific* genes (by which we mean specific lineages, entities that form a continuity in time in their structure or form) but about the chance of survival of an *average* gene within the genome. This is necessarily so: through meiosis, a random half of the genes are discarded, random in the sense that there is no way to tell beforehand which genes will be transferred to the next generation. So when talking about the good of the gene, there is no way to interpret this gene other than as an abstraction. Hence, when biologists are talking about the advantages of sexual reproduction over asexual reproduction that compensate for the 50% loss of genes, they mean that this advantage is there when the chance of survival of the average gene is greater with sexual reproduction than with asexual reproduction, despite the fact that the chance of elimination is 50% at every generation.

At the same time, this never becomes explicit. Even worse, these biologists sometimes use language that seem to contradict the gene-centered view altogether. As an example, we have seen Ridley claim that, 'The success of the genes that defended you so well in the last generation may be the best of reasons to abandon these same gene combinations in the next'. If adaptations are for the good for 'the gene', this can only be interpreted as the probability of the survival of the average gene within a genotype. But here Ridley suddenly comes up with a 'you', suggesting that sex is for the good of an individual of some sort. (A vagueness that must be familiar to the reader at this stage!)

- Another thing we have to observe is that the queen of evolutionary problems confronts us when one attempts to explain sex and considers the gene to be the unit of selection, but that this problem is not one-to-one related to the problem of creative teleonomy that was dealt with in Chapter II. Let us imagine that during meiosis, not one but two gametes would always be produced, and both of these gametes would contribute to the next generation. In other words, not one, but two individuals would be produced in sexual reproduction, without any genes left in parent organisms that would not be transferred to the next generation. Here, there would be no cost of meiosis. But this form of sexual reproduction could still not be explained as an adaptation. Sexual reproduction would still be exhibited by creative teleonomy (directed to the creation of new genetic codes) and not conservative (directed to the stability or replication of a genetic code of which the DNA coding for sexual reproduction is part). In other words, the creative aspect of the teleonomy exhibited in sexual reproduction is not necessarily related to the cost of meiosis. With the same logic, it would also mean that *if* a convincing model were proposed that would solve problem

the second, that is, a model that would find a convincing 50% advantage to balance the 50% cost of meiosis, the problem that is the subject of this study would still exist. After all, this model would still rest on the flawed idea that the gene is the unit of selection of the sexually reproducing organism.

So what is the relationship between the conclusions of Chapter II and the queen of evolutionary problems? What does this problem reveal? This conundrum must be seen as nothing else than an indication of the flawed nature of the assumptions of evolutionary biologists in the form of the gene-centered model on evolution. In the previous chapter we have elaborately analyzed the choice of the gene as unit of selection. We saw that Dawkins proposed the gene as unit as it is the candidate that is left over after all other candidates were eliminated: the gene is simply the *only* candidate that can serve as a unit of selection. But although Dawkins claims that he has thus defined the gene in such a way that he ‘cannot help being right!’ [Dawkins 1976: p. 35], this choice comes at a great cost. In fact, the queen of evolutionary problems reveals the *reductio ad absurdum* that is implied therein. After all, the gene might be a unit that corresponds to the description of a replicator, but during sexual reproduction only half of an organism’s genes make it to the next generation through the process of meiosis. But this is not the only issue; it is not only that a half of the genes are discarded – there is also no way to tell which ones. If ‘the gene’ is the unit of selection, then *which* gene is that unit? A human being contains approximately 23 000 genes on each of the 23 pairs of chromosomes, so are only those genes the unit of selection that perchance – through homologous recombination – ended up in the offspring? If so, the unit of selection can only be determined a posteriori and is simply a question of blind chance. And it is this profound difficulty, as we have seen, that forces evolutionary biologists to interpret ‘for the good of the gene’ in this abstract, statistical way.

In essence, the cost of meiosis is the price Darwinists have to pay for choosing a unit of selection that seems to be in line with their theoretical description of a replicator, and a reflection of the profound difficulties they encounter when they attempt to do so. It is the malformed outcome of a search grounded on a false conceptual framework, the unsatisfying result of bending over backwards to find anything that behaves as a replicator. The queen of evolutionary problems therefore reveals the highly problematic nature of the gene-centered view of evolution, and is an additional indication of it being fundamentally flawed.

VI Discussion

The history of science indicates that a well-established theory can take a lot of battering and get into a tangle of absurdities and contradictions, yet still be upheld by the Establishment until an acceptable global alternative is offered.

— Arthur Koestler

§1. In this chapter we will attempt to provide a wider context to the conclusions of the previous chapters. We will start by assessing the possibility that alternative versions of the theory of natural selection can be developed that would provide a sufficient explanation of living beings, including sexual reproduction.

In this chapter we will try to provide a wider context to the conclusion of this study that current versions of theory of natural selection are not able to account for sexual reproduction. This part will be of a different nature than the previous chapters. The common theme running through this work is the vagueness that has surrounded Darwinian terms, concepts and explanations, and we have made an attempt to overcome this vagueness by a rigorous laying bare of the fundamental problem of accounting for sexual reproduction. In this last chapter, in which we will discuss the ramifications of the conclusions of this study, we are forced to be less unequivocal. The reason is that we cannot indisputably determine the consequences of this study unless more research has been done. The possibility

of a Darwinian explanation for sex can at this stage not be fully excluded (in fact the question can be raised whether such a fundamental conclusion could ever be drawn at all).

Moreover, an analysis of Kuhn's model of scientific revolutions will inspire us to search for an alternative paradigm to account for living beings, a search that due to its scope cannot be completed in this work. At the same time, the likeliness of the validity of some far-reaching conclusions makes this discussion an essential operation without which this study cannot end. At the very least, this chapter can serve as a guideline for further research.

Let us start by considering the possibility of a Darwinian explanation for sex after all. Throughout this work we have stressed that sexual reproduction cannot be aligned with *current* versions of the theory, which leads to the essential question whether *other* versions of the theory could be developed that would provide an explanation for sexual reproduction. After our detailed exploration of the theory of natural selection, how realistic is it to expect the emergence of other interpretations of the principle of natural selection, or perhaps scenarios in which a combination of mechanisms has been able to result in the evolution of complex features such as sexual reproduction?

In terms of other interpretations of the principle of natural selection, it is difficult to see how these could emerge. After having dealt with Darwin's version of the theory of natural selection and after having seen its fundamental limitations, we concluded that the replicator-model of natural selection is the only model that would allow for sufficient explanations through natural selection, including sexual reproduction. But we were not successful at all in translating this model to empirical reality, stumbling over fundamental problems. We have also categorically excluded the possibility that genetic drift or sexual selection could have stood at the basis of sexual reproduction.

When considering combinations of mechanisms that we might have overlooked or not considered before, we realize the difficulty in seeing how an explanation for sex could thus be achieved. Let us look at the possibility that sexual reproduction evolved from asexual reproduction in relatively small steps. Thus, the majority of the genetic code standing at the basis of sexual reproduction was shaped in an evolutionary process of adaptation through natural selection acting on asexually reproducing organisms, but after a few steps, this feature radically changed its characteristic so that it led to sexual reproduction. This scenario, however, is extremely problematic. First of all, for this scenario to be likely to happen, one should be able to demonstrate that a feature existed (or still exists) that evolved through natural selection working on asexual reproducing entities (and thus contributed to the stability or replication of the replicator of which it was part) while being genetically very similar to sexual reproduction. It is hard to imagine how such a feature – a feature that had such a completely different function – should look like. An additional difficulty is that the step from this feature to sexual reproduction needs to be very small (in terms of mutations needed) as we are lacking a mechanism – such as natural selection or sexual selection – that can account for the accumulation of specific changes. How could we imagine a feature that serves the need of an asexually reproducing organism which, in a few steps, evolves into sexual reproduction with its highly specific characteristics such as distinct reproductive organs, meiosis, mating behavior and fertilization (hereby greatly simplifying the complexity of sexual reproduction)? Saving the theory of natural selection with such a scenario could hardly pass for a sound scientific explanation, especially if we consider that sexual reproduction is a dominant, ubiquitous and extremely complex phenomenon. All this strongly suggests that the inability to account for sexual reproduction does not only apply to current versions of the theory, but to the theory of natural selection as such.

§ 2. According to Karl Popper's definition of falsification, the conclusion that the theory of natural selection is unable to account for sexual reproduction would imply a falsification of the theory, as it is established that it cannot explain a certain feature of living beings.

The relation between the theory of natural selection and its (potential) falsification is a delicate one. Various authors have claimed that the theory of natural selection is untestable and tautological, and therefore cannot possibly be falsified. The most prominent of these critics was Karl Popper, who throughout his career questioned the falsifiability of the theory of natural selection. For Popper this was an essential question, because he considered falsifiability as an elementary characteristic of any genuine scientific theory (see Hull [1999] for a chronological overview of his ideas). One of the problems with the theory of natural selection in the context of its falsifiability in Popper's view is that it, unlike comparable theories in chemistry and physics, does not easily allow for experiments. The theory of natural selection deals with changes in biological phenomena that take place over long periods of time, and these phenomena cannot be easily experimented with or tested in laboratory settings [Popper 1978: p. 344]. Another problem for the theory of natural selection in light of its falsifiability, Popper held, is that the theory of natural selection does not really predict anything, and therefore cannot be tested on these predictions. Popper says:

Take 'adaptation'. At first sight natural selection appears to explain it, and in a way it does; but hardly in a scientific way. To say that a species now living is adapted to its environment is, in fact, almost tautological. Indeed we use the terms 'adaptation' and 'selection' in such a way that we can say that, if the species were not adapted, it would have been eliminated by natural selection. Similarly, if a species has been eliminated it must have been

ill-adapted to the conditions. Adaptation or fitness is *defined* by modern evolutionists as survival value, and can be measured by actual success in survival: there is hardly any possibility of testing a theory as feeble as this. [Popper 1976: p. 137]

As ‘adapted’ means almost the same as ‘being able to survive’, being adapted effectively means the same as ‘being alive’. As all living beings are therefore per definition fit and adapted to their environment, this couldn’t possibly serve as a prediction by which the theory of natural selection can be tested.

