FACULTY OF SCIENCE
UNIVERSITY OF COPENHAGEN

PhD thesis

Christian Baron

Epistemic Values in Behavioural Ecology and Paleontology

Academic advisor: Claus Emmeche

Submitted: 03/01/10

Content:

Abstract: This thesis investigates the role of epistemic values, understood as methodological criteria of judgment, in two areas of evolutionary biology; behavioural ecology and paleontology. The focal point of the investigation on behavioural ecology is the debates on a cluster of problems related to the origin and maintenance of biological labour division, altruism, the theory of group selection vs. other kinds of selectionist accounts, and the handicap hypothesis concerning the reliability of biological signaling. The focal point of the investigation on paleontology is a cluster of problems that are all connected with the discussion on the evolutionary interpretation and significance of the Cambrian fossils of Burgess Shale, and include the scientific debates on their systematic interpretation, their morphological disparity, and the role of contingency in evolution. Based on a comparative study of publications connected to various scientific controversies in the two domains of inquiry it put forwards three general claims concerning the role of epistemic values in science that are empirically supported by the case studies: 1) There is a relation of reciprocal underdetermination between epistemic values and other important variables in the scientific process; 2) It is considerably easier for an individual scientist to convince other scientists of the validity of his of her conclusions if they are based on a set of values that are compatible with the dominant epistemic ideals of the scientific community of which the scientist is a member, and 3) the actions of individual scientists in scientific controversies constitute an important level of analysis in the investigation of epistemic values, where interesting phenomena occurs that may otherwise go unnoticed when focusing exclusively on the scientific collective. It concludes that the existence of a relation of reciprocal underdetermination between epistemic values and other important epistemic variables discussed by this study, is a serious hindrance for any universalist approach that attempts to establish the unification of the sciences on a uniform application of epistemic values - and that such a project may be counter-productive. The dissent created by disagreements about how epistemic values are to be applied, is necessary in order to ensure a critical scrutiny of decisions that are based on these values. It is only by discussing them that we may be able to evaluate them critically.

Thesis Objective: To investigate to role of epistemic values in science with an emphasis on evolutionary biology: how they are applied; how they come into conflict; and how their application may change as a result of other intellectual developments.

Section I: Introduction and Overview

This thesis is about the role of epistemic values in evolutionary biology. It explores some aspects of the complex role epistemic values (understood preliminary as methodological criteria of judgment) play in science, focusing on scientific controversies within the domains of behavioural ecology and paleontology.

The thesis consists of four major sections. Section I is composed of this introduction as well as a synopsis paper (*On epistemic values, their role in science and how to analyse them*) that introduces the concept of epistemic values and discusses the most important approaches that has been used to address them. It also argues that reciprocal underdetermination is a key feature of the relation of the variables important for the understanding of epistemic values in science. An empirical approach therefore becomes a necessary part of the toolkit needed to investigate their role in scientific practice. Making a basic distinction between between epistemic values as communal imperatives and epistemic values as methodological judgment, the latter are chosen as the object to be investigated in this thesis, and controversy studies are chosen as the main approach of investigation. Taking a multi-level approach to the investigation of epistemic values, it locates the primary levels of interest in the relations between the individual researcher's idiosyncratic applications of epistemic values as criteria of judgment and those dominant within the scientific collective. Comparing different theoretical attempts to describe scientific collectives, the paper takes a pragmatic stance towards these, arguing that their explanatory merit must be justified according to the specific instances in which they are used. The paper concludes with a series of research questions and expectations that can be used to investigate particular instances of embodiment, where epistemic values, in the form of methodological rules or norms, have a concrete effect on decisions made as part of the scientific process.

The two following sections contain case-studies that address the application of epistemic values in the context of specific scientific debates. The approach taken to these case-studies is somewhat hermeneutical in the sense that some of the discovered misgivings of the analytical perspective chosen in Section II are regarded as 'lessons learned' that are usable in the process of choosing a different analytical perspective in

Section III. There is thus a difference in the choice of analytical perspectives between the two sections. However, as will be clear by reading this thesis, I do not believe that these differences render the case-studies incomparable, as many of their important findings may stand fairly independent of the analytical perspective chosen.

Section II is concerned with a cluster of related scientific problems within behavioural ecology. These include the classic problem of division of labour (which has been discussed primarily within the context of social insects); the origin and explanation of (apparent) altruism in nature; the role of group vs. kin, gene and individual selection; and the possible role of handicaps in ensuring the reliability of biological signaling. Section II consists of a sectionary introduction and two papers that are both intended for publication within peer reviewed journals. The first paper (*How the problem of division of labour became a question of group vs. kin selection: a conflict of formal and compositional biology*) examines the history of the problem of division of labour within myrmecology. This paper is currently in review in the *Journal of the History of Biology.* It argues that a conflict between adherents of two styles of biological theorizing, formal and compositional biology, strongly influenced how the problem of division of labour was perceived and approached by biologists and myrmecologists at different periods during the 20th century. Initially construed as a problem for Lamarckian inheritance, it experienced several redefinitions, later perceived as a question of colony integration and the coordination of parts within wholes, and, with the expansion of formal biology, as a question of how to explain the existence of apparent altruism in nature. These transformations were intertwined and embedded into the larger narrative of the advent and later hardening of the modern evolutionary synthesis and with changes in the relative appeal of the compositional and formal style within the biological community.

The second paper (*The Handicap Principle and the Argument of Subversion from Within*) examines the very disparate attitudes that various scientists have taken towards a classical argument against the evolution of altruism by group selection – the so-called *argument of subversion from within.* Focusing on the related debates on group selection, altruism and the handicap principle, this paper argues that the disagreements between John Maynard Smith and Amotz Zahavi over a number of important evolutionary issues were at least partly grounded in their disparate applications of epistemic values. In turn, these disparate applications were related to other important epistemological and ontological commitments, as the antagonists disagreed both over the hereditary basis for altruistic behaviour and in the confidence they ascribed to mathematical modeling. Comparing these findings with the theoretical distinction between formal and compositional styles of biological theorizing, it concludes that although this distinction has some explanatory merits, this theoretical scheme does not adequately cover the idiosyncrasies of Zahavi's approach – a case that illustrates that the peculiarities of *individual* scientists may play an important role in the shaping of scientific controversies.

Section III is concerned with a cluster of related scientific problems within the domain of paleontology that are all connected with the debates on the evolutionary interpretation and significance of the Cambrian fossils of Burgess Shale. The analysis presented here is based on a case-study that has earlier been published in Danish (Baron 2004) and whose main results are here brought to an English audience for the first time, with the intent of providing the basis for a comparative analysis with the findings of Section II. However, as will be explained in the introduction of Section III, the theoretical stance defended here, differs in several aspects from the one defended by Baron (2004) – most notably in its abandonment of Kuhn's theory of paradigms as the primary theoretical perspective upon which the analysis of this debate should be based. It also differs from the original study in the fact that it uses the actions of individual researchers in order to address how the semi-independent intellectual developments within *different* scientific thought collectives may interact which each other.

Like Section II, the main part of Section III consists (apart from the sectionary introduction) of two papers. The first paper (*Epistemic values in the Burgess Shale debate*) has recently appeared in the journal *Studies in History and Philosophy of Biological and Biomedical Sciences* (Baron 2009). Taking its departure in the relation between a collective's shared epistemic values and the idiosyncrasies of the individuals who apply them as means to various ends, this paper explores the role of individual idiosyncrasy in this application of epistemic values in the context of a discipline (paleontology) that seeks to establish scientific authority within the larger domain of evolutionary biology. The focal point of this analysis is the repeated claims of paleontologists that the study of fossils provides their discipline a 'privileged historical perspective', not shared by students of the extant biosphere. The first part of the paper explores how paleontologists has shifted between two strategies that employ opposing views on the classical positivist and physicalist ideal of science in their attempt to implement this perspective. The second part of the paper addresses this claim of privileged access to the historical dimension of evolution in a situation, where a theoretical upheaval occuring independent of the epistemic problem at hand, completely shifts the standards for evaluating the legitimacy of various knowledge claims. The paper concludes that although the various strategies employed to defend this claim of privileged access have themselves been disparate (and to some extent even contradictory), each of them have in common that they impinge on the acceptance of a specific epistemic ideal or set of values and that their success or failure depend on the compatibility of this ideal with the surrounding community of scientists.

The second paper in Section III (*A web of controversies: complexity in the Burgess Shale debate*) uses the Burgess Shale controversies as a case-study arguing that controversies within different domains may interact as to create a situation of "complicated intricacies" where the practicing scientist has to navigate through a context of multiple thought collectives. Each of these collectives may to some extents have its own epistemic dynamic - complete with a specific set of theoretical background assumptions; certain peculiarities of practice and some fairly negotiated standards for investigation and explanation. But the intellectual development in one of these collectives may occasionally "spill over" with far reaching consequences for the treatment of apparently independent scientific problems that are subject to analytical scrutiny in other thought collectives. For the practicing scientist, it is necessary to take this complex web of interactions into account in order to be able to navigate in such a situation. Based on these findings, the paper concludes that traditional encapsulated approaches, where scientists are treated as members of a single enclosed thought collective that stands intellectually isolated from other similar entities (unless the discipline is in a state of paradigmatic crisis) are inadequate in explaining the complicated relations and interactions between different domains of intellectual inquiry.

The final section of this thesis, Section IV, consists of the conclusion (which is perhaps more rightly labeled as the 'closing discussion'). Comparing the findings of the analyses presented in the other sections, it put forwards three general claims concerning the role of epistemic values in science that are empirically supported by the case studies. The first point is in line with the expectations (of Section I) that there is a relation of reciprocal underdetermination between epistemic values and other important variables in the scientific process. This claim is supported by the fact that several of the participants in the controversies may share (and give the same epistemic priority to) a given value, but may nevertheless end up on opposites sides of the fence because they disagree about exactly how this value is to be implemented.

The second general point that is empirically supported by the investigations in Section II and III is that it is considerably easier for an individual scientist to convince other scientists of the validity of his conclusion if they are based on a set of values that are compatible with the dominant epistemic ideals of the scientific community of which he or she is a member. This may seem to be a trivial point, but the case studies investigated here actually shows instances where this compatibility skews the analytical ability of a scientific community to the extent that the majority of its members accept propositions that are made on clearly unfounded grounds. However, this situation is further complicated by the fact that a scientist may also choose directly address and criticize the normative foundations for a scientific practice. If a scientist presents an otherwise epistemically sound argument into a scientific environment that is hostile to the argument's normative foundations, this does not necessarily entail that they will fall on deaf ears. The dominant epistemic values of a scientific thought collective are embedded within the scientific practice of that collective. The fruitfulness of that practice must be addressed (and viable alternatives provided) if that argument for changing values is to be successful.

The third general point of the conclusion is that the actions of individual scientists in scientific controversies constitute an important level of analysis in the investigation of epistemic values where interesting phenomena occurs that may otherwise go unnoticed when focusing exclusively on the level of the collective (or supra-collective). At the level of the individual, a bounded domain of the scientific community shows itself to be quite porous, and the entanglement and interaction between the intellectual developments in different semi-independent thought collectives becomes an important area of inquiry.

Another important analytical possibility inherent in this approach is that it, to a higher degree than analyses focusing on more exclusively on the scientific collective, may allow the investigator to couple the analysis of epistemic values with other important sociological variables that may play an important role in scientific controversies, such as, for instance, scientific prestige and authority. Thus, the cases investigated here indicate that it may be more difficult to retract from an argument when representing a minority of dissent than when representing the majority view. By going against the perceived consensus the dissenter has already invested a large amount of scientific prestige in claiming that everybody else is wrong. That capital may be lost, if it turns out that this investment was made on faulty premises. Taking the majority position, one does not make such a risky investment, however.

As a final thought, addressing the relevance of this investigation in connection with the larger themes of the unification or disunificatíon of the sciences, Section IV argues that the existence of a relation of reciprocal underdetermination between epistemic values and other important epistemic variables discussed by this study, is a serious hindrance for any universalist approach that attempts to establish the unification of the sciences on a uniform application of epistemic values. In also argues that such a project may be counter-productive. If epistemic values underdetermine theory-choice, the dissent that is created by disagreements about how these values are to be applied, is necessary in order to ensure a critical scrutiny of theory-choice – or for that matter any kind of choices where these values are involved. It is only by discussing these various uses that it is possible to evaluate them critically. And such a critical evaluation is much needed in the scientific community, where the fact that a controversy has reached closure and consensus does not necessarily mean that it has been settled in any epistemically satisfactory way.

General Acknowledgements: The making of this thesis has benefited from the help of several people. I thank employees and associates at the Center for the Philosophy of Nature and Science Studies at the University of Copenhagen for help and support, especially including Tom Børsen and my superviser Claus Emmeche, who provided helpful critique in the final stages of this thesis. I also thank employees and associates at the Center for

Social Evolution at the Biological Institute, University of Copenhagen, especially J. Koos Boomsma and Jes-Søe Pedersen, for opening their doors for an intruder, as well as the employees and associates at the Center for Biology and Society at the Arizona State University for doing the same. A number of people have also been helpful during the production of the papers presented in this thesis. These are specifically acknowledged in each case.

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On epistemic values, their role in science, and how to analyse them

Abstract: This paper discusses the most prominent approaches that have been used to address the role of epistemic values in science. It seeks an answer to the following three questions: what may we reasonably suppose about epistemic values; by which means do we uncover them when they are at play; and how do we study their implications for scientific practice? Taking a multi-level approach to these questions, it argues that reciprocal underdetermination is a key feature of the relation of the important variables for the understanding of epistemic values in science. An empirical approach therefore becomes a necessary part of the toolkit needed to investigate the idiosyncratic instances in which these values are applied by individual scientists. Furthermore, the paper puts forward a series of research questions that can be used to investigate particular instances of embodiment where epistemic values, in the form of methodological rules or norms, have a concrete effect on decisions made as part of the scientific process.

Introduction

This paper introduces the concept of epistemic values and discusses the most important approaches that have been used to address them, in order to give a preliminary answer to three questions:

a) What may we, as informed by the theoretical analyses of epistemic values given by philosophers, historians and sociologists of science, reasonable suppose about the nature of epistemic values in science?
b) By which means do we uncover epistemic values when they are at play in specific situations within the domain of science?
c) How do we study their implications for scientific practice?

The investigation is within the domain of what Ziman (2000) has termed 'academic science' – i.e. science where the research goals are formulated by the scientists themselves with a relative degree of autonomy, as opposed to situations of 'post-academic science' where the interplay between the formulation of research goals and the economic and political interests of various funding agencies has reached such an extent that it becomes a subject in itself. Comparing the universalist approaches to epistemic values of the Vienna Circle, Popper and Merton, with the contextualist approaches of Fleck, Kuhn, Laudan, Daston and Hacking, I argue that reciprocal underdetermination is a key feature of the relation between the variables important for the understanding of epistemic values in science. An empirical approach therefore becomes a necessary part of the toolkit needed to investigate their role in scientific practice. Taking a multi-level approach to the investigation of epistemic values, I put forward a series of research questions that can be used to investigate particular instances of embodiment where epistemic values, in the form of methodological rules or norms, have a concrete effect on decisions made as part of the scientific process.

What are epistemic values?

Put shortly (and broadly) epistemic values are criteria for good scientific conduct. Within academia they go under different labels such as epistemic virtues, norms, methodological rules or outright 'values' but terminology aside, they serve an important function in the thinking and actions of scientists that permeate every aspect of the scientific process. They are the criteria by which scientists evaluate whether their findings may be considered to be on a sound basis, and to distinguish good science from 'bad' science, or pseudo-science. Following the distinction of Cialdini (1996, p. 574) we may say that social norms exist in two basic forms. The first kind describes what most people *do.* It refers to social actions that are common or typical. Such norms may be called *descriptive norms.* These norms may motivate our behaviour by giving us evidence of what most other people think is effective conduct in a given situation. The second kind of norms describe the moral rules that we find *desirable.* It refers to shared expectations as to what constitute desirable conduct. Such norms reflects what people *approve* or *disapprove.* These norms may be called prescriptive norms, or (as Cialdini labels them) *injunctive norms* (because they do not merely inform our behaviour; they enjoin it). Epistemic values are of the latter kind.[1] We may preliminary distinguish between epistemic values that are about desirable conduct *within* the domain of science and the

[1] Perhaps it would be prudent to give a short early account of how I use the concepts of *norms* and *values.* Both terms are used rather interchangely here as synonymous with criteria for good conduct. In the following both norms and values therefore refer to what Cialdini has termed *injunctive norms.* When referring to values connected to scientific research, we may to some extent distinguish between *epistemic* values (e.g., parsimony or accuracy) that concerns the choice of a preferred explanation or investigation procedures; and *moral* values (e.g., demand for informed consent in medical research) that concerns just or morally good behaviour in general. It will also apparent from the following account that a decision is underdetermined by the values that are used to justify them – and that the application of epistemic values

and more general moral (or ethical) values that are about desirable conduct in society at large. However, following Douglas (2009, p. 85, 90) we may also be somewhat skeptical about the viability of this distinction. As noted by Douglas, the claim that it may possible to make a sharp distinction between epistemic and non-epistemic values is based on the contention that ethical values play no role in the evaluation of scientific theories. Such a position, however, would entail that scientist should be exempted having a moral responsibility from the consequences of making errorneous empirical claims - a position that Douglas regards as untenable.[2] Although this issue will not be the focal point of the investigations conducted in this thesis, we may preliminary contend that while epistemic values are not moral values *per se,* it may be that at least some of them may have a moral component and even a moral origin.

We may make a further distinction between epistemic values as *methodological criteria of judgment,* and epistemic values as *institutional and communal imperatives* that regulates the social behaviour of scientists. Among the latter imperatives we find the norms and values that allegedly ensure the pursuit of free critical inquiry within academic science. These include demands for impartiality and disinteredness, communicability of results and reciprocity in the exchange of scientific material like mutant stocks. Among the methodological criteria of judgment we find some familiar scientific criteria that are used to justify a choice of investigation procedure or a preferred explanation. Here we find simplicity, repeatability, testability, falsifiability, accuracy, precision and even truth.[3] Some of these criteria, for instance simplicity, may be known by other names (e.g. Ockham's razor and the principle of parsimony). Likewise, it may be unclear, and a

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may be considerably affected by the individual features that differentiate the members of a scientific community.

[2] See Douglas 2009. p. 66ff, for a full explication of this position. The basic argument behind her position is that scientists, like everyone else, are morally responsible for the consequences of their choices, including the consequenses of making empirical claims (this is especially important, as scientists, as scientific advisers, are central for many instances of political decision-making). Note that Douglas does not demand that a scientist should be able to foresee every possible consequences of making a factual claim. The moral responsibility that Douglas bestows on scientists is limited to situations where we may reasonably conclude that a scientist should have been able appreciate the uncertainty of making a factual claim, and the risk connected to the consequences of being wrong, but failed to do so due to recklessness or negligence.

[3] I am, of course, not trying to make a complete list here.

source of disagreement, how exactly one implements an epistemic value, and whether changing the label also implies changing the epistemic value itself.[4]

One might also add that epistemic values come in different scales. Specific epistemic values may aggregate into larger ideals or ideologies that prescribe a certain practice for a scientific discipline or even the whole of science. Or maybe it is the other way around so that the adoption of a grand epistemic ideal or ideology entails the adoption of a scientific practice that prioritizes a specific set of epistemic values. In any case, here we both find attempts to establish a 'universal ethos for science' as wells some of the grand '–isms' of science: reductionism, empiricism, positivism or physicalism. Some of these –isms may have ontological components as well (e.g. physicalism), but their relevance to scientific inquiry only becomes apparent in the context of their normative character. As with the specific epistemic norms, it may be unclear, and a source of disagreement, how exactly these '-isms' are 'implemented into', or just identified within scientific practice. Hence we may find different versions of them in academia, e.g. (for reductionism): genetic reductionism, behaviourism and even psychological reductionism ("everything is in your childhood").[5]

As it will be clear by now, understanding the role of epistemic values in academic science, is a complex task. Enter the field of epistemic values, and you enter a field of inquiry where few issues are settled despite being hotly debated for many years. Add to this the fact that the relation between epistemic and moral values is unclear, and that new post-normal (*sensu* Ravets & Funtowicz 1993) and post academic (*sensu* Ziman 2000) trends within science tend to complexify the situation even further. An overview is therefore needed.

Universalist approaches to epistemic values

[4] The notion of implementing is of course be problematic here. It implies that some epistemic value, e.g., parsimony, somehow has an abstract historical or logic priority to its actual implementations or concretizations. It may of course be the more plausible to assume that (in at least some cases) such values are abstracted from concrete discussions about how to adapt, improve or modify already existing practices of scientific investigation, thus not having any prior existence to the individual instances of application. However, as this is not an essay in axiology, I will not pursue the ontology or epistemology of values in general. The much more modest scope here is to see how epistemic values play a role in the research process within some fields of biology.

[5] An overview (in Danish) of some of the most important epistemic ideals in science is given in Baron, 2004, p. 49ff.

A good place to start an analysis of many philosophical topics in science studies is to begin with the modernist attempts to reach a unified science that occupied many thinkers within the domains of the philosophy and sociology of science in the first half of the twentieth century. This topic is no exception. No doubt, two intellectual trends from this period have put their mark on current thinking on the subject of epistemic values - even though (or perhaps precisely because) many later authors disagree with them.

Early polemics about the scientific method

The first of these is the 'hunt for the scientific method' – a trend most prominently pursued by the Vienna Circle, and their notable critic Karl Popper. Central in these efforts was the attempt to make sharp (and universal) demarcation criteria between scientific and non-scientific claims.[6] Different demarcation criteria were used by the logical positivists and Popper, who disagreed whether the scientific method was 'inductive' or 'deductive' and whether scientific theories were noted by their possibility for empirical *verification* or *falsification.* For these authors, epistemic values were understood as criteria of judgment that supported the application of the scientific method – the precise content of which, was a subject of disagreement. By attempting to explicate the criteria by which a scientific theory could be tested empirically, these authors both explicated and referred to a series of epistemic values that continue to play an important role both in our understanding of what science actually *is,* and in the concrete practice that is employed in many scientific communities.[7]

This is perhaps most clearly illustrated in the work of Popper and in his critique of the logical positivists. For logical positivists like Carnap, a central feature of scientific theories was that they could be verified through empirical observations. Armed with a correspondence theory of truth, Carnap sought to establish the means by which the

[6] The philosophical effortts to secure a sharp demarcation between scientific and non-scientific claims should not be conflated with the efforts to secure a sharp demarcation between epistemic and non-epistemic values. This latter attempt is connected with the so-called 'value-free ideal' of science – an ideal that is often wrongly attributed to the logical positivists in general. But as described by Douglas (2009, p. 44ff) this ideal did not rise to prominence within the domain of philosophy of science before the 1950's and 1960's.

[7] See also Baron 2004, p. 50 for an account (in Danish) of the similarities in the approach of Popper and the logical positivists. Of course, as will be noted below these similarities did not mean that there were not also important differences as well.

probability of a scientific theory being true could be increased by way of further observations and inductive reasoning.[8]

Criticizing this project for being unable to solve the problem of induction, Popper claimed that the logical positivists' criterion of verifiability did not adequately capture what should be the essential feature of a scientific theory. Rather than truth and verifiability, Popper believed that the essential distinguishing characteristic of a scientific theory lay in its ability to make empirical *prohibitions.* In other words – the most distinguishing feature of a scientific theory was not that it was true (Popper considered this to be irrelevant to its status as a scientific theory) but that it was refutable. Addressing this topic in his *Conjectures and Refutations*, Popper stated the following:

"(1) It is easy to obtain confirmations, or verifications, for nearly every theory – if we look for confirmations.
(2) Confirmations should count only if they are the result of *risky predictions*; that is to say, if, unenlightened by the theory in question, we should have expected an event which was incompatible with the theory – an event which would have refuted the theory.
(3) Every 'good' scientific theory is a prohibition; it forbids certain things to happen. The more a theory forbids, the better it is.
(4) A theory which is not refutable by any conceivable event is non-scientific. Irrefutability is not a virtue of a theory (as people often think) but a vice.
(5) Every genuine *test* of a theory is an attempt to falsify it, or to refute it. Testability is falsifiability; but there are degrees of testability. Some theories are more testable, more exposed to refutation, than others; they take, as it were, greater risks.
(6) Confirming evidence should not count *except when it is the result of a genuine test of the theory* and this means that it can be presented as a serious but unsuccessful attempt to falsify the theory. (I now speak in such cases as 'corroborating evidence'.)
(7) Some genuinely testable theories, when found to be false, are still upheld by their admirers – for example by introducing *ad hoc* some auxiliary assumption, or by re-interpreting the theory *ad hoc* in such a way that it escapes refutation. Such a procedure is always possible, but it rescues the theory from refutation only at the price of destroying, or at least lowering, its scientific statues. (I later described such a rescuing operation as a a '*conventionalist twist*' or a '*conventionalist stratagem*'.)

One can sum up all this by saying that the *criterion of the scientific status of a theory is its falsifiability, or refutability, or testability.*" (Popper 1963, pp. 36-37)

[8] See Carnap, 1928.

This polemic from *Conjectures and Refutations* expresses very clearly the epistemic value held most highly by Popper, namely refutability or falsifiability (which is used as synonyms). However, it also shows that Popper considered certain epistemic values to be important when it came to assess the status of a scientific theory (as being a *scientific* theory), and others to be less important or even unimportant. Though obviously sharing several important epistemic values and ideals (testability, clarity, simplicity and a hostility to metaphysics) with his contemporary adversaries of the Vienna Circle, Popper disagreed with them about how several of these were to be implanted in the scientific method, and also rejected a central epistemic value in the thinking of the logical positivists, namely truth, to be irrelevant for the question in hand. As to testability, Popper took great pain to explain, that although he shared this criterion with the logical positivists, it entailed quite a different vision of the scientific method for him, than it did for them. As stated under point five, a theory's testability, for Popper, laid in its falsifiability, which is, of course, one of the key points, where he disagreed with the members of the Vienna Circle. The simplicity of theories (also known as Ockham's razor or the principle of parsimony) played an important role both in the thinking of the logical positivist and in the thinking of Popper – presumably because of their common anti-metaphysical inclination. However, for the logical positivist, the importance of simplicity was to be understood in the context of their agenda to solve the problem of meaning of scientific claims by reducing them to simple observation statements. Based on this premise, they considered metaphysical statements to be meaningless. In the manifesto of the Vienna Circle, *Wissenschaftlige Waltauffassung* it was stated that

> "…there is a sharp boundary between two kinds of statements. To one belong statements as they are made by empirical science; their meaning can be determined by logical analysis or, more precisely, through reduction to simplest statements about the empirical given. The other statements, to which belong the one cited above,[9] reveal themselves as empty of meaning if one takes them in the way that metaphysicians intend." (Bergmann *et al,* 1929).