These claims regarding testability and possible tautological nature of the theory of natural selection have been the source of a vehement debate amongst biologists and philosophers of science (see Heijdra [2009] for a detailed overview). However, this debate does not concern us in this study; despite the problematic aspects of the theory of natural selection in light of its falsifiability, according to Popper there is another, and much less controversial method by which the theory of natural selection is falsifiable, and it is this method that relates closely to what we have done in this study. The basis of this method of falsification, which Popper outlined at a later phase of his career [1978], is the proposition that *if* the mechanisms of the theory of natural selection stand at the basis of the design in organisms, these organisms should be organized and behaving in a specific way. Organisms or features can falsify the theory of natural selection if their design, structure or behavior exhibit characteristics that cannot be aligned with that theory. The test for the theory of natural selection, then, is not a scientific experiment, neither does it involve the actual observation of the process of natural selection when taking place, nor the prediction of specific characteristics of living beings. Testing the theory of natural selection means the observation of living beings and their features and processes; if they are explainable as evolved through natural selection, sexual selection or genetic drift, the theory stands; but

if they cannot be explained, the theory falls. Darwin himself also referred to this method of falsification, when he mentioned in *The Origin of Species*:

If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down. [Darwin 1968: p. 219]

In other words, natural selection would be refuted if living beings are found to contain organs which could not have been formed gradually, which is a necessary condition for it to have been formed through an evolutionary process of adaptation through natural or sexual selection. Simply the existence of such an organ would imply the falsification of that theory. Likewise:

If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection. [Darwin 1968: pp. 228–229]

David Hull remarks, ‘Popper should have been very favorably impressed with the author of the *Origin of Species* because here he is specifying in advance which phenomena would be fatal to his theory’ [Hull 1999: p. 488]. Although the theory of natural selection does not predict, as Popper showed, what *specific kinds* of varieties of living beings will evolve, the theory of natural selection does predict some of their characteristics. Life that evolved through the principle of natural selection is characterized by certain features that all organisms will share. Or, as George C. Williams explains:

[...] natural selection is a real scientific theory. It logically predicts that there are certain sorts of properties that organisms

must have, and others, such as adaptations for the ‘benefit of the species’ [...] that they could not possibly have. [Williams 1966: p. x]

Natural selection can lead to design, but not to all forms of design, to adaptations, but not to all kinds of adaptations. These features can be described negatively, as done by Darwin who excluded the possibility of the existence of organs that could not have formed gradually, or positively, as done by Popper who claimed that all aspects of living beings that are evidence of design should be ‘useful’. In any case, the theory of natural selection will impose fundamental restrictions on the possible forms of life that will evolve, and these restrictions can serve as potentially falsifying criteria.

The existence of complex organs which could not possibly have been formed by numerous, successive, slight modifications has frequently been brought up for discussion by critics of the theory of natural selection. In fact, most of the scientific skepticism of Darwinism has centered on the notion that there is no evolutionary path imaginable that could lead to some of the complex features of living beings [Behe 1998: loc. 665–672]. Features of organisms, such as eyes and wings, are of such astonishing complexity and consist of so many parts that have no role or function outside the context of an integrated whole, that it is hard to imagine how they could have been formed by numerous, successive, slight modifications. In the words of Phillip E. Johnson:

Many organs require an intricate combination of complex parts to perform their functions. The eye and the wing are the most common illustrations, but it would be misleading to give the impression that either is a special case; human and animal bodies are literally packed with similar marvels. How can such things be built up by ‘infinitesimally small inherited variations, *each* profitable to the preserved being’? The first step towards a new

function – such as vision or ability to fly – would not necessarily provide any advantage unless the other parts required for the function appeared at the same time. [Johnson 1991: p. 34]

According to the theory of natural selection, the evolutionary path towards a new feature such as an organ must be formed by the successive accumulation of very small changes, or mutations. However, to be preserved, all these many intermediates would need to have an adaptive advantage even before the completed organ would come into being in which all these components find their function in this astonishingly complex machinery, something that is considered extremely unlikely.

But the problems we encounter on the macro level are child's play when we consider organisms on the biochemical level, as Michael J. Behe claims in *Darwin's Black Box* (1998). Life is ultimately a molecular phenomenon; living beings are machines made of molecules. But science only started to elucidate the workings of life at this level from the mid-1950s onwards. Before that time, biologists, including Charles Darwin, were ignorant of the molecular basis of life, which could have resulted in the idea that the basis of life was simple. But in Behe's eyes this 'black box', the biochemical basis of life, turned out to be astonishingly more complex than one could ever have imagined. Moreover, the problem with these biochemical systems is that they are *irreducibly complex*, composed of several interacting parts that contribute to the basic systems where the removal of any of the parts causes the systems to stop functioning. Therefore, Behe claims, they cannot have arisen by numerous, successive, slight modifications, each step in that evolutionary process being useful for the preserved being.

When contemplating the astonishing complexity of cellular features and processes, Behe's point might seem compelling. It is without doubt mind-boggling to reflect on the complexity of the blood clotting cascade or the workings of the eye, while trying to imagine how these systems could have evolved from simpler or 'less

complete' predecessors through natural selection acting upon a series of naturally-occurring mutations. But the fundamental problem here is that being mind-boggling, or being extremely unlikely is not the same as impossible. As Behe himself mentioned, 'there is no magic point of irreducible complexity at which Darwinism is logically impossible' [Behe 1998: loc. 3614–3620]. For that reason, as Johnson also admitted, 'whether one finds the gradualist scenarios for the development of complex systems plausible involves an element of subjective judgment' [Johnson 1991: p. 36]. This method of falsification, therefore, will necessarily remain feeble.

But concluding that the theory of natural selection cannot explain sexual reproduction implies that we have falsified the theory, and in a *much more direct and objective way* than proposed by Behe and Johnson, whose methods are ultimately based on an 'unlikelihood'. We have seen that the theory of natural selection can lead to design, but not to all forms of design, to adaptations, but not to all kinds of adaptations. As Popper mentioned, the design that the theory of natural selection can account for is one that is 'useful'. To be more specific: the design that the theory of natural selection can account for, is not a design that is useful for just anything, but the design that is useful *for something* that makes sense in the theory of natural selection. And, as Darwin argued, this 'something' excludes, for example, anything 'formed for the exclusive good of another species'. But the very problem with explaining sexual reproduction is that no such legitimate 'something' can be identified this feature is useful for. In our study, we concluded that adaptations can only be explained as features that contribute to the preservation and replication of a replicator of which this feature is part, but that with sexual reproduction, this relation between an adaptation and a replicator does not exist. In other words, the fact that sexual reproduction cannot be explained by the theory of natural selection implies that sexual reproduction is a falsification in the form described above and is, in the words of Hull, a phenomenon that is fatal to the theory of natural selection.

§3. *In this section we will be looking at Thomas Kuhn's model for the progress of science. We will conclude that according to his model, the outcome of this study challenges the naturalistic paradigm, although according to Kuhn's definition we cannot speak of a falsification of the theory of natural selection.*

In *The Structure of Scientific Revolutions* (1962), the philosopher and historian of science Thomas Kuhn presented a highly influential model for the progress of science. An essential concept in this model is the concept of the paradigm, which Kuhn defined as 'universally recognized scientific achievements that for a time provide model problems and solutions to a community of practitioners' [Kuhn 1996: loc. 76]. These paradigms are not mere theories or hypotheses, but ways of looking at the world, a set of basic ideas, assumptions and beliefs that serve as frameworks within which reality is understood, and serve as the basic organizing principles for scientific activities. The model defines what is to be observed and scrutinized, the kind of questions that are supposed to be asked and how these need to be structured, and how the results of scientific investigations should be interpreted. What Kuhn denotes by the term 'normal science', is the activity to force nature into the conceptual boxes supplied by the paradigm. The normal or paradigm-based research is described as a puzzle-solving activity, where scientists attempt to enlarge the paradigm, adding to its scope and precision.

Closely examined, whether historically or in the contemporary laboratory, [normal science] seems an attempt to force nature into the preformed and relatively inflexible box that the paradigm supplies. No part of the aim of normal science is to call forth new sorts of phenomena; indeed those that will not fit the box are often not seen at all. Nor do scientists normally aim to invent new theories, and they are often intolerant of those

invented by others. Instead, normal-scientific research is directed to the articulation of those phenomena and theories that the paradigm already supplies [Kuhn 1996: loc. 470].

In the course of time, some puzzles prove resistant to solutions. Facts appear that cannot be aligned with theory, phenomena identified that do not fit the conceptual box that the paradigm provides. In short, anomalies appear. Eventually, it becomes impossible to deny that there are problems which cannot be solved within the framework that the paradigm provides, leading to a crisis.

Sometimes a normal problem, one that ought to be solvable by known rules and procedures, resists the reiterated onslaught of the ablest members of the group within whose competency it falls. On other occasions a piece of equipment designed and constructed for the purpose of normal research fails to perform in the anticipated manner, revealing an anomaly that cannot, despite repeated effort, be aligned with professional expectation. In these and other ways besides, normal science repeatedly goes astray. And when it does – when, that is, the profession can no longer evade anomalies that subvert the existing tradition of scientific practice – then begin the extraordinary investigations that lead the profession at last to a new set of commitments, a new basis for the practice of science. The extraordinary episodes in which that shift of professional commitments occurs are the ones known in this essay as scientific revolutions. They are the tradition-shattering complements to the tradition-bound activity of normal science. [Kuhn 1996: loc. 206–219]

The crisis would be resolved if a new paradigm emerged, in which normal science can proceed as usual. Kuhn presents various examples of scientific revolutions and paradigm shifts in the field of physics and chemistry that follow this structure, such as the

discovery of oxygen at the end of the 18th century, and the Copernican, Newtonian and Einsteinian revolutions in physics.

Kuhn's model provides an interesting framework to analyze the outcome of this study. Let us first recall how sex causes severe headaches amongst evolutionary biologists. Its existence being called 'the queen of evolutionary problems', sexual reproduction conforms almost perfectly to Kuhn's description of an anomaly. While it was initially comfortably assumed as *explanans* in Darwin's explanatory framework and later uncritically considered to be for the good of the species by supplying variation, issues became complicated when biologists in the 1960s and 1970s were compelled to discard those versions of the theory of natural selection, and were forced to interpret adaptations as being for the good of the gene. But then, if sexual reproduction – like all adaptations – is an adaptation for good of the gene, why are half of those genes discarded during sexual reproduction? What can be the benefit of sex so that it compensates for 50% of the genes being lost during sex? This profound paradox caused the problem of sex to be dubbed an 'enigma', 'the queen of evolutionary problems', a problem that is still not solved to this very day. Using Kuhn's words, sex has without doubt resisted 'the reiterated onslaught of the ablest members', at times causing 'despair and bafflement' [Ridley 1993]. Sex has been, in other words, an anomaly *par excellence*.²⁸

In this study, we have laid bare the cause of this anomaly. Sex cannot be 'aligned with professional expectation' because it is a

²⁸ One can argue that the unit of selection (a concept so fundamentally affected by sexual reproduction), or more specifically, the failure to appoint one that is generally acknowledged as such in the scientific community, is an anomaly as well. A theory that, on the one hand, explains design and teleonomy primarily by reference to the 'for the good' of something, but on the other hand, cannot equivocally decide what the 'something' is, and in its search moves from the individual up to the species and then all the way down to the other extreme, the gene, can equally be seen as a fundamental problem for the theory of natural selection.

phenomenon that is alien to current versions of the theory of natural selection and does not fit the theoretical framework. In their search to find a level within the biological organization that conforms to their description of the replicator, evolutionary biologists were forced to appoint the gene as the unit of selection as the only option left. But this appointment came at a great cost, revealing itself as the 'cost of meiosis' when, as an implication of the gene-centered view on evolution, they attempted to explain sexual reproduction as an adaptation that evolved for the good of the gene. In this study this unsolved conundrum is shown to be caused by an unsuccessful attempt to place sexual reproduction within the framework of the theory of natural selection.

As we have seen, Kuhn claims that an anomaly challenges more than a theory; it challenges an entire paradigm, a set of basic assumptions and beliefs that serve as the basis of these theories. An anomaly reveals a problem that cannot be solved within the conceptual box that a paradigm provides. In line with Kuhn's framework, the conclusion that sex cannot be explained by the theory of natural selection also amounts to more than just challenging the theory. The paradigm for which sexual reproduction is an anomaly is not merely the theory of natural selection, but its underlying set of ideas and basic assumptions that serve as the framework through which the biological world is understood and interpreted.

In order to recognize this, we return to the introduction of this study where we reflected on the significance of Darwin's theory outside the realm of biology. The idea that species are static was more and more challenged throughout the 18th and 19th centuries, but evolution only found a compelling scientific explanation through the theory of evolution by natural selection. But Darwin's theory had a much broader significance. Modern science commenced with the explanation of physical phenomena in the 16th and 17th centuries, but its advancement outside physical phenomena was for a long time hampered by a lack of success in explaining

biological phenomena. Their seemingly goal-directedness or purposiveness, as well as their astonishingly complex design formed a fundamental problem which defied a scientific explanation.

Darwin's theory of natural selection was therefore so successful and of such great significance because it seemed to solve this dichotomy between the inanimate and animate world. Through the theory of natural selection, living beings, their design and end-directed processes, could be scientifically explained as a result of natural, mechanistic processes without having to refer to an intelligent creator. Through this, Darwin's *Origin of Species* removed the last hurdle to a complete naturalistic interpretation of life and the universe, in which nothing is assumed to exist outside the natural world, and nothing to operate but natural laws and forces. Darwin 'naturalized' the design of the organic world and the apparent end-directedness of living beings. As we already quoted Dennett, 'in a single stroke, the idea of evolution by natural selection unifies the realm of life, meaning, and purpose with the realm of space and time, cause and effect, mechanism and physical law' [Dennett 1984: p. 21]. Or, as another scholar noted, 'the undeniable purposiveness of biological structures and functions frustrated many attempts towards a mechanistic interpretation of living phenomena. Natural selection is the key to the mystery, the salvation from teleology, this 'original sin' of all living beings' [Montalenti 1974]. Through the theory of natural selection, living beings could be explained in a naturalistic way, implying that '[...] there is nothing beyond the natural, physical world, no *supernatural* creative intelligence lurking behind the observable universe, no soul that outlasts the body and no miracles – except in the sense of natural phenomena that we don't yet understand' [Dawkins 2006: p. 14].

The inability to account for sex affects both problematic aspects of living beings – their design as well as their end-directedness. Let us look in more detail at each of these problems. *The problem of design* for naturalism – assuming there is nothing beyond the natural

world, efficient causes and physical forces – is how to account for the design of living beings, their high level of organization and complexity. If the universe is ruled by the free play of physical forces to which no goal, purpose and specific direction can be attributed, and where we cannot assume the existence of an intelligent designer, how can we account for the existence of objects that look *as if* they are designed?

The principle of natural selection was proposed as the solution. Natural selection would work as a non-random sieve on random mutations, selecting useful combinations of nucleotides – combinations that contribute to the stability or replication of the replicator. In this way, natural selection creates order and design out of chaos, or, as Monod puts it, the music in the biosphere is created from a source of noise. But we have seen that the design of sexually reproducing organisms, their sequences of DNA not behaving as replicators, cannot be explained in this way.

The problem of teleonomy is how to account for the fact that, assuming that no goal, purpose or specific direction can be attributed to physical forces, our planet is filled with objects that do display a specific direction. Or, as Monod said, we are forced to ‘recognize the teleonomic character of living organisms, to admit that in their structure and performance they decide on and pursue a purpose. In fact the central problem of biology lies with this very contradiction [...]’ [Monod 1971: p. 31]. Or, as David Buller remarked, ‘Ever since the rise of [the] scientific world view, the metaphysical problem of teleology has been that of explaining whether, and if so how, there can be goal-directed processes in a universe governed solely by efficient causation’ [Buller 1999: p. 6]. But the proposed solution was shown to not work. We elaborated on the difference between conservative and creative teleonomic processes in §6 of Chapter II: only a conservative teleonomic process can be explained through the principle of natural selection as the product of a long series of iterations of random variation through mutations,

and non-random 'natural selection' of those sequences that contribute to the stability or replication of the replicating string of DNA. By contrast, sexual reproduction is a creative teleonomic process as it is directed to the creation of new strings of code, and therefore cannot be explained in this fashion. The proposed key, natural selection, therefore does not work, and fails to solve 'the mystery' that displays itself in sex.

In line with the ideas of Kuhn, this consequently implies that not only the theory of natural selection is challenged, but that it also constitutes a problem for its underlying paradigm, naturalism. Through the inability to explain sexual reproduction, the generally accepted idea that the laws of physical science can furnish a sufficient explanation for the design and end-directed processes of biological phenomena is proven problematic. Sex constitutes a challenge for the naturalistic paradigm in general.

At the same time, this is the moment to make some important reservations and temper possible expectations. Kuhn disagrees with Popper's interpretation of falsification described earlier. According to him, Popper's phenomenon of falsification alone is not sufficient to cause a paradigm to shift. Or, to put it differently, for Kuhn, Popper's falsification is actually the occurrence of an anomaly, but for a falsification, a phenomenon Kuhn associates with a paradigm shift, more is needed.

Popper's anomalous experience is important to science because it evokes competitors for an existing paradigm. But falsification, though it surely occurs, does not happen with, or simply because of, the emergence of an anomaly or falsifying instance. [Kuhn 1996: loc. 2248]

Kuhn questions the existence of falsifying instances or experiences, i.e. instances that would refute a theory, altogether.

[...] anomalous experiences may not be identified with falsifying ones. Indeed, I doubt that the latter exist. As has repeatedly been emphasized before, no theory ever solves all the puzzles with which it is confronted at a given time; nor are the solutions already achieved often perfect. On the contrary, it is just the incompleteness and imperfection of the existing data-theory fit that, at any time, define many of puzzles that characterize normal science. [Kuhn 1996: loc. 2237]

Applied to the findings of this study, we could say that Kuhn would likely claim that despite the fact that we have elaborately argued that sexual reproduction cannot be explained by current versions of the theory of natural selection, and that we have shown that the problems with sexual reproduction are more fundamental than previously assumed, sexual reproduction will remain an anomaly. It is only when this anomaly is seen as too large *and* an acceptable alternative is provided, that a falsification, or paradigm-shift, can take place. Falsification is 'a subsequent and separate process that might equally well be called verification since it consists in the triumph of a new paradigm over the old one' [Kuhn 1996: loc. 2248]. While for Popper, sexual reproduction might falsify the theory of natural selection, for Kuhn, sex can at most serve as an anomaly, an anomaly which became significantly more serious after the conclusions of this study and challenges the naturalistic paradigm, but will still only lead to a paradigm-shift or falsification if the anomaly is widely accepted as such *and* a viable alternative paradigm through which nature can be interpreted, is offered. This study might have made this anomaly more severe, but the latter remains an indispensable element for a paradigm-shift to take place.