[9] The statements referred to as examples here, and given in an earlier passage in the text, are the following: "there is a God"; the primary basis of the world is unconscious" and "there is an entelechy which is the leading principle in the living organism". (Bergmann *et al.* 1929).

Popper, however, did not try to solve the problem of meaning, which he considered to be a verbal 'pseudo-problem' (Popper 1963, p. 40). Rather, he tried, at least by his own accord, to solve the problem of demarcation *per se.* Popper did not claim metaphysical claims to be meaningless, but rather that they were irrelevant to scientific inquiry. Instead he conceived simplicity as a necessary tool for his vision of science as a trial-and-error process, or as he called a process of *conjectures* and *refutations.* For Popper, the importance of simplicity in this process lay in its ability to strengthen the refutability of a theory:

> "… what is usually called the simplicity of a theory is associated with its logical improbability and not with its probability, as has often been supposed. This, indeed, allows us to deduce from the theory of science outlined above, why it is always advantageous to try the simplest theories first. They are those which offer us the best chance to submit them to severe tests. The simpler theory has always a higher degree of testability than the more complicated one." (Popper 1963, p. 61)

Differences about the understanding of epistemic values are central in the thinking of both the Vienna Circle and Popper, thus lay at the heart of the disagreement between them. This illustrates a point that will be repeated many times in the following: even the most common epistemic values within the part of academia that occupies itself with natural science, are not understood unequivocally by its members.[10] As this example illustrates, this may also be the case for people who seek to make these epistemic values the universalist foundation for a unified science.

The Ethos of Science

Were the Vienna Circle and Popper to differ in their approach to the scientific method, they were united in their rejection of the totalitarian regimes that rose to power in the decades after the first world war, and in their efforts to establish a platform for securing scientific rationality as a domain safe from the invasion of totalitarian anti-intellectualism. In this they shared a common goal with another contemporary scholar who approached the role of epistemic values in science from the perspective of the sociology of science, seeking to establish a set of general norms that were universally

[10] Of course the example gives refers to philosophers of science, rather than scientists themselves. As will demonstrated in the following however, this point applies equally to scientists as well.

held by the scientific community at large. In 1942, Robert K. Merton published his thoughts on the normative structure of science in the first issue of the *Journal of Legal and Political Sociology* in a paper entitled “Science and Technology in a Democratic Order”. Here Merton presented the CUDOS norms - a set of epistemic values that he argued constitute a universal ethos of science. The word *cudos* comes from greek and means recognition but it was also used as an abbreviation for the set of values and norms, that Merton held to be binding on any practitioner of science:

> “These imperatives, transmitted by precept and example, and reinforced by sanctions are in varying degree internalized by the scientist thus fashioning his scientific conscience or, if one prefers the latter-day phrase, his super-ego. Although the ethos of science has not been codified, it can be inferred from the moral consensus of scientists as expressed in use and wont, in countless writings on the scientific spirit and in moral indignation directed toward contraventions of the ethos.” (Merton 1942/1973, p. 269).

Thus, whereas the epistemic values that were treated by philophers like Carnap and Popper were conceived as criteria of judgment used supporting the application of the right *methodology* in scientific investigations, Merton conceived them as general *institutional* imperatives that were necessary if the institution of science were to maintain its credibility as a source of independent, critical and free inquiry. The CUDOS itself consists of four such institutional imperatives, entitled *communism* (later dubbed *communalism* by writers such as Ziman 2000, in order to avoid confusion with communism as a political ideology); *universalism; disinterestedness* and *organized skepticism.*

The principle of *communism,* or *communalism,* requires that scientific knowledge should be public (and published) knowledge; that the results of research should be published; that there should be freedom of exchange of scientific information between scientists everywhere, and that scientists should be responsible to the scientific community for the trustworthiness of their published work. There is no “ownership” of scientific knowledge - a scientist claim to “his” intellectual “property” is limited to recognition and esteem. Given this institutional emphasis on recognition and esteem as the sole property rights of scientists, scientific priority in discoveries becomes a prime concern of scientists. The institutional conception of science as part of the public domain is connected with an imperative for communication of findings. Merton noted that secrecy is the antithesis to this norm while full and open communication is its enactment, and that this communal character of science was further reflected in the recognition by scientists of their dependence, upon a cultural heritage to which they lay no differential claims. And finally, in what may today be regarded as a preliminary capture of some of the problems that academic scientist encounters in an industrial or post-academic setting, Merton noted that the communism of the scientific ethos is incompatible with the definition of technology as "private property" in a capitalist economy (Merton 1942/1973, 273-275).[11]

The principle of *universalism* is based on the simple premise that truth-claims, whatever their source, are to be subjected to *preestablished impersonal* criteria. The acceptance or rejection of such claims by the scientific collective is required to be independent of the personal or social attributes of their protagonist. Race, nationality, religion, class and personal qualities are as such irrelevant for this question. Science is ideally and essentially an international enterprise. Even though chauvinist claims of a special "national" science have appeared in times, these deviations from this norm actually presuppose its existence in the first place. That such pressures can be exerted on scientific universalism illustrates that the institution of science is part of a larger social structure to which it is not always integrated. If this larger culture opposes universalism, the ethos of science is subjected to serious strain. This may especially happen in times of international conflict, when the dominant definition of the situation is such as to emphasize national loyalties. In such a situation the scientist is subjected to the

[11] The status of the norms of the CUDOS as *institutional values,* is illustrated by Merton's review of James D. Watson famous autobiography *The Double Helix* (1968)*,* concerning his and Francis D. Crick's pursuit of the chemical structure of DNA, for which they were ultimately awarded with the Nobel Prize in Physiology or Medicine in 1962. This highly personal account of the process was scorned by several reviewers and participants (notably Crick), for having put too much emphasis on the competitive character of science (and hence on the self-interest of scientists). Merton, however, noted that:

"All this competition and jockeying for position might seem to suggest that science tends to recruit egotistic personalities, contentious and exceedingly hungry for fame. However that may be – I doubt it – it does not explain these behaviour patterns […] it appears rather, as we see in Watson's memoir that the competitive behaviour of scientists results largely from values central to the scientific enterprise itself. The institution of science puts an abiding emphasis on significant originality as an ultimate value, demonstrated originality generally means coming upon the idea or finding first. Recognition and fame does appear to be more than personal ambitions. They are institutionalized symbols and rewards for having done one's job exceedingly well." (Merton 1968, p. 215-216) conflicting imperatives of scientific universalism and of ethnocentric particularism (Merton 1942/1973, pp. 270-272).

According to Merton, these pressures also illustrate that science does not thrive equally in all societies. An example is societies that are strongly divided into unequal social classes or castes, and where there is no free access to scientific pursuits for the inferior castes. Such a situation however is, according to Merton, inherently unstable, where extra-scientific justifications for this exclusion must constantly be sought, while lip service to the principle of universalism are still being paid within the realm of science. Since he believes universalism to be a dominant guiding principle in the ethos of democracy Merton also believes that a society following this ideal has the best chances of being able to fulfill the needs demanded by the imperative of scientific universalism:

> "However, inadequately it may be put into practice, the ethos of democracy includes universalism as a dominant guiding principle. Democratization is tantamount to the progressive elimination of restraints upon the exercise and development of socially valued capacities. Impersonal criteria of accomplishment and not fixation of status characterize the open democratic society. Insofar as such restraints do persist, they are viewed as obstacles in the paths to full democratization." (Merton 1942/1973, p. 273)

The principle of *disinterestedness* requires that the results of bona fide scientific research should not be manipulated to serve considerations such as personal profit, ideology, or expediency. As elsewhere, Merton made a point here of distinguishing between institutional and motivational levels of analysis, and he noted that the quest for distinctive motives appears to have been misdirected. Disinterestedness does not equate with altruism which is a motivational state (and nor does interested action equate with egoism). Rather, it is a distinctive pattern of institutional control within the scientific community, that compels the scientist to conform to this norm, with the risk of sanctions should the norm be violated, and, so far the norm has been internalized, with the risk of psychological conflict.

Merton also argued that ”the virtual absence of fraud” in the annals of science could not be attributed to the personal qualities of the scientist but to the institutional control installed by the scientific ethos.[12] An integral part of this institutional control lay in the final norm of the CUDOS system, the principle of *organized skepticism.* According to Merton, this principle is both a methodological and an institutional mandate. The principle of organized skepticism requires that statements should not be accepted on the word of authority, but that scientists should be free to question them and that the truth of any statement should finally rest on a comparison with observed fact. He further notes that this epistemic value may frequently put science at odds with other institutions, where the temporary suspension of judgment and detached scrutiny of beliefs may come in conflict with preestablished dogma:

> "Conflict becomes accentuated whenever science extends its research to new areas toward which there are institutionalized attitudes or whenever other institutions extend their control over science. In modern totalitarian society, anti-rationalism and the centralization of institutional control both serve to limit the scope provided for scientific activity." (Merton 1942/1973, p. 278).

Perhaps it is most clearly in quotation above, and in the critical nature of the last of the CUDOS norms that we see the intellectual connection between Merton's thinking and the attempts of the Vienna Circle and (especially) Popper, to establish a universal philosophical foundation for the scientific method. Central in both these types of approaches were a vision of science as an endeavor that sought to establish a universal platform for rational and critical thinking. The epistemic values proposed as part of this endeavor were by their authors considered to be a must for any scientist. Followed correctly, they would ensure science's status as a rational activity.

Contextualist approaches to epistemic values

Although a later generation of scholars took issues with certain parts of the universalist ambitions of these thinkers, it is clear that they did not conceive science to be an activity taking place in a social vacuum. On the contrary, many of their concerns were precisely connected with the negative effects of social and political pressures on science.

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[12] One might of course question this use of negative evidence. Does the absence of *discovered* fraud means that it did not occur? Or is it because the control systems for discovering it were to weak? Questions such as these have popped up in connection with prominent cases of allegedly misconduct in high-profile science, for instance, within nano-science, the case of Jan Hendrick Schön (see Beazley *et al.* 2002).

These concerns expressed themselves both in the anti-metaphysical stance of the Vienna Circle (who believed metaphysical ‘dogma’ to be a hindrance for societal progress) and in Merton’s contention that the ethos of democracy and the ethos of science are especially compatible together.

In retrospect, perhaps the main critique of the universalist stance, was that its absolutist perspective was unable to adequately address the role of contextual elements (institutional philosophical) in setting the standards for the investigation, including:

1) Which kinds of questions and problems are scientifically legitimate.
2) Which kinds of solutions are scientifically acceptable.

The inadequacy of a universalist treatment of these questions becomes apparent when considering one of the basic distinctions that informed the thinking of both the logical positivists and Popper – the distinction between the *context of discovery* and the *context of justification.* Originally introduced by Hans Reichenbach (1938) this distinction served as a tool for relegating matters concerning the discovery of scientific findings or theories to the realm of psychological analysis and having no bearing on how these claims were evaluated or justified. It was the realization that such a distinction could not be upheld (at least not as sharply as had been supposed) that became a basic premise for the development for a line of thinking on epistemic values, that I find most appropriately labeled *contextualist.* Whereas universalist approaches had considered epistemic values to be *absolute,* and a must for any scientist, contextualist approaches took epistemic values to be *historical* and *contingent* – in other words to be entities that could arise, change and dissolve as the result of historical and cultural developments. As such they offered at best a somewhat shaky foundation for science, as they themselves could be subjected to critique and discussion as part of academic disagreement. And the understanding of them had to based on the investigation of their particular implementation in scientific *practice.*

The prime entity of analysis for this enterprise was the scientific collective – *the scientific community*. Though at times struggling to demarcate this entity, the role of collective norms and values in disciplining scientific practice was already recognized in the writings of Merton and measurable means to demarcate them would later be employed in the forms of mapping of textbook uses or citation index analysis.

Thought styles and thought collectives

An early exponent of the contextualist approach was no doubt Ludwik Fleck, a contemporary of the 'universalists' thinkers who were treated in the previous passages, although the significance of his thinking was to be realized much later.

In the *Genesis and Development of a Scientific Fact,* Fleck offered a new perspective in his ideas of thought styles in medicine and science as tools for interpreting and understanding empirical observations. The premise for Fleck's analysis was a complex case taken from the history of medicine: the medical conception of the causes of syphilis from the 15th Century to the beginning of the 20th Century. From initially being regarded as a veneral disease resulting from immoral behaviour and "bad blood", Fleck traced the radical transformation of the concept of syphilis (facilitated by the introduction of molecular diagnostic tools, like antibodies, that made it possible to prove the existence of sub microscopic particles in blood and tissue samples coming from infected patients), to its modern conception, where it is regarded to be the result of a pathogenic microorganism. Arguing this shift to be as much the result of a change in thinking as the result of experiment and observation, Fleck concluded that scientific reasoning was locked within *thought collectives* (german: *Denkkollektiv*), an idea that became central to his conception of science. According to Fleck a thought collective was to be defined as a community of persons mutually exchanging ideas or maintaining intellectual interactions,[13] and he designated this entity the role of "carrier" for the historical development of any field of thought as well as the given stock of knowledge and cultural habits that were part of the collective belief system. Each collective was therefore accompanied by a specific style of thinking or *thought style* (german: *Denkstil*):

[13] An individual could therefore, according to Fleck (1935/1979, p. 45) belong to several thought collectives at once. As part of a research community, a scientist would belong to one collective, but as a member of a political party, a social class or a nation he would belong to others. What Fleck did not address in his description of the thought collective, however (and what will become a paramount point when addressing the role of the individual) was the possibility that a scientist may be a member of several *scientific* thought collectives.

"Like any style, the thought style also consists of a certain mood and of the performance by which it is realized. A mood has two closely connected aspects: readiness both for selective feeling and for correspondingly directed action. It creates the expressions appropriate for it, such as religion, art, customs, or war, depending in each case on the prevalence of certain collective motives and the collective means applied. We can therefore *define thought style as* [the readiness for] *directed perception, with corresponding mental and objective assimilation of what has been so perceived.*" (Fleck 1935/1979, p. 99)

Fleck further noted that a thought style is characterized by common features in the problems of interest to the thought collective, by the judgment which the thought collectives considers evident, and by the methods which it applies as its means of cognition. Thus, a thought style was also characterized by a common set of epistemic values (as methodological criteria of judgment) that the members of the thought collective would apply to their problems of interest in a similar manner. The thought style might also be accompanied by a technical or literary style characteristic of the given system of knowledge (ibid.).

This contextualist framework led Fleck to reject universalist ambitions to create any absolute and objective criteria for judging the suitability of scientific theories, claiming that such absolute criterion of judgment to be as invalid for fossilized theories, as a chronologically independent criterion would be for evaluating the adaptability of the Brontosaurus.[14] Challenging Carnap to discover for himself the social conditioning essential for scientific knowledge, he stated that:

"Carnap's system … will perhaps be the last serious attempt to construct the "universe" from "given" features and from "direct experience" construed as ultimate elements … Concerning his viewpoint ... one would hope that eventually he might discover the social conditioning of thought. This would liberate him from any absolutism in the standards of thought, but of course he would also have to renounce the concept of 'unified science." (Fleck 1935/1979, p. 177).

As can be seen from above, the thinking of Fleck did in fact encompass elements that would be characteristic in the thinking and interpretation of later contextualist approaches to epistemic values. Among these were a skeptic stance towards the

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[14] Curiously, paleontologists no longer recognizes the existence of the "Brontosaurus" as an evolutionary fact. Systematic revisions has derived this genus its status as an independent taxonomic entity, and the bones that were previously associated with it are now being assigned to the genus *Apatosaurus.*

possibility for attaing absolute truth in scientific research (since scientists supposedly were locked into scattered thought collectives, each of which were constituted by a specific thought style), and the contention that the state of science did not just develop by the unidirectional and progressive accumulation of new knowledge claims, but also in the overthrowing of old ones.

The Disciplinary Matrix

Both of these elements can, of course, be found in the writings of one of the most prominent philosophers of science of the twentieth century, Thomas S. Kuhn. Like Fleck, Kuhn's account took the scientific collective or community as his basic unit of analysis, and described a model of scientific change, that divided scientific activity into three types or states: *normal science*, *crises* and *scientific revolutions.* Central to this model was his notion that the activities of the scientific community were embedded within a set of contextual presuppositions – a *paradigm.* During periods of *normal science* (which, according to Kuhn, was the usual state of affairs within science), scientists were mostly occupied with expanding the paradigms implications on problems well-defined within the paradigms framework, not questioning the framework itself. Kuhn called this activity "puzzle-solving", and noted that should findings appear as a result of this puzzle-solving, that were not in accord with the paradigm, they would at first be ignored or explained away. Eventually however, if enough of such anomalies accumulated, this might lead some scientists to reject this framework, proposing an alternative paradigm and initiating a scientific *crisis.* Unlike periods of normal science the paradigms framework would be openly discussed during a crisis period. According to Kuhn this debate may be severely hindered, however. Precisely because the participants disagree about the basic framework (the paradigm) for evaluating scientific claims or arguments, they do not (or no longer) share the same understanding of their scientific vocabulary and terminology. Central scientific concepts may therefore be understood differently by proponents of disparate paradigms, something that may lead to partial breakdowns in communication, i.e. *incommensurability*. If an alternative paradigm proves strong enough it may convince the majority of scientists to reject the old one. This would create a *scientific revolution* within the field, which would then enter a new state of normal science, where the alternative paradigm becomes the dominant framework for scientific research.[15]

Famous (and much criticized) for this paradigm account of science in *The Structure of Scientific Revolutions* (1962), it is in fact in Kuhn's later writings that we find the most explicit treatment of the topics most relevant to this text, the role of epistemic values (which he understood as methodological criteria of judgment in the tradition of Popper and the logical positivists). Attempting to explicate the contextual elements of a paradigm Kuhn introduced the concept of the disciplinary matrix (Kuhn 1969). The disciplinary matrix consists of four components, *symbolic generalizations; metaphysical* or *ontological assumptions, exemplars,* and *values* (by which he meant epistemic values in the form of methodological criteria of judgment). By 'symbolic generalisations' Kuhn meant the schematical or logical expressions that represent general laws or relations. Examples include Ohm's law V = RI or the Hardy-Weinberg law in population genetics. Metaphysical or ontological presumptions denote claims about the nature and properties of the world and its contents such as the idea of the universe or the human being as a machine. By 'exemplars' Kuhn refers to textbook or labouratory examples that students learn as examples of how scientific practice is to be conducted. Examples here (within biology) include lab experiments with the fruit fly *Drosophila melanogaster* and calculation of random mating models in population genetics.

Unlike these three components, whose content he considered to be specific for each particular scientific community, Kuhn believed the final component of the disciplinary matrix, the (epistemic) values, to be more widely shared among natural scientists as a whole. Thus, epistemic values, such as simplicity or precision, did have a more "universalist" ring to them, but Kuhn warned against believing that the application of epistemic values was a trivial affair. Although certain kinds of scientific judgments concerning, for instance accuracy might be relatively (though not entirely) stable from one time to another and among members of a scientific community, Kuhn noted that

> "… judgments of simplicity, consistency, plausibility, and so on often vary greatly from individual to individual. What was for Einstein an insupportable inconsistency, one that rendered the pursuit of normal

[15] The central reference for Kuhn's paradigm theory of scientific development is, of course, Kuhn (1962).

science impossible, was for Bohr and others a difficulty that could be expected to work itself out by normal means." (Kuhn 1969, p. 184).

Kuhn also noted an aspect of epistemic values that was perhaps even more important: in situations, where epistemic values are applied, different values will often dictate different choices, when they are regarded separately. One theory could be more accurate but less consistent than another and Kuhn noted that though epistemic values were widely shared by scientists, and that commitment to them was constitutive of science, their application was sometimes deeply affected by idiosyncratic features of the individual member of the scientific community.

Thus, despite the choice of the scientific community as the prime level of analysis in his paradigm account of science, Kuhn's understanding of the role of epistemic values showed a clear recognition of an important level of individual choice when it came to how these values were applied to judgment. But, although arguing for a strong element of individual idiosyncrasy in the application of epistemic values, Kuhn also stated that since these values were shared by the scientific collective, they still had a significant function as guiding principles even when they were not used in an unanimous way. The fact that epistemic values could be applied in various ways did not mean that it could be applied in any way chosen. Defending himself against charges that his position led to a completely relativist and irrational view of science, Kuhn noted that

> "Though the values they [i.e. scientist working within the framework of a paradigm during a period of normal science] deploy at times of theory-choice derive from other aspects of their work as well, the demonstrated ability to set up and to solve puzzles presented by nature is, in case of values of conflict, the dominant criterion for most members of a scientific group. Like any other value, puzzle-solving ability proves equivocal in application. Two men who share it may nevertheless differ in the judgments they draw from its use. But the behaviour of a community which makes it preeminent will be very different from that of one which does not." (Kuhn 1969, p. 205)

How is one to describe this situation theoretically? The analysis that Kuhn presents here seem somewhat reminiscent of an old claim from Quine concerning the relation between data and theory-choice. Quine claimed that theory-choice is *underdetermined* by data in the sense that the available evidence is not in itself enough to decide between rival hypotheses or theories.[16] We may also follow the distinction of Newton-Smith (2001) who described a weak version and a strong version of Quine's claim concerning the relation between data and theory-choice. According to the weak version, this problem may perhaps be solved by gathering more, decisive, evidence. In the strong version of Quine's claims any scientific theory has an incompatible theory to which it is empirically equivalent.

Now, if theories are underdetermined by data (whether we accept the weak or the strong claim), then we would presumably expect other variables, like ontological commitments or methodological criteria of judgment to come into play in decisions of theory-choice. One might also add that the underdetermination of theories by data arise because the precise content of these variables are themselves not agreed upon. Thus, we find an important source for this underdetermination of theory by data in the fact that scientists employ different criteria of judgment or interpret empirical evidence on the basis of different ontological commitments. Presumably they would have reached consensus if they agreed, not only in factual beliefs and the credibility of the available data (which may also be a source of disagreement), but also on all methodological and ontological presumptions. However, the quote of Kuhn states that this is *not* necessarily the case. Even in situations where scientists work in a period of normal science within the same paradigmatic framework, there will be an idiosyncratic element in their application of epistemic values. The adoption of a specific set of methodological criteria of judgment does not entail the adoption of a ubiquitous conception of how these criteria are to be interpreted and applied in concrete instances. Although these criteria may occasionally be used to decide between rival theories and hypothesis, they cannot, according to Kuhn, provide any logic-proof justification for a preferred theory-choice – and, one might add, nor do they provide the logic-proof justification for any other choices relevant for the scientific investigation. Paraphrasing Quine's claim, one might say, that Kuhn believed that *scientific choices are underdetermined by epistemic values.*[17]

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[16] Quines original formulation claimed that theories were undetermined. See W. V. O. Quines "Two Dogmas of Empiricism" (1951). Historically this argument was first pursued by the French philosopher Pierre Duhem (1906). The claim has since been known as the 'Quine-Duhem' thesis.
[17] For further explication of the claim that the choice of theories is underdetermined by epistemic values, see Longino 1990.

The Aims of Science

This very point became pivotal in the treatment and critique of Kuhn launched by philosopher and historian of science Larry Laudan. In his *Science and Values: The Aims of Science and Their Role in Scientific Debate* (1984) Laudan granted that theory-choice are underdetermined by epistemic values, but chided Kuhn for giving a picture of them as being too fluid and ambiguous to be of any major role in scientific decision-making.[18] Arguing that an important distinction must be made between belief and preference, Laudan believed that while methodological rules underdetermine belief in factual claims they simultaneously determine a preference that will exclude certain prospective beliefs as impermissible. Thus while one class of beliefs may be equally permissible, because they all have an equally high empirical support, there will, at the same time, be another class of beliefs that will be impermissible, because they do not have the same degree of empirical support as the first class:

> "For instance the rules and evidence of biology, although they do not establish the unique correctness of evolutionary biology, do exclude numerous creationist hypotheses – for example, the claim that the earth is 10,000 or 20,000 years old – from the permissible realm and thus provide a warrant for a rational preference for evolutionary over creationist biology." (Laudan 1984, p. 29)

Arguing that an understanding of choice of belief must take its departure in the acceptance that scientists, when making decisions about theories, choose the best theory they can find, rather than the best theory possible, Laudan noted that

> "The crucial point here is that even when a rule underdetermines choice in the abstract, that same rule may still be unambiguously dictate comparative preference among extant alternatives. It will do so specifically when we are confronted with a choice between (in the simplest case) two candidate theories, one of which is (methodologically) permissible, and the other not." (Laudan, 1984, p. 29)

Thus, if we, according to Laudan, once grant that theory appraisal is a comparative matter, where scientists are generally making comparative judgments of adequacy among available rivals rather than absolute judgments, then it becomes clear

[18] One may perhaps argue, having the second quotation above in mind, that this interpretation of Kuhn is not entirely fair.

that comparative preference may be warranted even when the selection of the best possible theory is beyond our justificatory resources.

What are we, then, to do with instances where scientists disagree about the rules of the game? According to Laudan part of the answer lies in the role of cognitive goals and aims in the scientific process. Thus, one role of aims in resolving methodological disagreements is to eliminate certain methodological rules, by virtue of their irreconcibility with those aims. By imposing constraints on the class of permissible rules in situations where certain rules are conducive to achieve a given aim, while others are non- or counterconducive, shared goals can often mediate in controversies about rules (Laudan 1984, pp. 36-37).