The situation we face is that no such alternative is easily available. In the background of this study, we have already reflected on the narrowness of the discussion surrounding the theory of natural

selection, offering no scientific alternatives to account for living beings and only finding creationism as an alternative paradigm ('God or Darwin'). And it is not just that creationists are inspired by dogmas unacceptable for the scientific mind that makes their paradigm unfit to serve as a viable alternative; the conclusions of this study do not point in the direction of a validation of their viewpoint either. Creationism, at least as espoused by biblical literalists, does not support the idea of evolution. However, the existence of this process is not challenged in this study, 'only' its underlying mechanisms suggested by the theory of natural selection. Evolution, that classical antagonist of creationism, still stands! Also, when we conclude that the design of living beings cannot have been formed through the mechanisms belonging to the theory of natural selection, this conclusion does not imply that we subsequently have to assume special creation to account for this (concluding this would, again, assume that God or Darwin would be the only options available). Thus, none of the two dominant paradigms – naturalism and creationism – readily supplies a suitable box to place living beings in, and thus no alternative paradigm is at hand.

§ 4. Finding an alternative paradigm to account for living beings transcends the scope of this study, but an attempt will be made to place the conclusions of this study in a philosophical context by discussing relevant doctrines and theories. We will start by revisiting some fundamental biological concepts.

So far, we have concluded that sexual reproduction cannot be accounted for in current versions of the theory of natural selection. As it is highly improbable that alternative versions of the theory can be developed that would account for sexual reproduction, the inability to account for sexual reproduction is likely to apply to the theory of natural selection as such, which equals a falsification of the theory in a Popperian sense. In line with Kuhn we concluded

that because of this, not only the theory of natural selection is challenged, but also its underlying paradigm, naturalism. At the same time, a Kuhnian paradigm shift will only take place if an alternative paradigm is identified through which a more satisfying account for living beings can be provided. Assessing whether such a paradigm exists or can be established, however, transcends the scope of this study, although still an attempt will be made to at least place the conclusions of this study in a proper philosophical context. This will be done by discussing those doctrines and theories that relate to the renewed insights into the characteristics of living beings which can be derived from this study.

In the attempt to sketch the possible contours of a new, more suitable paradigm, we must widen the narrow scope of the naturalistic-creationistic discussion. 'God or Darwin' turned out to be a simplification, disregarding various philosophical systems and scientific theories that have dealt with the explanation of life in general, and design and end-directedness in particular. These systems, which were perhaps too easily neglected or disregarded as not being based on the allegedly superior method of reason and observation, have to be firmly brought up for discussion again. We must extend the narrow scope of the naturalistic-creationist discussion, and see whether a broader look incorporating doctrines that were perhaps erroneously discarded, provides us with the concepts and terms that can help us to understand the idiosyncrasies of living beings.

Before we start this quest, however, there is another step we have to take, and that is to disentangle our view of living beings from Darwinian concepts and terminology. Having dominated biology for the last 150 years, its terms and concepts have shaped the way we look at living beings, a way of looking, however, which with the 'breaking down' of the theory through sexual reproduction would be flawed. Darwinism has compelled us to interpret biological phenomena using at least some terms and concepts that would be

proven false, but at the same time has also led us to neglect aspects that do not fit the theory. A refutation of the theory would mean that we have to reconstruct our way of looking at living beings, discarding outdated biological concepts and terms while at the same time clearly identifying which ones remain valid. We have to get rid of our Darwinian glasses and attempt to take a fresh look at living beings incorporating the insights derived from this study. In the rest of this section, we will focus on this first task, an attempt to perceive organisms disentangled from Darwinian concepts and vocabulary while identifying and retaining valid ones, and – where needed – to reinterpret some of their essential characteristics.

Most urgently, a rejection of the theory of natural selection through its inability to account for sexual reproduction forces us to revise our – Darwinian – view on teleonomy. The theory of natural selection dictates that the end-direction of teleonomic processes and behavior is the stability or replication of the replicator of which the feature exhibiting these processes is part. This notion has been proven false. The attempt to interpret teleonomic processes and behavior in this fashion failed when dealing with sexual reproduction. However, the refutation of the theory of natural selection does not alter the fact that processes and behavior of organisms *are* end-directed. The term teleonomy we applied is purely descriptive. As Pittendrigh rightfully argued, end-direction is inextricably bound up with living beings; the term ‘organism’ is derived from the term organization, and organization is always relative to some end. The question that still stands after rejecting Darwinism, being deprived of the theory that forces us to interpret the end-directedness of living beings in terms of the stability or replication of the replicator, is *what* the teleonomic processes and behavior are directed to, what their end-direction, or ‘ultimate goal’ is.

At the same time, a breaking down of the theory of natural selection through its inability to account for sexual reproduction does not imply that we have good reasons to believe that features

of living beings did not originate through an evolutionary process. As discussed in the introduction, the idea that organisms evolve and that different species can be traced back to common ancestors is not challenged in this study, nor do we question the notion that the evolutionary process is one of adaptation whereby organisms become better equipped to survive in their environments (what we did challenge were the proposed mechanisms behind that process). We will therefore continue to describe the features of living beings as ‘adaptations’.

Let us turn to observation and try to assess if we can identify an alternative ‘ultimate goal’ of living beings. What do the data of experience reveal about the direction of teleonomic processes and behavior? Superficially, we could still stick to the description we used when dealing with Darwin’s *Origin of Species*, namely, ‘survival and reproduction’, whereby survival refers to the survival of the individual alone. But what is ‘reproduction’? This term might appeal to an intuitive notion, but let us try to determine in more detail what it stands for.

Reproduction can occur asexually and sexually. Sexual reproduction is prevalent in higher plants and animals [Williams 1975]. The description of asexual reproduction is relatively straightforward; it refers to the creation of new individuals containing the same genetic material as their (single) parent. Sexual reproduction, on the other hand, denotes the creation of new individuals using the material of two parents. Here, reproduction can be described in much more detail.

Especially with higher animals, the choice of mating partners is not random. The act of sexual reproduction is often preceded by an at times elaborate process of the selection of mating partners, which are chosen or rejected based on certain characteristics.²⁹ Thus, sexual reproduction is not directed to the creation of just new individuals, but this creation is characterized by a certain level of specificity.

We have already dealt with Darwin's account of sexual selection. For Darwin, sexual selection was mostly a mechanism that explained how features that do not provide a direct advantage in terms of survival, can evolve. But the preference for mating partners will first and foremost allow for, and result in, the selection of the *fittest* individuals. Males compete for females, which means that the strongest individual will tend to reproduce. We see this clearly in certain mammals living in social groups, such as lions, whereby only the strongest males in the hierarchy are allowed to mate. But also the selection for secondary characteristics described by Darwin can be interpreted as a selection for the strongest, fittest individual – the ability to display the most beautiful song or plumage will certainly have a correlation with the fitness of that individual. Sexual selection will therefore facilitate that the fittest individuals will populate the next generation.

But there is also a factor of *randomness* in sexual reproduction. Not all forms of sexual reproduction are accompanied by the selection of mating partners; see for example wind-pollination in certain species of plants. Here there is no selection of mating partners, and which individuals will contribute to the next generation is more or less a matter of chance. Moreover, during meiosis, gametes are produced, and due to homologous recombination, these gametes contain a random mixture of maternal and paternal DNA. Here we see that meiosis and homologous recombination work directly towards this randomness, the latter being a function of these mechanisms. If we assume that features like meiosis are adaptations, we must inherently assume that an additional advantage of sexual reproduction must lie in this randomness. Think of the advantages that were earlier discussed: sex as a producer of variable offspring

29 A refutation of the theory of natural selection does not invalidate the term 'selection' in the meaning of 'sexual selection', contrary to selection in 'natural selection'.

to thrive as environments change through time, and sex as an enabler of organisms to remain competitive in a world where other organisms are poised to take advantage of any weakness.³⁰

In summary, these observations show that teleonomic processes and behavior are directed to *the creation and maintenance of a transient and ever changing population of individuals through selecting the best material through sexual selection and providing variation*. It is this description of organisms' ultimate goal, the 'end' behind 'survival and reproduction' that we will utilize in our attempt to place the findings of this study in the right philosophical context.³¹

While we are, through observation and analysis, able to construct a more accurate description of the end-directed processes and behavior of living beings discarded from Darwinian concepts and vocabulary, we have derived no new insight into the *origin of design*. We started this study with a description of the working of the mammalian eye, and how the theory of natural selection claims to account for its origin. We now assume that the mechanisms belonging to the theory of natural selection cannot provide a sufficient account for biological features. We have also seen (in the

30 Note that in the previous chapter these notions were seen as untenable within the gene-centered model of evolution as it is considered unlikely that delivering variation could provide a 50% advantage above asexual reproduction to balance the 50% cost of meiosis. However, as we abandoned the gene-centered model of evolution in particular, and the attempt to interpret the benefit of sex in a quantitative way in general (both linked to the theory of natural selection), these objections do not concern us here. The criticism of the DNA repair hypothesis that was discussed in the previous chapter is, however, not related to this quantitative aspect and therefore this criticism is not affected by a refutation of the theory of natural selection. Therefore, the DNA repair hypothesis will not be revisited as a possible advantage of sexual reproduction.

31 Whether this description applies to all human behavior, e.g. behavior of intellectual or artistic nature, is an open question. This description definitely applies to processes and behavior of plants and animals, and the more primal of those of human beings.

introduction of this work) that proposed evidences for the operation of the mechanism of natural selection are surprisingly poor, and are confined to instances whereby small changes, often degenerating existing features, caused a selective value in exceptional cases. Although the theoretical possibility is still left that *some* features could be explained through the mechanisms of natural selection, sexual selection or genetic drift, we concluded that, reasoning from the knowledge of current versions of the theory of natural selection, this cannot constitute the whole, or even a significant part of the story. But what then really the by far most important and dominant mechanism *is* behind the origin of design, this study does not shed a new light on.