However, it is important to stress, that although the invocation of shared goals may sometimes make methodological consensus possible, this is not, according to Laudan, a cure-all for all manner of methodological disagreements. For instance, it may happen that both parties in a controversy are advocating methodological rules that are, so far as we can see, equally effective in achieving the cognitive aim in question. Even more commonly are situations where a broad range of epistemic values are simultaneously endorsed (say, simplicity, coherence and empirical accuracy), but where the methodological rule tends to promote the realization of one of these values at the expense of others. In such situations there seems little possibility that methodological disagreements could be solved by bringing aims explicitly into play. And of course, there are plenty of cases, where methodological disagreements arise from even deeper disagreements about cognitive aims. The history of science is rife with controversies between, for instance, instrumentalists and realists, reductionists and antireductionists, advocates and critics of simplicity, proponents of teleology and advocates of purely efficient causality. According to Laudan the existence of such controversies, along with the fact that they often eventually reach consensual closure, exposes the weaknesses in the accounts of scientific debates inherent in the works of classical philosophers of science like Popper, Hempel or Reichenbach. This account (which Laudan calls the 'hierarchical model') assumes the existence of three levels of disagreements within science; a level of disagreement concerning factual claims; a methodological level of disagreement concerning methods or investigation procedure and what Laudan refers to as an ‘axiological’ disagreement concerning cognitive aims and goals. This model assumes that disagreements at the factual level are resolved at the methodological level, and that disagreements at the methodological level are resolved at the axiological level. However, the hierarchical model gives us no reason to anticipate that disagreements at the axiological level can be resolved at all, and the fact this is done frequently within science shows is a testimony to its inadequacy.

Another fallacy of the hierarchical model is that it assumes a clear cut separation between factual beliefs and methodological considerations. As an example of the problems of this assumption Laudan cites the discovery of the Placebo effect. Before the recognition of the Placebo effect, simple control experiments (where one group of the patients were given the drug to be tested and another were given nothing) were considered as sufficient tests of therapeutic efficiency. The recognition of the Placebo effect within the medical community led to the adoption of single-test that make appropriate allowance for reports of efficacy based largely on the patients expectations of betterment. Likewise, in a similar development, the recognition that those administering drug tests could unconsciously transmit their own therapeutic expectations to the patients they were examining, led to the adoption of double-blind tests of medication and other therapies (Laudan 1984, p. 39).

As this example shows factual beliefs shape our methodological attitudes, and for Laudan this example illustrates that subject areas like the methodology and epistemology of science, whose central focus is with the assessment of various rules of inquiry and validation should be conceived, at least to a much greater extent than they normally are, as empirical disciplines. Such a naturalization does not, however, mean that these disciplines should renounce on their normative aims and transform into purely descriptive enterprises:

> “Granting for a moment that there is no hard-and-fast line between normative and descriptive activities, the presumption that an empirical theory of knowledge would be void of normative claims is nonsense. Once we realize (as this chapter should make clear) that methodological norms and rules are assert empirically testable relations between ends and means, it should be clear that epistemic norms, construed of course as conditional imperatives (conditional relative to a given set of aims), should form the core of a naturalistic theory of scientific knowledge.” (Laudan 1984, p. 40)

Based on these considerations, Laudan proposes an alternative to the hierarchical model of justification, the so-called *reticulated model,* whose main feature is that aims, methods and factual beliefs form a network of shifting and interdependent justificatory relations. According to this model disagreement at any level may be resolved by justificatory arguments coming from any other level. Not only may aims justify the choice of a preferred method or theory, but factual beliefs may be relevant to the appraisal of methods (as in the case of the Placebo effect) or may provide constraints on appropriate cognitive goals by deeming certain goals to be impossible to reach. Likewise, considerations about available methods may shape scientists' perceptions about the attainability of a specific cognitive goal, or may even lead to claims that the goal is so ambiguously or imprecisely stated as to be reachable by empirical means at all. Changes taking place at one or more level of the hierarchy may thus be warranted on the basis of factors obtaining at any other level (Laudan 1984, pp. 50ff).

Moral Economies

Although both the reticulated model and Laudan's general position of 'normative naturalism' were met with accusations of endorsing epistemic relativism,[19] his holistic conception of the justificatory relations between epistemic values, factual beliefs and cognitive goals certainly seems to have some merit. One of its interesting consequences is that it adds a historical dimension to the study of methodology. If factual beliefs inform methodological rules, then it is to be expected that these rules may change and develop historically as a consequence of our changes in factual beliefs. Historical studies of actual developments and changes in epistemic values, and the development of conceptual tools that may be helpful in such an enterprise, are thus warranted.

A candidate for such a conceptual tool is the *moral economy.* The concept of moral economies of social groups was originally introduced by the historian E. P. Thompson (1971) but has been developed and refined as a tool for understanding the

[19] Most notably here is the exchange between Laudan and Worrall. See Laudan 1989 and Worrall 1988; 1989.

function of values in the practice of scientific collectives by Daston (1995).[20] Daston describes the moral economies of science as sets of norms or values that are shared by a scientific community as a thought- and emotional collective.[21] Whereas the term 'moral' in moral economy refers here both to its psychological and the normative resonances of the term[22] 'economy' refers, not to money, but rather to an organized system that display certain regularities, regularities that may be explicable but not always predictable in detail. A moral economy is thus a balanced system of emotional forces, with equilibrium points and constraints. Moral economies are embedded within the scientific practice and habits of the community (though they are not determined by them), and they are historically contingent in the sense that they arise, change and dissolve as a result of historical and cultural developments.[23]

According to Daston there are certain demands to moral economies. Firstly they must be internally coherent and consistent. There must be an internal balance between the different values of a moral economy. Not all values can be logically combined. Inconsistency between the values of a moral economy would cause a breakdown of the stability that is a necessary element if a moral economy is to maintain its power as a set of guiding principles for a research collective. And secondly there must be a balance between the values of a moral economy and the values of the surrounding society, if frictions between them are to be avoided.

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[20] An account (in Danish) of Daston's concept of moral economies has earlier been given in Baron, 2004, p.28ff. As will be clear, however, the analysis presented here differs from this account in several respects, most notably in its critical attitude towards *exactly which kinds of epistemic values* (i.e. communal imperatives of methodological criteria of judgment) moral economies are supposed to describe.

[21] Daston's initial analysis is based on the conception of epistemic values as methodological criteria of judgment. However, as will be clear from story of Kohler's analysis of the Morgan fly group given below, this is not the only way to conceive the norms and values of moral economies.

[22] It should be noted, though, that Daston emphasized that moral economies is *not* a matter of individual psychology. Although moral economies are about mental states, these are the mental state of *collectives* of scientists, not of lone individuals. Daston (1995, p. 5).

[23] It should be noted that it is to some extent unclear at which level the concept of moral economies operate. According to Daston's *definition* moral economies are connected to specific communities. But her *de facto* use, for instance in the analysis of different kinds of objectivities (see below) seems to suggest that moral economies may be a cross-community phenomenon covering several different communities. I do not believe this scale problem disqualifies the moral economy concept's applicability and usefulness as an analytical tool, however. Recognizing that scientists operate under shared sets of values is a helpful assumption if one is to analyze their role and dynamics. The collectives that operate under a certain sets of guiding principles may be embedded in even larger collectives (as in the case of Kohler's analysis of the fly group – see below) - or a set of guiding norms may be shared by various collectives pursuing similar cognitive goals in different specialist fields (as in the case of Daston's analysis of different kinds of objectivities). As demonstrated by Kohler these relations may be far from trivial.

As examples of how epistemic values prescribe specific scientific practices when combined, Daston goes through historically instantiated applications of practice related to three central concepts in science: quantification, empiricism and objectivity. According to Daston each of these concepts is applied in various ways that illustrate the existence of several moral economies in science. Hence, a concept like (e.g.) quantification covers not one but several different meanings and practices.[24] Each of these meanings of quantification are employed in a variety of scientific communities with disparate cognitive goals and with disparate moral economies.

Thus, in scientific communities occupied with precision measurement, the primary epistemic values are accuracy and precision.[25] Combined, these epistemic values support a practice that directs the measuring scientist towards a focus on painstaking detail and a self-discipline of diligence, fastidiousness, thoroughness and caution. Other epistemic values have low priority in this moral economy, however. The practice of measurement aims at integrity sometimes in defiance of the collective, since the more precise the measurement the more it stands as a solitary achievement of the measurer, rather than as the replicable common property of the group. The price paid may be a loss of communicability of results and scientific sociability. Measuring accurately acquires skill, expertise and experience with the experimental apparatus, and this first hand experience may be difficult (if not impossible) to communicate fully to others not having the same background. Although scientists devoted to precision measurements never meant to withdraw from the scientific community, there are historically instances, where their rigorous pursuit of this goal effectively isolated them from other experimentalists and theorists (Daston, 1995, p. 10-11).[26]

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[24] These include 1) abstract models that may of may not refer to measurements or observations; 2) measurements that may or may not refer to a mathematical model of the phenomena under investigation; 3) estimates that are neither grounded in theory nor measurements; 4) methods of data representation and analysis like graphs and tables; and 5) the creation of new entities, for instance index numbers such as the gross national product. See Daston 1995, p. 8.

[25] Daston makes a sharp distinguishing between accuracy and precision. For Daston, accuracy concerns the fit of numbers or geometrical magnititude with some portion of the world and presupposes that a mathematical model can be anchored in measurement. Precision concerns the clarity, distinctness and intelligibility of concepts, and stipulates by itself nothing about whether those concepts match the world (Daston 1995, p. 8).

[26] As an example Daston cites Kathryn Oleszko's study of the habits and ethos of astronomers in the Franz Neumann's physics seminar that was established in Königsberg in 1834. See Oleszko 1991, pp. 250-252, 287, 392-393, 378-386.

A contrast to the balance of epistemic values in this moral economy of quantification can often be found flourishing under conditions of weak or confused authority – for instance, in situations where a scientific collective occupied with an interdisciplinary problem is constituted by members with a diverse and heterogeneous educational and theoretical background.[27] In such a situation a moral economy may arise where a quantifying practice is established around a combination of communicability and impartiality as primary epistemic values. Here, the aim of quantification is not to secure individual conviction, but rather to secure the acquiescence of a diverse and scattered constituency. In this quantifying practice communicability and impartiality combine to the end of damping controversy and compelling consensus. Behind it lies the contention (expressed originally by Leibniz) that lack of clarity was at the root of almost all controversy and that this lack of clarity could be cured by a goodly dose of numbers. Although these attempts to silence dissent through quantification are, to some extent, also founded upon the allegedly certainty of mathematically based knowledge, their dominant appeal is the promise of reaching consensus through communication and shared understanding. The price paid for this gain is a loss of information about the specific observatory conditions. If local details (such as the individual researcher's skill and experience; which brand of instrument was used; the exact degree of humidity of the air in which the measurement was taken etc.) were not filtered out, these quantified results would lose their portability, and, hence, their value as tools in scientific communication.

As can be seen by these examples, Daston envisages the "balance" of moral economies as a situation, where certain epistemic values are weighted highly as guiding principles for a given scientific practice, whereas others are given less significant weight – or not weighted at all. This metaphor of the "balance" also indicate that the emphasis of Daston's original analysis of the moral economy concept, are laid on the on the conception of epistemic values as methodological criteria of judgment (since these, as noted by Kuhn, may often support conflicting approaches). Despite this fact, however, the epistemic values that were included in her analysis were actually of combination of methodological criteria and communal imperatives. In the moral economies of

[27] Within biology this situation can, perhaps most obviously, be found in some areas of ecology and evolutionary biology.

quantification that was mentioned above the two central values of the moral economy of precision measurement, accuracy and precision clearly have the status of methodological criteria of judgment. However the two central values of the other moral economy, communicability and impartiality seems to be more related to Merton's principles of communism and universalism (two of the communal imperatives of the CUDOS system), as all of these values are concerned with ensuring that scientific claims are easily accessible and that their acceptance or rejection are based on criteria independent of personal biases. In this respect the values of the second moral economy serves an important function as communal imperatives (similarly to the norm of the CUDOS), although, in all fairness, it should be noted that they at the same time also function as methodological criteria, in the sense that they provide the standards for judging a certain practice of quantification to be 'better suited' for ensuring a sober and rational scientific debate. This reminds us that the distinction between epistemic values as methodological criteria and as communal imperatives is not always one of mutually exclusive categories.

This suggests either that the concept is unclear in content or that is has a fruitful 'fuzziness" that allows it to address the relation between these two types of epistemic values. As other analyses of moral economies show, it is certainly possible to lay the emphasis primarily on communal imperatives instead. Such a study (that follows a different route than Daston, building directly on Thompson's original analysis) can be found in Kohler's (1999) detailed investigation of the moral economy of the "fly group" – a scientific community studying the genetics and mutations of *Drosophila* (the common fruit fly) under the leadership of Thomas Hunt Morgan in the early part of the 20th century. Here, epistemic values are conceived as a kind of communal imperatives in the spirit of Merton's CUDOS norms. Kohler describes the moral economy of the fly group as consisting of two related sets of interconnected values.[28] Each of them was connected with different aspects of scientific practice of this community, one of them with the internal practices of Morgans fly group and the other with the practice of exchange of mutant stocks, between the Morgan group and other scientists working with *Drosophila.*

[28] Kohler describes each of them as separate moral economies, *the [internal] moral economy of the fly group* and *the moral economy of exchange,* although he notes that the moral rules of the Drosophila exchange system clearly were adaptations of the Morgan fly groups customs of communal work to a wider community.

According to Kohler, the internal communal practice of the fly group was guided by a moral economy with three central elements. First and foremost, members of the fly group enjoyed a complete and unhindered *access* to communal stocks of mutant flies, research paraphernalia and know-how. Compared to many other contemporary scientific communities the work of the fly group was intensely communal and egalitarian.[29] A very high percentage of papers that came out of the fly group were multi-authored – now a common custom in science, but rare in those days.