At the same time, it is important to note that a rejection of the theory of natural selection as suggested in this study does not force us to change our view on the biochemistry of living beings. It does not alter our understanding of the chemical processes of organisms, nor of our knowledge of the structures and functions of cellular components such as proteins, carbohydrates, lipids, and nucleic acids.³²

To conclude, this leaves us with the following. This study does not force us to change our view on the biochemistry of living beings, nor question the existence of an evolutionary process of adaptation, although we have gained no insights into its dominant underlying mechanism or mechanisms. What we did accomplish is to redefine the end-direction of sexually reproducing living beings

³² What it does revise is our view on the relation between DNA and proteins. The theory of natural selection dictates that adaptations exist for the stability or replication of a replicator, a role which was reserved for strands of DNA. But with a refutation of the theory of natural selection, this necessary relationship between DNA and proteins is lost. With the rejection of the theory of natural selection, there is no need to treat the relation between DNA and proteins as a hierarchical one whereby the one exists for the good of the other, a relation which was shown to be problematic (see note 13 on p. 58).

disentangled from Darwinian concepts, and we concluded that it can be best described as being directed to the creation and maintenance of a transient and ever changing population of individuals through selecting the best material through sexual selection and providing variation. In the next section we will explore alternative doctrines that relate to these renewed insights and descriptions.

§ 5. Doctrines and theories that will be analyzed to see whether they are related to the renewed insights derived from this study are called theistic, finalistic, and vitalistic. In this section, we start with looking at theism.

Alternative ways to interpret living beings already revealed themselves when we discussed the challenges in accounting for design and teleonomy in a naturalistic fashion. The problem of design was, assuming that the universe is ultimately physical in nature, how to account for the design (the high level of organization and complexity) of living beings. If the universe is ruled by the free play of physical forces to which no goal, purpose or specific direction can be attributed, and there is no supernatural creative intelligence lurking behind the observable universe, how can we account for the existence of objects that look as if they were designed? The problem of teleonomy is how to account for the fact that, assuming that no goal, purpose or specific direction can be attributed to physical forces, our planet is filled with objects that do display a specific direction. One alternative to naturalism, therefore, is that there is a supernatural creative intelligence lurking behind the observable universe. Another alternative is that the universe is *not exclusively* ruled by physical forces to which no goals, purposes or specific directions can be attributed.

Let us start with the first alternative, that there is a supernatural creative intelligence after all. In that case, the structure of living beings finds its root and explanation in an act of design. The

teleonomy of these beings, then, is grounded in the morphological structure of these living beings. The challenge for this doctrine, which can be labeled as *theism* as it assumes the existence of God next to the physical world, however, is to incorporate the notion of common descent, a notion which contradicts the traditional, biblical idea of creation. A theistic doctrine providing an alternative paradigm for living beings that incorporates the conclusions of this study therefore has to come to grips with the notion of evolution by common descent. Michael Behe, a supporter of intelligent design, adheres to the notion of common descent, although his ideas on how an intelligent designer could be associated with the process of evolution are not clearly defined (see Behe [1998]).

However, there is a more important issue – in fact a crucial one – to be dealt with before we can determine in which direction we have to look for an alternative paradigm, and that is the question whether the conclusions of this study compel us to revise our view on a fundamental element that was *part* of the Darwinian explanation of teleonomy. Let us again look at the explanation of teleonomy through the theory of natural selection. As we have seen while analyzing the works of Jacques Monod, this explanation consists of two elements. First, teleonomy is explained by reference to the structure of living beings, more concretely, to the structure of allosteric proteins. This structure itself is based on the sequence of amino acids in proteins, which in turn are based on the sequence of nucleic acids on the strands of DNA. In short, the teleonomy is *based on the (micro)structure* of living beings. Second, this DNA sequence, its specific sequence, is explained as the result of the mechanisms belonging to the theory of natural selection. In other words, the explanation of teleonomy as supplied by the theory of natural selection, is that teleonomy is explained by the morphological structure, and this structure is subsequently explained by the theory of natural selection. In this study, this latter element was shown to be false. Within current versions of the theory of natural

selection, neither the principle of natural selection, nor sexual selection or genetic drift, can completely explain the structure of living beings, because sexual reproduction is out of explanatory reach of these mechanisms. But theism – as does naturalism – assumes that teleonomy, the end-directedness of living beings, arises from living beings' particular (micro or macro) structure. It thus assumes that the end-directed processes of living beings can be explained *mechanistically* through efficient causes working on the structure of living beings. Theism and naturalism share the first element of the Darwinian explanation of teleonomy. The question that needs to be answered is therefore whether the conclusions of this study – the end-direction of living beings is not the stability or replication of a replicator, but can be best defined as the maintenance of a transient and ever changing population of individuals through the selection of the best material through sexual selection and the generation of variation – have consequences for that element in the explanation of teleonomy as well. In other words, can we explain mechanistically the type of end-directed process that we concluded sexual reproduction to be?

In answering this question, existing research can help us only in a limited way. The field of research that occupies itself with the mechanistic explanations of teleonomy (the explanation of end-directed processes by means of physical forces and efficient causes working on the structure of organisms) is the rather loosely defined and multidisciplinary field of systems theory, or cybernetics. In this field, living beings are interpreted as complex systems, and their goal-directed behavior and processes explained and interpreted mechanistically in terms and concepts such as programs, self-organization, preferred states, and closed feedback loops.³³ Often, physical models are presented as analogies for biological teleonomic systems. Classic examples are homeostatic temperature

33 See for example Kauffman [1995], Toepfer [2012] and Christensen [1996].

systems or goal-seeking torpedoes that are presented as models for biological systems, whereby, just as in living beings, allegedly preferred states and feedback loops stand at the basis end-directed processes (see also Hull [1974]).

A characteristic of this field, however, is that it either treats (and attempts to explain) end-directedness in a general, unspecified sense, or treats teleonomy in a relatively narrow context, namely, in relation to notions that revolve around the system itself, such as in 'self-replication', 'self-organization', or 'self-repairing' ends. The explanation of direction in a general, unspecified sense we see, for example, with Mayr when he argues that 'a program might be defined as coded or prearranged information that controls a process (or behavior) leading it toward a *given end*' [italics JVR], or that 'all teleonomic behavior [...] depends on the existence of *some end point, goal or terminus* which is foreseen in the program that regulates the behavior' [italics JVR], this end-point being, for example, 'a structure, a physiological function, the attainment of a new geographical position or a consummatory [...] act in behavior' [Mayr 1988: p. 45]. The same holds good for David Hull when he writes that one way in which teleonomic systems are characterized is by *certain* preferred states, and that the preferred states are brought about by mechanisms such as causal feedback loops, especially negative feedback loops [Hull 1974, italics JVR]. Reference to 'self' we also encounter frequently, for example, with Christensen when he talks about 'self-organization', 'self-repairing', or 'self-replication' in relation to teleonomy [Christensen 1996], or Kauffman for whom self-organization was the central theme of his work *At Home in the Universe* [1995].

Although one can argue that these scientists have thus been successful in mechanistically explaining the possibility of end-directedness in general, or end-directedness associated with these systems themselves, it is a different matter to account for a teleonomy that is directed to 'the maintenance of a transient and ever

changing population of individuals through selecting the best material through sexual selection and providing variation' (which we concluded the end-direction of living beings amounts to). Just as self-replication is a relatively straightforward concept to understand from a chemical point of view (despite the problems with accounting for the repetitiveness of replication; see note 13 on p. 58), so are concepts like 'self-replication' or 'self-repairing' easier to be reconciled with a mechanistic, cybernetic explanation than with something we concluded the end-direction of sexually reproducing organisms to be. A primary task in our search for an alternative paradigm, therefore, is to determine whether systems theory can account for this 'ultimate goal'.

This task, however, is of such nature that it will not be undertaken in this study. It would require elaborate research and analysis that falls outside the range of this work. What we can do, however, is to sketch the consequences if this explanation were proven impossible. If the teleonomy of living beings cannot be explained mechanistically by reference to the (micro or macro) structure of living beings, then we will have not only disqualified naturalism, but also the earlier defined form of theism that assumes that the end-directed process of living beings can be explained mechanistically through efficient causes working on the structure of living beings. We have then not only shown that the structure of living beings cannot be explained through the theory of natural selection, but also that this structure cannot explain the teleonomy of living beings. And that conclusion would bring us to a whole new range of alternative doctrines, namely finalistic and vitalistic theories and doctrines. We will look at these in more detail in the next section.

§ 6. Finalistic and vitalistic doctrines are discussed as alternatives in case the mechanistic explanation of teleonomy were proven impossible. The difference between naturalistic, theistic, finalistic and vitalistic doctrines is explained by using the analogy of a machine.