The principle of *equity* of ideas was an equal part of the internal moral economy of the fly group. Within the fly group ideas flowed freely as a communal resource. Credit was given not to a person who came up with a good idea, but to the one(s) who first made the idea work experimentally. Not all problems of assigning credit were settled by the principle of equity. To those members of the fly group, who had lots of ideas and a habit of steady, productive work, this rule seemed eminently fair. But to others with different work habits (a prominent case was Hermann Muller, who was extremely quick to see the ramifications of ideas, but who worked very deliberately with a taste for grand experiments that took years to prepare and complete) it did not. Muller, for example, came to feel that many of the fly group's best ideas had been his, and concluded that Morgan had concocted this rule in order to deprive him of his due of credit. But in fact the rationale behind this approach was that the work mattered most, more than personal credit (Kohler 1999).

The same rationale guided the handling of the third element of the internal moral economy of fly group, the principle of *dispersed authority.* Research agendas and choice of problems were not imposed by Morgan or other senior scientist, but emerged from the communal work of the fly room's buzztalk. Contrary to the custom in many other academic departments, the senior researcher did not regard students or visitors as disciples who would follow their lead and enhance their status, and all the experienced workers of the fly group took responsibility in helping students (which officially were all Morgans since only he had professorial status) select the topics for their dissertation.

[29] The custom of equal and open access is apparent even in the physical space of the fly room at Columbia University. It consists of one common space, the only door being the one to Morgans office, which was always open (Kohler 1999).

The values of the internal moral economy of the fly group was taught by personal example, not by explicit verbal transmition. This highlights another feature of moral economies, namely that they are rarely explicitly directly expressed, but rather transmitted tacitly through the socialisation process into the communal practice of the community in question.

As noted these values were not restricted to the fly group itself, but were extended and adapted to a wider community of *Drosophila*-working scientist through a custom of free exchange of mutant stock. As with the internal moral economy of the fly group, the moral rules of this exchange were guided by the imperative that the collective advancement of the scientific work came before other considerations.

Though these rules were seldom articulated, they can, according to Kohler (1999) be readily discerned in the letters that followed the exchanges of mutant stocks between scientists. One of these moral rules was the principle of *reciprocity.* If a qualified researcher asked for a mutant stock, the fly group provided them free of charge and with no strings attached, save that the privilege of receiving stocks entailed the obligation to reciprocate if asked.

Another element in the moral economy of exchange was the principle of *disclosure.* The recipients of the mutants stocks were expected to give donors full information about the experiments they intended to do with them. The principle of disclosure was vital for dispelling suspicions and securing trust among potential rival. Failure to give this information was taken as a reason to suspect the recipients' intentions and to cut them out of the exchange system (although the situation was rarely allowed to develop this far).

Finally, the exchange system entailed a principle of *limited ownership.* While scientific problem might temporarily belong to the exclusive domain of specific individuals, the tools of investigation (i.e. specific developed stocks) were regarded as the property of the whole community of fly researchers. There were certain limits to this: in the case of specially invented stocks (like Calvin Bridges's multiply-marked mapping stock, or versatile triploids or translocations) it was customary to get permission to use them from their inventors. It was taken for granted that such a permission would not be refused. But not to ask was also taken as a reason to suspect that the borrower might be a poacher.[30]

Taken together the system of two complementary moral economies described by Kohler can (as shown below) be seen as constituting one way of realizing Merton's (1942) classical CUDOS values of academic science in the context of labouratory life of the *Drosophila* genetics community. In the moral economomies of the fly group and the exchange systems, the principle of *communism* is most clearly reflected in the demand of unhindered *access* to mutant stocks; the free flow of ideas within the fly group (the principle of *equity*) and the *limited ownership* of scientific problems. The requirement of *universalism* (that science be independent of race, colour, or creed) is reflected in most of the values described above: the demand for unhindered *access* to mutant stocks; the principle of *dispersed authority* concerning the choice of research problems, the *limited ownership* of these problems, and the *equity* of ideas are all principles that serves as hindrance to any attempt to monopolize fruit fly research. There are also several elements in the values and practices of the fly group that reflects the imperative of disinterestedness, including (again) the principles of unhindered *access* to stocks; *equity* of ideas; and *limited ownership* of scientific problems – three principles which acted together in hindering the monopolization of scientific investigations. Furthermore the principle of *disclosure* meant that if any researchers were in fact having secret or hidden interests or research agendas, they could potentially risk finding themselves asking in vain for the mutant stock that were needed for the experiments in question. Finally the requirement of *organized skepticism* (that statements should not be subject of free critical inquiry and not accepted on the word of authority) is reflected in the principle of *limited ownership* of scientific problems that allows other researchers the possibility of interfering in a research process that they consider gone awry, in the demand for unhindered *acces* to mutant stock and in the principle of *reciprocity* (both allowing for the possibility to make critical evaluations based on experiment); and in the principle of *dispersed authority* (allowing researchers the free choice to critically check any purported results).

[30] In most cases violations of this rule was simply a beginner's ignorance of etiquette. Such was the case when Gert Bonnier, a Swedish geneticist, failed to get Bridges's permission before using one of his stocks. As a result of this, other fly researchers wondered if he could be trusted with further stocks.

As the example of Kohler's study show, it is quite possible to make good use of the moral economy concept in analyses that address epistemic values as communal imperatives. In fact as Merton appears as one of the introductory references to Daston's account of the values and norms of moral economies, there is no indication in her original paper that she would regard Merton's CUDOS norms to be of a different kind than her own moral economies.[31] What seems to be a salient feature of Daston's analysis of the moral economies of sciences, is the fact that she makes no distinction neither between different kinds of epistemic values nor between moral and epistemic values *per se.* Nevertheless, her analysis of various historically instantiated moral economies gives several examples of the interplay between the moral values and epistemic values of society and science – an area where the methaphor of the 'balance' plays an equally important role. One example is the historical applications of the concept of objectivity in the 19th century scientific practice. One of the various applications of this concept (by Daston termed 'mechanical objectivity') played on the ideal of self-control – an ideal that was justified by an ascetic-Christian notion of Man as inherently sinful and as therefore needing restraint. Within science this ideal of self-control was transformed into a demand that the scientist needed to restrain himself in the process of data collecting, and fight his inner urges to judge, interpret, anthropormorphize, aestheticize or in any other way violate the raw facts of nature. This moral imperative facilitated a scientific practice concerned with authenticity of data, procedural correctness and the automatization of data collecting (Daston 1995). Thus, as can be seen from this analysis, in practice Daston actually *does* recognize that there is some kind of distance between the epistemic values of a moral economy (which may, according to Daston, have a moral component although that component has now become 'naturalized" to the scientific milieu) and general moral or ethical values as such. In that respect the moral economy concept serves to reconfirm the borders between science and society. I find this feature of the moral economy concept to be reassuring. As noted be Douglas (2009, p. 102), if one was to allow general moral or ethical values a direct role in the process of scientific investigation (equal to epistemic

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[31] This does not mean, of course, that Daston's account of epistemic values are *on a par* with Merton's, There are several areas of disagreement between Merton and Daston concerning epistemic values, the most prominent being her denial of their universalist nature.

values), it would endanger the whole notion of science as an independent intellectual inquiry, reducing scientific judgment to be a matter of moral preference.[32]

So, despite (or perhaps because of) its ‘fuzziness’, the moral economy concept does seem to have some usefulness as an analytical tool. In many ways it can be considered to be a “border concept” between science and society. On one hand, Daston uses the concept of moral economy as a tool for distinguishing science from other activities, in a way that may be comparable to Kuhn’s use of paradigms. But compared to, say, the characterization of values in Kuhn’s (1969) concept of the disciplinary matrix (which focuses exclusively on epistemic values) moral economies are characterized by having more fuzzy boundaries between the epistemic and the moral domain - something that makes the moral economy concept a useful metaphor in the study of the transport and transformation of values between society and science. It is especially this characteristic that may turn the concept of moral economies into a fruitful key to the dynamics between moral and epistemic values in scientific practice.

The moral economy concept thus serves as a descriptive category that can be useful in the process of fleshing out embedded values in decisions made with relation to scientific practice, and (as mentioned) in the investigation of the dynamical transport and transformation of epistemic and moral values between society and science. It should, however, be noted that it is to some extent unclear at which level the concept of moral economies operates. According to Daston’s *definition* moral economies are connected to specific communities. But her *de facto* use, for instance in the analysis of different kinds of objectivities seems to suggest that moral economies may be a cross-community phenomenon covering several different communities. One may, perhaps also add, that the emphasis on the scientific *collective* inherent in this concept (along with other theoretical concepts with similar collectivist emphasis) ignores the role of individual choice in the study of epistemic values. Even recognizing an “individual” level may not be enough. In many ways, the real “micro-level” where values come into play here, is the specific *situation* where decisions between alternatives have to be made. It cannot even be safely

[32] One might argue that this has in fact already happened in situations of ‘post-academic science’, where scientific research is conducted in the interest of private sponsors with a wish to ensure a specific result (for instance the development of a new drug) from this research. Here the independence of the scientific investigation may risk severe compromising by utilitarian demands. See Ziman (2000).

assumed that the values of a specific individual can be treated as an integrated coherent whole, as people may make very diverse decisions when faced with similar dilemmas in different situations.

I do not believe this scale problem disqualifies the moral economy concept's applicability and usefulness as an analytical tool, however. Recognizing that scientists operate under a shared set of values is a helpful assumption if one is to analyse their role and dynamics. The collectives that operate under a certain set of guiding principles may be embedded in even larger collectives - or a set of guiding norms may be shared by various collectives pursuing similar cognitive goals in different specialist fields (as in the case of Daston's analysis of different kinds of objectivities). Individuals operating under the hegemony of such a set of guiding norms may choose (perhaps unconsciously) to adhere to these principles, or to (consciously) deviate from them.

Styles of Reasoning

Having distanced ourselves from strict determinist interpretations of the different theoretical entities that attempt to describe and categorize the contextual foundations of scientific collectives, we may (again) raise the problem that spurred the formulation of Laudan's reticulated model: what bearing does the descriptive questions and concerns raised by contextualist approaches to epistemic values have on the normative concerns raised by the universalistic attempts in the first half of the 20th century to reach a general set of guiding principles for good scientific conduct?

One possible road to an answer to this problem would be to claim the existence of a finite plurality of general methodologies in science. Perhaps there exist several, "grand" classes or styles of scientific reasoning that pervade across the boundaries of scientific communities. Some of the tensions in Daston's analysis hints at this, as her *de facto* use of the moral economy concept at times suggest that it may be a cross-community phenomenon covering several different communities, rather than restricted to a particular historically instantiated community *per se.*

An example of such a position can be found in the final three-volume *opus magnum* of historian of science A. C. Crombies *Styles of Scientific Thinking in the European Tradition* (1994). Having undertaken the daunting task of delivering a complete account of the western history of science since the early greeks, Crombie identified six general styles of thinking, each of which he believed had played a central role in the development of certain scientific areas: 1) a style based on axiomatic postulation and mathematical proof; 2) an experimental style based on designed observation and measurement, 3) a style based on hypothetical modeling as a method of exploring the unknown properties of natural phenomena; 4) a taxonomic style using comparative methods to order the variety in any subject-matter; 5) a probalistic style based on the application of statistical analysis and finally 6) a style of historical derivation seeking to explore the origin and diversification of any subject-matter, whether language or organisms from the common source, and to explain the cause for that diversification (Crombie, 1994, p. xi).

Building upon Crombies' work, and preferring the term *styles of reasoning* (rather than styles of *thinking*), Hacking has attempted (while at the same time avoiding the debate about whether Crombies' scheme, that identifies exactly six central styles in the history of science, should be accepted) to explicate the content and meaning of this concept and its bearing on our understanding of science.[33] Like Fleck's thought styles, paradigms and moral economies, styles of reasoning are regarded to be constitutive of scientific work, and embedded in contingent systems of thought that sets the standard both for what is good scientific practice. Thus, every new style introduces a range of novelties including

> "…new types of objects; evidence; new sentences, new ways of being a candidate of truth of falsehood; new laws or modalities; possibilities. One will also notice, on occasion new types of classification and new types of explanation." (Hacking, 2002, p. 189)

Explicating this concept Winther (2005, p. 46) adds new ways of unifying, understanding and modeling. In other words, styles of reasoning represent distinct ways of reasoning, hypothezising, evaluating, investigating, organizing and so on.

[33] Hacking *styles of reasoning* should not be conflated with Fleck's *thought styles*, or, for instance Harwoods (1987) *national styles* in science or Maienscheins (1991) *epistemic styles.* The concept of style has caught the attention of a variety of scholars with somewhat disparate theoretical approaches. For a comparison of these, see Vicedo (1995).

With this rather encompassing account of what a style is, it may be prudent to note what a style is *not.* It is not (at least not in any trivial sense) a “theory of the world” that can be verified or falsified. It may be possible that a style can be shown to be unfruitful. But the complete extinction of a style seems to be a much rarer event than with paradigms and moral economies.[34] Of the six styles originally described by Crombie, Hacking notes that they are still going strong, despite the fact that the oldest of them originated in Ancient Greece.

Hacking also notes that a style of reasoning provides the frame and the criteria that determine a whole range of important elements that sets the standards for solving scientific problems. In this sense, it determines what counts as objectivity. A style of reasoning determines which kinds of questions and problems are scientifically legitimate; it gives procedures for how to decide and distinguish between different possible approaches to solve these questions, and for deciding which kinds of solutions are scientifically acceptable. In other words, a style of reasoning determines the procedure by which we find out whether certain sentences are true or false. But there is also an element of self-authenticating circularity in styles, as the sentences of this kind only become candidates for truth or falsehood in the context of a specific style of reasoning. It is Hacking’s contention that no higher standards are given to which a style must answer, and that the self-authenticating character of styles of reasoning is a first step in understanding what gives science its “quasi-stability” (Hacking 2002, pp. 189-191).[35]

Does this solution solve the tensions and problems Laudan described between universalist and contextualist perspectives? In my opinion not. First of all because it is not clear how exactly one identify a style. In Crombie’s investigation styles are defined ostensibly, by pointing to major trends in the history of science *a posteriori* – as a result of history rather than being grounded in philosophical justification. The lack of clearly identifying criteria makes the style concept fairly elusive. This criticism may of course to some extent be directed against competing entities like paradigms or moral economies as well. But here the problem seems to be even more pressing especially because, unlike

[34] Hacking gives two examples of possible ”dead styles”: Renaissance medicine and withchcraft (Hacking 2002, p 194-195)

[35] He does, however, doubt that the late Crombie would agree with this, noting that if such a disagreement existed, it would have philosophical in character rather than historical.

paradigms and moral economies, Hacking is most ready to admit that styles may hybridize and intertwine (2002, p. 183). This, of course, renders the criteria for how to identify a style at best obscure. This is illustrated by the fact that, among historians and philosophers writing about styles there is no clear consensus about precisely how many styles exists, and how to identify them. Thus Winther (2005; 2006) whose conception of scientific styles in general builds on Hacking, differentiates two "styles of theorizing" within biology,[36] based on a conceptual distinction (considered by Winther to be pivotal) between *laws* and *parts*. Thus, the primary focus of one of these styles, denoted "formal biology", is put on mathematically formulated laws and models that represent quantitative relations among parameters and variables. This style might be interpreted as a possible instantiation of Crombie's third style: hypothetical modeling. It is regarded by Winther to be dominant in disciplines like theoretical population genetics and theoretical ecology, and in a critique of his fellow philosophers of biology, he notes that this style has received much attention by philosophers, who have tended to treat it as if this approach was the only respectable way of doing biology (and perhaps doing science in general). However, much biology cannot be accounted for within this framework, as it focuses not on the discovery, or formulation, of mathematical laws or models, but on the relation between parts and their organizational whole. This, in turn, is the focal point of the other style of theorizing which Winther denotes *compositional* biology. This style is based on the notion of the organic world as organized in a nested hierarchy of parts and wholes, and focus on the discovery of their respective functions and capacities. This style (which has no apparent counterpart in the scheme of Crombie), tends to be employed in a variety of biological disciplines, including fields like functional and comparative morphology, and molecular, cellular and developmental biology (Winther 2006, p. 471).

This ostensive character of styles means that they are vulnerable to the same critique that has been directed toward other similar attempts to describe collective entities at the level of the scientific community or supra-community. Their elusive boundaries mean that delimiting them from one another may be no easy task. Crombie's original scheme of six styles of reasoning may be tempting to adopt, but none of these six styles

[36] Winther alternately denotes them *styles of scientific investigation* (2005) and *styles of theorizing* (2006). Here, I will use the latter term.

seems to cover the "compositional style of theorizing" described by Winther.[37] At the same time, Winther's contention that there is a style of thinking/reasoning/theorizing in biology that has the relation of parts and wholes as their explanandum rather than laws, models or any of the other types of explanatory focal points covered by Crombie, certainly has some merit.[38] One may therefore, with a certain right, claim that the identification of this or that style is, at least to some extent, arbitrary.[39]

As a further point of criticism, one may note that Hacking, by both claiming styles to be self-authenticating *and* claiming that there are no higher standard to which a style must answer, seems to walk a dangerous line close to relativism. If a style is a closed domain of a certain *type* of reasoning (with accompanied differences in objects of study, ontological presumptions and preferred epistemic values), one can easily imagine that the same kind of incommensurabilities in the communication between proponents of different styles could arise between proponents of different paradigms.[40] But in the case

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[37] It should be noted however that although the compostional style has no apparent counterpart in the scheme of Crombie, this does not mean that the history of this style of theorizing is totally absent in his works. The before mentioned six styles are used by Crombie to organize his exposition of the huge material included in his account of the history of European science. Interestingly, the history of the style of theorizing characterized by Winther as compositional biology (including the famous reflections of Kant on teleology in living nature) can be located, within Crombie's scheme, under the lable of "the analogical model" – a subspecies of his style no. 3: "hypothetical modelling"..

[38] Note here especially that Winther's compositional style of theorizing corresponds neither to Crombie's experimental style of designed observation and experiment (style nr. 2); his taxonomic style of comparative methods and ordering (style nr 4); or his style of historical origin, derivation and diversification (style nr 6). Within the domain of biology it would appear that all of these styles of reasoning are employed in various domains of inquiry. Following Crombie, the experimental style of reasoning, for instance, seems to be widely appropriated within physiology, whereas both the taxonomic style and the style of historical derivation are employed in comparative morphology, systematics and parts of evolutionary biology. Following Winther's approach, however, one could equally justly argue that a compositional style of theorizing is employed in certain areas within all these biological disciplines, and that it appears just as 'grand' and pervasive across community boundaries as Crombie's original six styles.

[39] Though it need not be arbitrary with respect to a certain subject of investigation.

[40] There might be an unresolved tension in Hacking's account of styles of reasoning here. As noted earlier, Hacking states that every new style, among other things, introduces new 'objects', 'new sentences' as well as (occasionally) 'new types of explanation'. Taken together, this seems to indicate that a style also develop a specific kind of vocabulary comparable to the 'lexical taxonomies' that was described by the later Kuhn in his attempts to explicate his incommensurability thesis (see Kuhn 1991) However, as described above styles of reasoning are at the same time conceived to be cross-community phenomena, and Hacking are, as noted, quite ready to admit that styles may hybridize or intertwine. This would indicate that it is possible to reach a metaperspective from which such hybridisation may be reached on even terms, but such a metaperective is by Hacking's own account not possible, as he states that no higher standard are given to which a style must answer. As far as I can see this, can only be solved either by abandoning the claim that there is no higher standard to which a style must answer (hence, accepting the possibility of a higher metaperspective), or accept that proponents of competing styles may experience the same kind of partial breakdown in their communication that according to Kuhn may befall proponents of competing paradigms.

of Kuhnian paradigms, these obstacles may be overcomed by translators that are able to "go native" within the various paradigms (Kuhn 1969, p. 201). This seems to presuppose the existence of a "meta-domain" of understanding (perhaps located in the common use of everyday languages) wherein proponents of different paradigms may reach each other. However, for Hacking, no such option exists. But if that is the case, the challenge Laudan gave to contextualists, that they should be able to explain the widespread existence of consensus in science (despite the equally widespread existence of ontological and theoretical disagreements), is met even more poorly by Hacking's account of the scientific styles of reasoning than by Kuhn's classic paradigm account. Furthermore, unlike the methodological norms in Laudan's reticulated model, styles are not informed or modified by factual beliefs. Once coming into existence, they persist through time until extinction.[41] Thus, although claiming himself to be an 'arch-rationalist', it appears somewhat difficult to see what exactly it is in Hacking's account that gives us any reason to defer the concept of styles of reasoning any final advantage *vis-à-vis* competing concepts like thought styles, paradigms or moral economies. Instead, it appears that all of these suffer from the same weaknesses. They are defined ostensibly, which means that their full implication only becomes apparent when discussing them in relation to particular examples. Although we may (because of the their prospective explanatory power) be principally inclined to accept the existence of scientific thought styles, paradigms, moral economies and styles of scientific thinking, reasoning or theorizing, for the moment their merit within science studies seems to lie primarily in their capacity as heuristic devices.

Discussion: notes on how to study epistemic values in science

Given the manifold and diverse attempts to capture the role of epistemic values in science described in the previous pages, one may easily lose track of the many positions and perspectives that has been explicated on this topic. How do we approach epistemic values in science? What may we reasonably suppose about them; by which means do we

I have here decided to follow the latter road, as I believe it preserves most of the elements that are pivotal to Hacking's account of scientific styles.

[41] It should be noted though, that the extinction of styles of reasoning may be informed by factual beliefs. The widespread abandonment of a belief in preternatural forces in the intellectual circles of Europe was probably detrimental for the witchcraft style of reasoning. See Allen 1996.

uncover them when they are at play; and how do we study their implications for scientific practice?

A complete all-encompassing answer to these questions goes beyond this essay, and even beyond the thesis of which it is a part. However, with the foregoing analysis in mind, I believe, that there are a number of conclusions that can be reasonably made.

First of all, it may be possible to distinguish between two kinds of epistemic values in science. Both of them are what we (following the terminology of Cialdini) called 'injunctive norms' – that is they refer to shared expectations as to what constitutes desirable conduct and reflects what people *approve* or *disapprove.* One of these kinds is what we may call communal imperatives. These values (such as the principles of *access* and *reciprocity* that were described in Kohler's analysis of the moral economy of Morgan's *Drosophila* research group) regulate the social actions of scientists within the scientific community. Violations of these norms may result in isolation, and withdrawal of favors, and, in the most serious cases (for instance, when people fail utterly to give any satisfactory account for how certain scientific results have been reached), in claims of scientific misconduct.[42] The second kind is the values that we usually know as methodological criteria of judgment. These values (such as the principles of accuracy and precision as described in Daston's account of the moral economy of precision measurers or the principle of falsifiability that was central to Popper's view of what should be the primary virtue of scientific theories) are used to justify specific epistemic choices in scientific practice, such as choices of investigation procedure or preferred explanation. Violations of these norms may be frowned upon by other scientist (especially if they are unsatisfactorily justified), but they rarely result in accusations of misconduct despite the fact that scientists may slander violators with the label 'unscientific'.

Secondly, it seems clear that the universalistic idea, or hope, of reaching one single encompassing scientific method, should be abandoned. There are several reasons for this. One of them is that, as noted by Laudan, methodological norms themselves are informed by factual beliefs and may thus develop (and even progress) as the result of parallel developments in our knowledge claims. Another is that, as Daston has

[42] An example of this can be found in the case of nano-scientist Jan Hendrick Schön. See Beazley *et al.* 2002.

demonstrated, there is a price of following a specific set of epistemic values. A third reason, noted by Kuhn, is that a plurality of approaches may actually be fruitful for scientific development. There may be some time in the future where these difficulties can be encompassed, but for the moment, it seems clear that the normative concerns that were raised by these scholars must be approached in other ways.

However, it also seems clear that the contextualist perspectives that have been offered so far have been unable to meet Laudan's challenge: the ability to explain the widespread existence of consensus in science, despite the equally widespread existence of ontological and theoretical disagreements. Neither Kuhn's account of a paradigm's disciplinary matrix, the moral economy concept, or Hacking's styles of reasoning (and the related concept of Winther's styles of theorizing) seems to be able to explain the existence of scientific consensus as equally satisfying as the universalistic accounts of the Vienna Circle or Popper. Nor for that matter does Fleck's original notion of thought collectives and thought styles.

The issue here seems to be *underdetermination.* Following the explication of underdetermination that were given previously in the last paragraphs about Kuhn's disciplinary matrix, we may state that both theory-choice and concrete investigation procedures are logically underdetermined by epistemic values. But one of the important feature's of Laudan's analysis (which serves as a motivation for his reticulated model of scientific justification) is that this is not the only kind of underdetermination that is at play. Theories are also underdetermined by factual belief. Likewise, factual beliefs are underdetermined by the scientific theories used to support them. Moreover, the preference and application of epistemic values are (as Kuhn takes pain to describe) logically underdetermined by the paradigms that supposedly serve as the normative and metaphysical foundations for this application. And, following Daston's analysis, we may expect that combinations of epistemic values, as in moral economies, changes the context in which they are applied, but even moral economies underdetermine the scientific practice into which they are embedded, and hence, the application of epistemic values.

In my opinion, it is precisely this property, the widespread existence of reciprocal underdetermination of the variables important for this topic that warrants the naturalistic move proposed by Laudan. If the relation between, say, epistemic values and theory-choice, was one of logical necessity, an algorithm-based "armchair" approach to epistemic values might suffice.[43] But as this is clearly not the case, an empirical approach becomes a necessary part of the toolkit needed to investigate the role of epistemic values in science. Only by taking an empirical approach may we gain knowledge of the idiosyncratic applications of epistemic values of scientists in their decision-making.

By what route should one undertake such an empirical investigation? The answer to this question is vital as it partly determines which kind of knowledge it is possible to obtain about epistemic values. One way to go about this question is of course to ask scientists directly. Using questionnaire interview, such an approach has been followed by Prpic (1998). Studies like this are certainly necessary, because they help revealing to us, which values scientists *believes* are important. However, the possible pitfalls of such an approach are easy to see. It may be that the stated values are merely referred to by lip service and play no important role in the scientific practice – and that a closer study of this practice will reveal that other, and more important, epistemic values are at play. No doubt this problem was realized by authors such as Kohler (1999), who suggests that the communal imperatives of a scientific community may be studied by paying attention to the etiquette concerning the exchanges of scientific material (in this case of mutant stocks of the fruit fly) between different scientists. Such an approach seems especially fit for disclosing the communal imperatives of a scientific community.