Theories and doctrines that challenge the mechanistic element in a naturalistic explanation of teleonomy – the notion that by reference to the (micro)structure of organisms teleonomy can be explained mechanistically – are called *finalistic* and *vitalistic*.³⁴ By finalistic doctrines we mean those doctrines that hold that goals or ends

34 As the term ‘teleology’ is ambiguous and can refer to several types of explanations as well as other phenomena, we will avoid its usage. For example, the term teleology in the context of ‘teleological processes’ can refer to the existence of end-directed processes in nature. This was defined as teleonomy in this study. In this sense, teleology describes and fully recognizes end-directed processes and behavior, without making any naturalistic or non-naturalistic claims about the causes of these processes or behavior. In this way, the use of the term is purely descriptive. Mayr [1988] further distinguishes between teleomatic, teleonomic and teleological systems. Teleomatic systems are classified as end-resulting, teleonomic as end-directed, and teleological as end-seeking, and these distinctions are intended to capture the differences between inorganic, biological and intelligent systems [Christensen 1996]. In this study, however, all these processes are grouped as teleonomical, all exhibiting end-directedness. Also, teleology used in the context of ‘teleological language’ can refer to language in terms of goals, functions and purposes that is frequently used in biology. For example, ‘the function of the kidneys is to eliminate the end products of protein metabolism’, or ‘the function of blood is to transport nutrients and oxygen’. Whether the use of teleological language is legitimate is a source of discussion amongst biologists, although most Darwinists concede that the use of this language does not imply non-naturalistic notions [Mayr 1998]. Moreover, many biologists believe that such language is indispensable for describing and explaining a large variety of biological phenomena [Nagel 1979: p. 276]. Teleological notions are important as heuristic devices and are integral parts in the explanation of the presence of parts in living beings as naturally selected systems [Toepfer 2012]. This use of the term teleology, therefore, does not imply non-naturalistic notions. Moreover, teleology in the context of ‘teleological behavior’ can relate to intentional purposive human behavior and the supposedly purposive behavior of the higher animals. An example of this teleological behavior is: I go to the shop because I want to buy bread. Or: the deer runs away because it wants to flee from a predator. Goal-directed behavior is in this case the action undertaken by a conscious agent for the sake of achieving a

are true causes for living processes. Ends and goals are immanent in nature, and processes and functions exist that are intrinsically performed for the good of the goal or end. In other words, certain natural changes take place and certain natural attributes exist for the sake of some end. Not only do these changes and attributes

goal. As Nagel [1979] argues, although in this case action can be explained teleologically (the intention of buying bread caused me to go to the shop), this explanation is still a causal explanation when one considers 'buying bread' a mental state that is the causal determinant of the action. In other words, it is not the goal that brings out the action; it is the agent's mental state of wanting the goal that does so [Nagel 1979: p. 278]. Next, teleology in the context of an 'evolutionary direction' can refer to the existence of a direction in the phylogeny, the idea that evolution of organisms is somehow directed to a certain end. We see this notion of progressionism or orthogenesis in Henri Bergson's (1859–1941) *élan vital*, a living, creative force that he saw as driving evolution, or with Teilhard de Chardin (1881–1955), who believed that evolution occurs in a directional, goal-driven way. The term teleology in the context of 'teleological explanations' can also refer to dualistic explanations. This type of explanation, which is based on the Platonic model, sees the world as the end-product of a divine craftsman [Lennox 1992]. This is sometimes described by the term 'external' or 'extrinsic' teleology. Extrinsic teleology essentially corresponds to creationism. It assumes that the end-directedness of organic functions and processes is caused by an outside agent who designed these beings with those goals or purposes in mind. In that view, the ends of processes and behavior are causes of these processes mediated through an external agent or creator. Organisms are end-directed because their creator made them so. Finally, there is the term 'immanent' or 'internal teleology', which can be used to refer to finalism as well as the stream of vitalism that assumes a quasi-conscious agent inside natural objects. It 'carries two distinct connotations [...] which should not be confused. The notion of "immanence" may simply stress that the goal or function involved is a goal or function of the individual organism under consideration, rather than of an "external" designer. But it may also carry connotations of "quasi-conscious" agent inside natural objects, so to speak [...] [Lennox 1992]. This term is associated with the philosophy of Aristotle, but despite the fact that there is unanimity on the importance of teleology to Aristotle, there is no consensus about which meaning Aristotle adhered to [Johnson 2005].

contribute (or are directed) to some end, they take place and exist *because* they contribute to an end [Lennox 1992]. Whereas naturalism and theism only assume the existence of efficient causes, finalism explains processes and function additionally by reference to final causes. Just as a heart pumps because it transports oxygen and nutrients to the body, processes and functions exist for the good of the organism or species. This notion points to an alternative for the mechanistic explanation of the end-directed processes and behavior of living beings through the structure of living beings, if this turns out to be required. Ends and goals are immanent in nature, and processes and functions exist that are intrinsically performed for the good of the goal or end.

The mechanistic element in a naturalistic explanation of teleonomy is also challenged in *vitalistic* theories. Vitalism refers to two different concepts.³⁵ First, the idea that *vital forces* operate on the level of organic nature. Vital, directive forces manifest themselves in living beings, forces that cannot be reduced to physical or chemical ones. The second form of vitalism, which was influential in the 19th and 20th century, involves the idea of a '*quasi-conscious*'

³⁵ Vitalism can also have a more general meaning in the sense that the processes of life are not explicable by the laws of physics and chemistry alone. In that sense vitalism is a purely negative doctrine that does not suggest how these processes should be understood otherwise. Vitalism can also refer to murky and outdated notions such as those that living beings are made of different substances, or that living and non-living beings are made of the same material, but that living beings contain an additional vital substance, such as a fluid [Hull 1974]. These notions are outdated because of our current knowledge of biochemistry, a science that has made enormous strides since the beginning of the 19th century. The synthetic synthesis of urea, the discovery that the body heat is due to the combustion of food, and the discovery of the protein were all fundamental events that eliminated the distinction between life and non-life. This development culminated in the latter half of the 20th century, resulting in the understanding all basic organic process, from embryology to metabolism and heredity, on a biochemical level.

agent inside natural objects. It is this agent that causes the immanent intentionality of living beings [Lennox 1992].

In summary, we can further specify the finalistic and vitalistic doctrines that offer an alternative to the mechanistic explanation of the end-directed processes and behavior of living beings (in case this explanation were necessary as the teleonomy of living beings cannot be accounted for through the (micro)structure of organisms) as those that explain teleonomy by reference to final causes (finalism), vital forces or quasi-conscious agents that are peculiar to the organic world.³⁶

All the doctrines that we have considered until now – naturalism, theism, finalism and vitalism – can be described by using the analogy of a machine. For *naturalism*, living beings are like machines, as the teleonomic processes and behavior exist by virtue of the constitution, or structure, of the organism. Processes are mechanistically explained through the organisms' specific order of its specific parts. Moreover, as Monod argued, organisms are *self-constructing* machines. Their structure (morphology or phenotype)

36 In the 19th and 20th century, vitalistic doctrines were most often invoked to explain the ontogenesis (embryology) or evolution of living beings. For example, Hans Driesch (1867–1941) believed that his research on sea urchins compromised mechanistic theories of ontogeny, and proposed 'entelechy' to account for that phenomenon, which he defined as 'itself neither "an energy" nor "a material substance" of any special kind: such an assumption would lead to absurdities. Entelechy is an agent *sui generis*, non-material and non-spatial, but acting "into" space so to speak; an agent however, that belongs to nature in the purely logical sense in which we use this word' [Driesch 1914: p. 204]. Another well-known vitalist, Henri Bergson, proposes his 'élan vital' as a force behind evolution. This force pervades the whole of nature and represents itself in innumerable forms [Bunnin 2004]. In this study, however, we do not investigate embryology, nor do we assume the existence of an end-directedness in evolution. Instead, we solely look at sexual reproduction and see if this phenomenon requires a vitalistic, finalistic, or dualistic explanation.

is the result of morphogenetic interactions within the object itself that take place in the embryonic and juvenile stage. Additionally, these machines came into existence through the mechanism of natural selection. The design of organisms is the result of a blind evolutionary process of adaptation through (primarily) the principle of natural selection.

Theism also adheres to the machine-like interpretation of living beings. Teleonomic processes and behavior exist by virtue of the structure of organisms. However, according to this doctrine, these machines are created by an intelligent designer. This doctrine does therefore not oppose the mechanistic aspect of naturalism, but its ontology, as it assumes the existence of an intelligent designer. For both naturalism and theism, organisms are machines, but whereas the former claims these machines came into being through a process driven by blind mechanisms, the latter claims that these machines were created by an intelligent entity.³⁷

Finalism as well as *vitalism*, on the other hand, *do* oppose the machine-like interpretation of living beings. These doctrines claim

37 In fact, the machine-like interpretation of living beings, implying the existence of design in organisms, is used as an argument for the existence of a designer in the so-called 'argument from design', most notably known through Paley's watchmaker's analogy, 'In crossing a heath, suppose I pitched my foot against a stone, and were asked how the stone came to be there; I might possibly answer, that, for anything I knew to the contrary, it had lain there forever: nor would it perhaps be very easy to show the absurdity of this answer. But suppose I had found a watch upon the ground, and it should be inquired how the watch happened to be in that place; I should hardly think of the answer I had before given, that for anything I knew, the watch might have always been there. [...] There must have existed, at some time, and at some place or other, an artificer or artificers, who formed [the watch] for the purpose which we find it actually to answer; who comprehended its construction, and designed its use. [...] Every indication of contrivance, every manifestation of design, which existed in the watch, exists in the works of nature; with the difference, on the side of nature, of being greater or more, and that in a degree which exceeds all computation' [Paley 1802].

that living beings cannot be explained mechanistically, because in living beings – next to efficient causes and physical forces – final causes, vital forces or quasi-conscious agents are operative.³⁸

These doctrines – theism, finalism and vitalism – thus oppose naturalism on different levels. Theism can be called ‘supernaturalistic’ as it assumes the existence of a supernatural creative intelligence. This intelligence is the cause of the design of living beings, this design itself standing at the basis of their end-directed behavior. It thus opposes naturalism on the ontological level. Finalism, on the other hand, does not per definition assume an intelligent designer. While theism conflicts with naturalism on the ontological level (there is more than matter alone), finalism challenges the mechanistic aspect of naturalism, more specifically, its causality. For naturalism, only efficient causes exist, but finalism also assumes the existence of final causes. If theism targets the ontological aspect of naturalism and finalism its mechanicism, the form of vitalism that assumes the existence of a vital force also challenges the mechanistic aspect of naturalism, but in this case its *reductionist* aspect. Naturalism assumes that life is assembled out of non-living building blocks and that it should – at least in principle – be explainable on the basis of these elements and their accompanying forces, although these explanations can be accompanied by epistemological anti-reductionistic elements such as those derived from systems theory.³⁹ Vitalism, on the other hand, proposes that on the organic level, distinct *forces* emerge that cannot be reduced to those that operate on the level of chemistry or physics. On the other hand, the form of vitalism that assumes the existence of

38 Cf. Hans Driesch, ‘The main question of Vitalism is not whether the processes of life can properly be called purposive: it is rather the question if the purposiveness in those processes is the result of a special constellation of factors known already to the science of the inorganic, or if it is the result of an autonomy peculiar to the processes themselves’ [Driesch 1914: p. 6].

semi-conscious agents would precisely because of this assumed existence not allow itself for a machine-like interpretation.

This section was intended to list existing doctrines that could provide a framework for the explanation of the teleonomy that exhibits itself in living beings after we have assumed that this cannot be provided by the theory of natural selection. We have identified and labeled these doctrines as theistic, finalistic, and vitalistic. Moreover, we have encountered a principal question that needs to be answered in order to determine in which direction this alternative explanation of living beings is to be found, namely, whether the teleonomy that exhibits itself in living beings (and in sexual reproduction in particular) can be aligned with a mechanistic explanation. In this case, theism could provide an alternative paradigm, although it would have to fully come to terms with the existence of an evolutionary process of adaptation. In case this mechanistic explanation of the teleonomy that exhibits itself within living beings were proven impossible, we would have to look for solutions in finalistic or vitalistic doctrines.

In this section we did not dwell on the enormous philosophical and conceptual problems that are currently associated with these alternative doctrines. After all, for biologists vitalism has been a dead issue for more than eighty years,⁴⁰ finalism as a genuine metaphysical position has long ceased to play a role in science, and God

39 Discussions around the use of epistemological anti-reductionistic elements relate to the 'holism' vs. 'reductionism' debate in systems biology. Some 'holistic' streams of systems theory assume, while residing within the current scientific paradigm, that the complexity of organic systems is preventing an understanding of these systems on lower levels, thus acknowledging the existence of epistemological anti-reductionistic elements in the explanations of these systems [Gatherer 2010]. Those doctrines that propose anti-reductionistic elements in the form of vital forces, on the other hand, surely do not fall within that paradigm.

40 See also Mayr [1982]: p. 52.

IV · DISCUSSION

has been eliminated out of the mainstream scientific worldview since the 19th century. On the other hand, the scope of this study has forced us to restrict our search for a solution of the problem of sex to historical, existing doctrines, leaving open the possibility that an alternative would have to be looked for in quite another direction.

References

- Agrawal, A.F. [2006], 'Similarity Selection and the Evolution of Sex: Revisiting the Red Queen'. In: *PLOS Biology*, vol. 4 (8): e265. DOI 10.1371/journal.pbio.0040265
- Amundson, R. and G.V. Lauder [1998], 'Function Without Purpose: The Uses of Causal Role Function in Evolutionary Biology'. In: D. Hull and M. Ruse (eds.), *The Philosophy of Biology*. Oxford: Oxford University Press
- Ayala, F.J. [1970], 'Teleological Explanations in Evolutionary Biology'. In: C. Allen, M. Bekoff and G. Lauder (eds.), *Nature's Purposes: Analyses of Function and Design in Biology*. Cambridge, MA: MIT Press
- Ayala, F.J. [2010], 'Darwin's Explanation of Design: From Natural Theology to Natural Selection'. In: *Infection, Genetics and Evolution*, vol. 10 (6): pp. 839–842. DOI 10.1016/j.meegid.2009.09.014
- Barham, J. [2002], 'Theses on Darwin'. In: *Rivista di Biologia/Biology Forum*, vol. 95: pp. 115–148
- Behe, M. [1998], *Darwin's Black Box* (Kindle edition). New York, NY: Free Press
- Behe, M. [2007], *The Edge of Evolution* (Kindle edition). New York, NY: Free Press
- Buller, D.J. [1999], 'Natural Teleology'. In: D. Buller (ed), *Function, Selection, and Design*: pp. 1–27. Albany, NY: State University of New York Press
- Bunnin, N. and Y. Jiyuan (eds.) [2004], *The Blackwell Dictionary of Western Philosophy*. Oxford: Blackwell
- Cartwright, J. [2001], *Evolution and Human Behavior: Darwinian Perspectives on Human Nature*. Cambridge, MA: MIT Press

- Christensen, W. [1996], 'A Complex Systems Theory of Teleology'. In: *Biology and Philosophy*, vol. 11 (3): pp. 301–320. DOI 10.1007/BF00128784
- Cooper, T.F., D.E. Rozen and R.E. Lenski [2003], 'Parallel Changes in Gene Expression After 20 000 Generations of Evolution in *Escherichia coli*'. In: *PNAS*, vol. 100 (3): pp. 1072–1077. DOI 10.1073/pnas.0334340100
- Dawkins, R. [1976], *The Selfish Gene*. Oxford: Oxford University Press
- Dawkins, R. [1982], *The Extended Phenotype*. Oxford: Oxford University Press
- Dawkins, R. [1986], *The Blind Watchmaker*. New York, NY: Norton
- Dawkins, R. [1996]. *Climbing Mount Improbable*. New York, NY: Norton
- Dawkins, R. [2006], *The God Delusion*. London: Bantam Press
- Darwin, C. [1922], *The Descent of Man and Selection in Relation to Sex*. London: Murray
- Darwin, C. [1968], *The Origin of Species*. Harmondsworth: Penguin
- Dennett, D. [1995], *Darwin's Dangerous Idea*. New York, NY: Simon & Schuster
- Driesch, H. [1914], *The History and Theory of Vitalism*. London: MacMillan
- Eldredge, N. and S.J. Gould [1972], 'Punctuated Equilibria: An Alternative to Phyletic Gradualism'. In: T.J.M. Schopf (ed.), *Models in Paleobiology*. San Francisco, CA: Freeman, Cooper
- Fischer, R.A. [1930], *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press
- Gatherer, D. [2010], 'So What Do We Really Mean When We Say That Systems Biology is Holistic?' In: *BMC Systems Biology*, vol. 4:22. DOI 10.1186/1752-0509-4-22

REFERENCES

- Ghiselin, M.T. [1974], *The Economy of Nature and the Evolution of Sex*. Berkeley, CA: University of California Press
- Ghiselin, M.T. [1988], 'The Evolution of Sex: A History of Competing Points of View'. In: R.E. Michod and B.R. Levin (eds.), *The Evolution of Sex: An Examination of Current Ideas*. Sunderland, MA: Sinauer Associates
- Godfrey-Smith, P. [1998], 'Functions: Consensus Without Unity'. In: D. Hull and M. Ruse, *The Philosophy of Biology*. Oxford: Oxford University Press
- Haldane, J.B.S. [1955], 'Population Genetics'. In: *New Biology* 18: pp. 34–51. London: Penguin
- Hamilton, W.D. [1963], 'The Evolution of Altruistic Behaviour'. In: *The American Naturalist*, vol. 97 (896): pp. 354–356. DOI 10.1086/497114
- Heijdra, M.G. [2009], *Darwinian Explanations of the Origin of Language*. Amsterdam: Vrije Universiteit (Doctoral Thesis)
- Hempel, C. and P. Oppenheim [1948], 'Studies in the Logic of Explanation'. In: *Philosophy of Science*, vol. 15 (2): pp. 135–175
- Hempel, C. [1965], *Aspects of Scientific Explanation and Other Essays in the Philosophy of Science*. New York, NY: Free Press
- Hoekstra R.F. [2005], 'Why Sex is Good'. In: *Nature*, vol. 434: pp. 571–573. DOI 10.1038/434571a
- Hull, D.L. [1974], *Philosophy of Biological Science*. Englewood Cliffs, NJ: Prentice-Hall
- Hull, D.L. [1984], 'Units of Evolution: A Metaphysical Essay'. In: R.N. Brandon and R.M. Burian (eds.), *Genes, Organisms, Populations*. Cambridge, MA: MIT Press
- Hull, D.L. and M. Ruse (eds.) [1998], *The Philosophy of Biology*. Oxford: Oxford University Press
- Hull, D.L. [1999], 'The Use and Abuse of Sir Karl Popper'. In: *Biology and Philosophy*, vol. 14 (4): pp. 481–504. DOI 10.1023/A:1006554919188

- Johnson, M.R. [2005], *Aristotle on Teleology*. Oxford: Clarendon Press
- Johnson, P.E. [1991], *Darwin on Trial*. Washington, D.C.: Regnery Gateway
- Kauffman, S.A. [1995], *At Home in the Universe: Search for Laws of Self-Organization and Complexity*. New York, NY: Oxford University Press
- Kitcher P. [1998], 'Function and Design'. In: D. Hull and M. Ruse, *The Philosophy of Biology*. Oxford: Oxford University Press
- Kuhn, T.S. [1996], *The Structure of Scientific Revolutions* (3rd Kindle Edition). Chicago: University of Chicago Press
- Lange, F.A. [2000], *The History of Materialism and Criticism of its Present Importance*. London: Routledge
- Leigh Jr., E.G. [2010], 'The Group Selection Controversy'. In: *Journal of Evolutionary Biology*, vol. 23 (1): pp. 6–19. DOI 10.1111/j.1420-9101.2009.01876.x
- Lennox, J.G. [1992], 'Teleology'. In: E.F. Keller and E.A. Lloyd (eds.), *Keywords in Evolutionary Biology*: pp. 324–333. Cambridge, MA: Harvard University Press
- Lenski, R.E. [2004], 'Phenotypic and Genomic Evolution During a 20 000-Generation Experiment with the Bacterium *Escherichia coli*'. In: *Plant Breeding Reviews*, vol. 24 (2): pp. 225–265. DOI 10.1002/9780470650288.ch8
- Lifson, S. [1987], 'Chemical Selection, Diversity, Teleonomy and the Second Law of Thermodynamics. Reflections on Eigen's Theory of Self-Organization of Matter'. In: *Biophysical Chemistry*, vol. 26 (2–3): pp. 303–311. DOI 10.1016/0301-4622(87)80031-5
- Lloyd, E., 'Units and Levels of Selection'. In: E.N. Zalta (ed.), *The Stanford Encyclopedia of Philosophy* (Winter 2012 Edition). <http://plato.stanford.edu/archives/win2012/entries/selection-units>
- Mayr, E. [1978], 'Evolution'. In: *Scientific American*, vol. 239: pp. 46–55. DOI 10.1038/scientificamerican0978-46

REFERENCES

- Mayr, E. [1982], *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Belknap Press
- Mayr, E. [1988], 'The Multiple Meanings of Teleological'. In: *Towards a New Philosophy of Biology*, Cambridge, MA: Harvard University Press
- Mayr, E. [1997]. 'The objects of selection.' In: *PNAS*, vol. 94 (6): pp. 2091–2094.
- Maynard Smith, J. [1964], 'Group Selection and Kin Selection.' In: *Nature*, vol. 201: pp. 1145–1147. DOI 10.1038/2011145a0
- Maynard Smith, J. [1978], *The Evolution of Sex*. Cambridge: Cambridge University Press
- Michod, R.E. and B.R. Levin (eds.) [1988], *The Evolution of Sex: An Examination of Current Ideas*. Sunderland, MA: Sinauer Associates
- Monod, J. [1971], *Chance and Necessity*. New York, NY: Vintage Books
- Monod, J. [1973], 'On the Molecular Theory of Evolution.' In: R. Harré (ed.) [1975], *Problems of Scientific Revolution: Progress and Obstacles to Progress in the Sciences*: pp. 11–24. Oxford: Clarendon Press (The Herbert Spencer Lectures; 1973)
- Montalenti, G. [1974], 'From Aristotle to Democritus via Darwin: A Short Survey of a Long Historical and Logical Journey'. In: F.J. Ayala and T. Bodzhansky, *Studies in the Philosophy of Biology*. London: Macmillan
- Muller, H.J. [1932], 'Some Genetic Aspects of Sex'. In: *The American Naturalist*, vol. 66 (703): pp. 118–138. DOI 10.1086/280418
- Muller, H.J. [1964], 'The Relation of Recombination to Mutational Advance'. In: *Mutation Research*, vol. 1 (1): pp. 2–9. DOI 10.1016/0027-5107(64)90047-8
- Nagel, E. [1979], *Teleology Revisited and Other Essays in the Philosophy and History of Science*. New York, NY: Columbia University Press

- Nowak, M.A., C.E. Tarnita and E.O. Wilson [2010], 'The Evolution of Eusociality'. In: *Nature*, vol. 466: pp. 1057–1062. DOI 10.1038/nature09205
- Okasha, S. [2006], *Evolution and the Levels of Selection*. Oxford: Clarendon Press
- Paley, W. [1802], *Natural Theology or Evidences of the Existence and Attributes of the Deity, Collected from the Appearances of Nature*. London: R. Faulder
- Pittendrigh, C.S. [1958], 'Adaptation, Natural Selection, and Behaviour'. In: A. Roe and G.G. Simpson (eds.), *Behavior and Evolution*. New Haven, CT: Yale University Press
- Popper, K. [1976], *Unended Quest*. London: Fontana
- Popper, K. [1978], 'Natural Selection and the Emergence of Mind'. In: *Dialectica*, vol. 32 (3–4): pp. 339–355. DOI 10.1111/J.1746-8361.1978.TB01321.X
- Pross, A. [2005], 'On the Chemical Nature and Origin of Teleonomy'. In: *Origins of Life and Evolution of Biospheres*, vol. 35 (4): pp. 383–394. DOI 10.1007/S11084-005-2045-9
- Ridley, M. [1993], *The Red Queen: Sex and the Evolution of Human Nature*. London: Penguin
- Reeve, K. and L. Keller [1999], 'Levels of Selection: Burying the Units-of-Selection Debate and Unearthing the Crucial New Issues'. In: L. Keller (ed.), *Levels of Selection in Evolution*. Princeton, NJ: Princeton University Press
- Ridley, M. [2004], *Evolution*. Malden, MA: Blackwell
- Ruse, M. [1980], 'Charles Darwin and Group Selection'. In: *Annals of Science*, vol. 37 (6): pp. 615–630. DOI 10.1080/00033798000200421
- Salmon, W.C. [1989], *Four Decades of Scientific Explanation*. Minneapolis, MN: University of Minnesota Press
- Schopenhauer, A. [1966], *The World as Will and Representation*. New York, NY: Dover Publications

REFERENCES

- Schopenhauer, A. [1986], 'Über den Willen in der Natur'. In: *Sämtliche Werke. 3: Kleinere Schriften*. Frankfurt am Main: Suhrkamp
- Schuurman, R., et al. [1995], 'Rapid Changes in Human Immunodeficiency Virus Type 1 RNA Load and Appearance of Drug-Resistant Virus Populations in Person Treated with Lamivudine (3TC)'. In: *Journal of Infectious Diseases*, vol. 171 (6): pp. 1411–1419. DOI 10.1093/infdis/171.6.1411
- Shaw, G.B. [1921], *Back to Methuselah*. New York, NY: Brentano's
- Simpson, G.G. [1963], 'Biology and the Nature of Science'. In: *Science*, vol. 139 (3550): pp. 81–88. DOI 10.1126/science.139.3550.81
- Sober, E.R. [1984], *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. Cambridge, MA: MIT Press
- Toepfer G. [2012], 'Teleology and its Constitutive Role for Biology As the Science of Organized Systems in Nature'. In: *Studies in History and Philosophy of Science. c: Studies in History and Philosophy of Biological and Biomedical Sciences*, vol. 43 (1): pp. 113–119. DOI 10.1016/j.shpsc.2011.05.010
- Van Rossum, J.P. [2003], 'A Case Reopened: Teleology and its Consequences for the Unit of Selection Discussion'. In: *Rivista di Biologia/Biology Forum*, vol. 96: pp. 105–122
- Van Rossum, J.P. [2006], 'On the Unfitness of Natural Selection to Explain Sexual Reproduction, and the Difficulties That Remain'. In: *Rivista di Biologia/Biology Forum*, vol. 99: pp. 251–272
- Van Valen, L. [1973], 'A New Evolutionary Law'. In: *Evolutionary Theory*, vol. 1: pp. 1–30
- Von Bertalanffy, L. [1969], 'Chance or Law'. In: K. Koestler and J.R. Smythies (eds.), *Beyond Reductionism: New Perspectives in the Life Sciences*. New York, NY: MacMillan
- Visser, J.A.G.M. de and S.F. Elena [2007], 'The Evolution of Sex: Empirical Insights into the Roles of Epistasis and Drift'. In: *Nature Reviews Genetics*, vol. 8: pp. 139–149. DOI 10.1038/nrg1985

- Walsh, D.M. [2000], 'Chasing Shadows: Natural Selection and Adaptation.' In: *Studies in History and Philosophy of Science. C: Studies in History and Philosophy of Biological and Biomedical Sciences*, vol. 31 (1): pp. 135–153. DOI 10.1016/S1369-8486(99)00041-2
- Weismann, A. [1889], *Essays upon Heredity and Kindred Biological Problems*. Oxford: Clarendon Press
- Williams G.C. [1966], *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press
- Williams G.C. [1975], *Sex and Evolution*. Princeton, NJ: Princeton University Press
- Wilson, D.S. [1997], 'Multilevel Selection Theory Comes of Age.' In: *The American Naturalist*, vol. 150 (S1): pp. S1–S4. DOI 10.1086/286046
- Wilson, D.S. and E.O. Wilson, [2008], 'Evolution "for the Good of the Group"'. In: *American Scientist*, vol. 96 (5): pp. 380–389. DOI 10.1511/2008.74.1
- Winther, R.G. [2000], 'Darwin on Variation and Heredity.' In: *Journal of the History of Biology*, vol. 33 (3): pp. 425–455. DOI 10.1023/A:1004834008068
- Woodward, J. [2011], 'Scientific Explanation.' In: E.N. Zalta (ed.), *The Stanford Encyclopedia of Philosophy* (Winter 2011 Edition). <http://plato.stanford.edu/archives/win2011/entries/scientific-explanation>
- Wouters A.G. [2003], 'Four Notions of Biological Function.' In: *Studies in History and Philosophy of Science. C: Studies in History and Philosophy of Biological and Biomedical Sciences*, vol. 34 (4): pp. 633–668. DOI 10.1016/j.shpsc.2003.09.006
- Wynne-Edwards V.C. [1962], *Animal Dispersion in Relation to Social Behaviour*. Edinburgh: Oliver and Boyd

DARWINISM is one of the most successful scientific theories, and its validity is largely unquestioned within the scientific community. Most criticism comes from creationist streams of thought, and primarily focuses on aspects of improbability, such as on the alleged improbability of the origin of life, or of accidental mutations and natural selection yielding the astonishing complexity of living beings. In this work, a new criticism of the theory of natural selection is introduced. Its aim is to show that a salient characteristic of living beings, sexual reproduction, defies Darwinism, and not based on an improbability, but on an impossibility of explanation. Moreover, it is a critique that does not endorse creationism, but demands that the discussion about the explanation of organic phenomena should be held in a much broader philosophical context.

ISBN 978-90-9027200-9



9 789090 272009