Another way to approach epistemic values would be by using controversy studies. Such an approach seems especially revealing for how methodological criteria of judgment are applied to specific scientific problems, and the way a controversy reach closure may also inform us about the relations between individual applications of these criteria and the attitudes of the scientific collective(s) in which a controversy is taking place. Based on such an approach a range of questions may be asked, that may be answered empirically. What is the relation between the decision of a researcher in specific situations and the shared epistemic values of the scientific collective of which the scientist is a member? Does the individual researcher (consciously or unconsciously)

[43] I am not hereby denying the relevance of statistical inference and bayesian methods for the development of methodology.

follow a standard procedure or consciously deviate from it? Is there any disagreement among the participants in a scientific debate on how the values should be understood or applied? Are there any inconsistencies in an individual's applications of a specific epistemic value? Does the individual have to justify their choice in relation to the standards of different scientific communities and not just one? How do major developments within a field affect, how such justifications are perceived and evaluated by other scientists?

Although recognizing the importance both of questionary studies and of the 'material exhange' approach taken by Kohler, I have decided on taking a controversy approach in the investigations that will appear in the following pages. This is in part because my prime interest in this subject lies in the role of epistemc values as methodological criteria of judgment rather than as communal imperatives. But it is also in part because of the fact that detailed analyses of the idiosyncratic application of individuals in specific controversies are still somewhat 'Terra Incognita' within science studies. Although I also had the chance to engage with scientists that are either involved in these controversies, or are part of the scientific communities in which they are taking place, the main empirical source of investigation in this thesis has been that of published scientific papers and books.[44] This choice of approach is grounded in the simple fact that it is within these publications we find the public justifications that scientists give for their factual beliefs. It may well be that scientists use other methodological criteria of judgment during the actual process of investigation, when these beliefs are supposedly still being formed. But the justifications they give for their decisions in scientific publications are clearly of the kind that they're willing to defend in public. By focusing on scientific publications we are focusing on the end result of the scientific process, ignoring the false roads that were followed on the way. Therein lies also the weakness of this approach, for undoubtedly, there are lots of interesting dynamics (in which the

[44] It should be noted, however, that the information gathered in such social interactions has at times been pivotal for building up an understanding of the contextual settings in which these controversies take place, especially in the process of deciding which research questions to pursue and where to look for answers.

adherence to certain epistemic values may be expressed) going on in the scientific departments and research labs that never reaches a scientific journal.[45]

Finally, what role does entities such as thought styles and collectives, paradigms, moral economies and styles of reasoning/theorizing, play in such empirical investigations? This question may seem precarious because these entities are primarily designed to address the role of the scientific *collective*, while the initial point of investigation here will be the actions and attitudes of individual scientists. However, perhaps it would be more to the point insisting that this study of values takes the *relations* and *interactions* between normative presumptions at different relevant levels as its object of investigation. The "relevant" levels here *at least* include the level of the individual and the level of the collective. The level of the collective is constituted by the set of shared assumptions (including epistemic values) that identify the evaluative standard of reference for the legitimacy of theories, knowledge claims and investigational practices within a scientific community, or set of communities. The level of the individual is constituted by the range of epistemic values that are used by an individual researcher to justify specific choices of a preferred theory, investigation procedure or for the evaluation of the credibility of a given knowledge claim. There may be analytical situations, as when dealing with the relations between super- and sub-communities, where inclusion of the level of the supra-collective is necessary for understanding the problem at hand. Equally important however, is to include a sub-individual level that recognizes that scientists may not necessarily be coherent, or even consistent, in their application of epistemic values. As people may make very diverse decisions when faced with similar dilemmas in different situations, in many ways, the focal level where values come into play, will often be the specific *situations* where decisions between alternatives have to be made. A *situational* level thus becomes the initial focal point of analysis: what decision was made, by whom, and on what grounds?

Despite this choice of focus, I believe that these analytical tools do offer some help as heuristic devices. With the help of a constructive 'models are always wrong – some are useful'- approach, we may use their heuristic strength to ask relevant questions

[45] The argument that scientific papers misrepresent the process prior to publication was made long ago by Medawar 1963. A classic anthropological text on the behaviour of scientist's in a laboratory is of course Latour and Woolgar 1986.

about the application of epistemic values in specific situations. This pragmatic stance is based on the fact that all these concept suffers from the weakness that they can (so far) only be defined ostensibly, by pointing to their instantiation as concrete exemplars in scientific practice. Furthermore, that none of them offers any account of the scientific process that is convincing enough to confer them absolute advantages in comparison with competing concepts.

The consequence of this pragmatic stance is that use of these concepts as heuristic device has to be justified in relation to the specific case study that is under scrutiny. But boundary problems aside, I do believe that each of these analytical tools contain important contributions to our understanding of epistemic values as methodological criteria of judgment.

Hence, the analyses provided by Fleck in his account of thought collectives and thought styles gives us reason to expect that scientific reasoning are locked into certain epistemic domains (the thought styles) which are characterized by a common set of methodological criteria of judgment, that the members of the thought collective will apply to their problems of interest in a similar manner. But, although Fleck does not address this possibility directly, it also opens up the possibility that an individual scientist may be a member of several scientific thought collectives at once – a possibility that may indeed complexify any contextualist analysis of epistemic values.[46]

The analyses provided by Kuhn in his presentation of the disciplinary matrix gives us reason to expect that although an epistemic value may be widely shared by scientists, and even regarded to be constitutive of science, the members of a scientific community may vary greatly in their application of this value in individual instances. Or, as one may also put it; scientific choices are *underdetermined* by epistemic values

The analyses provided by Daston in her account of moral economies gives us reason to expect that the application of individual epistemic values is interdependent with the normative context in which they appear. Firstly, because epistemic values acquire more specific connotations, when appearing as part of a specific set of values, a moral economy, than when regarded as standing alone. Secondly a balance must be reached, or

[46] As we will later see (in Section III), this is actually the situation in the Burgess Shale debate, where both Stephen Jay Gould and his adversary Simon Conway Morris has to navigate in the context of the standards of several semi-indendent scientific thought collectives.

negotiated, between the (moral and epistemic) values of a scientific community and the moral values of the surrounding society, as a prolonged conflict between them may be detrimental to scientific activity.[47]

Lastly, the analyses provided by Crombie, Hacking and Winther explore the possibility of the existence of 'grand' scientific styles across scientific communities. In the light of the general agreement, even among contextualists like Kuhn and Daston, that most epistemic values exist as a cross-community phenomena (even though they may be applied and prioritized disparately in various settings), this move certainly has some merit. Among other things, a comparison of the analyses of these scholars with Daston's account of moral economies, highlights that Daston had taken the boundary problem too lightly in her account, and that it is not clear whether moral economies should be regarded as connected to specific communities, or whether they should be considered to be a cross-community phenomenon, in the same manner as scientific styles. It also opens up the possibility that epistemic ideals that may appear sharply opposed to one another in some situations, may hybridize and intertwine in others.

Armed with this insight, we approach an answer to three questions posed in the introduction, in a manner that points to the fact that the epistemological question of how to analyse epistemic values is interdependent with the ontological question of what epistemic values are. Based on the analysis given here, it is my opinion that the role of epistemic values in science can best be understood by investigating instances of their embodiment in scientific practice. Such an approach, however, implies that the second question can only be answered with the help of evidence showing how epistemic values, as methodological rules or norms (whether these are explicitly stated or must be dug out as implicit presumptions) may effect actual decisions made within scientific practice.

With this, we are now ready to commence the investigation.

[47] One should add though, that such a balance is not necessary reached by full accommodation of the scientific community to surrounding moral standards. History is rife with politically inclined scientists and scholars trying to fight this battle on society's battleground rather (or as well as) on science's. Perhaps the most prominent example of a scientist with this inclination was the late evolutionary biologist Julian Huxley (1887-1975) whose political engagement in liberal humanism and internationalism led to his appointment of the first director of UNESCO. Turning to the scholars mentioned earlier in this text, Merton's paper on the ethos of science, and the manifesto Vienna Circle were two examples of scholarly work concerned with the role of science in relation to society.

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Section II: Behavioural Ecology

It seems to be either an artifact of analysis or just a simple misguided conception that sociologists of science may sometimes tend to treat scientific controversies as if they were about single scientific problems. In many of the more complicated controversies, however, they are about a whole *cluster* of scientific problems. On a closer look apparently unrelated questions show themselves to be deeply entangled into one another; part of the theoretical disagreement may be about how a problem is to be defined (and therefore which kinds of solutions are feasible) – or major theoretical upheavals facilitate a general transformation of the questions that are under inquiry.

So we start, not by delineating a debate on a scientific problem, but by entering the debate of a 'set' of related problems, where a part of the investigation consists both in identifying them, and to reveal the character of their relations. Hence, although we may for theoretical reasons expect that certain problems may have some logical connections, the relevance (for the inquiry) of theses connections can only be identified *a posteriori.*

The set of related problems that are the subject of investigation in Section II are located within the domains of behavioural ecology and sociobiology. They include the classic problem of division of labour (which has been discussed primarily within the context of social insects), the origin and explanation of (apparent) altruism in nature; the role of group vs. kin, gene and individual selection; and the possible role of handicaps in ensuring the reliability of biological signaling. These are all topics related to what we might call the 'study of social evolution' – as they all address the behaviour and relations of individuals in the context of a larger integrated collective (the population, the colony, or the mating pair).

By entering the domain of social evolution, we enter a biological area where the belief in adaptive explanations is quite strong. This may of course also be said of other disciplines, but for historical reasons, the related fields of behavioural ecology and sociobiology, appear to be one of the most prominent strongholds of 'orthodox adaptationism'.[48] Within this field, the challenges to explain the social actions of animals

[48] Although the term 'adaptationism' was originally introduced by Gould and Lewontin (1979) as a strawman in an attempt outline their own skepticism towards adaptive explanation in evolution, i believe it

as fitness-improving behaviour that been facilitated by problems such as the origins of labour division; of altruism; and the role of group selection, has spurred biologists to a defense of adaptive explanations so strong (at times almost vehement) that it supersedes that found most other areas in biology. Given this history, it is perhaps not surprising that a range of prominent defendants of adaptationist views of evolution has a background in the study of social and behavioural evolution. This includes e.g. Edward O. Wilson, who is a specialist on social insects and coiner of the term ‘sociobiology; Richard Dawkins who studied ethology under the supervision of Niko Tinbergen (one of the fields founding fathers); and Robert Trivers, who originally had psychological training, and is the originator of the theory of reciprocal altruism.[49]

In other words, by entering the domain of social evolution, we enter (Neo-) Darwinian heartland. With the possible exception of theoretical population genetics, this is *the* area of inquiry where we would expect to uncover some of the epistemic ideals and values that occurs in a ‘typical’ adaptationist setting.[50] This is not to say that another choice of focus could not produce a different result. But a comparative study has to start from somewhere.

Apart from this introduction, Section II consists of two papers. The theoretical approach taken in these papers is based primarily on Rasmus Winther’s distinction between formal and biological theorizing that was presented in the previous pages. This choice is based on the fact that Winther’s original introduction of this distinction was made in the context of the interplay between biological and social science. Thus, several of the players in the stories that are unfolded in the two following paper, appear in the original analysis of Winther as exemplars of scientists employing one of these styles of theorizing. For the compositional style this includes William Morton Wheeler and Alfred

can be reasonably appropriated as a neutral term that denote views that places their prime emphasis on adaptive explanations on their overall conception of evolution. However, as most critics of ‘adaptionism’ presumably would be quite ready to admit that adaptive explanations must be given *some* role in our understanding of evolution (this includes, for instance, Gould and Lewontin themselves) the middle ground between extreme adaptionism and extreme anti-adaptionism must be conceived as a continuum of possible positions.

[49] It should be noted though that although Wilson, Dawkins and Trivers are all prominent figures in this area of inquiry, they will here be delegated to minor role in the stories that will be told in the following..

[50] Note that there may be more than one of such epistemic ideals at play here. One cannot, of course, assume that just because people are interested in the same scientific problems it would also mean that they shared the same set of epistemic values and applied them in a ubiquitous way. In fact as the case studies included in this section will demonstrate, this is certainly *not* the case here.

E. Emerson, both of whom play an important role in this history of myrmecology – the latter as part of the Ecology Group at the University of Chicago (which were used by Winther as an example of a scientific *community* that adheres to a compositional style). For the formal style, this includes Bill Hamilton, as well as Wilson and Dawkins. If there is any explanatory merit to this distinction, the closest place to look for it is by analyzing examples that are close, but not quite identical, to the context in which they were put forward.

Exploring this question, the first paper (*How the problem of division of labour became a question of group vs. kin selection: a conflict of formal and compositional biology*) examines the history of the problem of division of labour within myrmecology. It argues that the transformations of how this problem was perceived and approached by biologists and myrmecologists at different periods during the 20th century was strongly influenced by a conflict between adherents of formal and compositional biology. The problem of division of labour was initially construed as a problem for Lamarckian inheritance, but has experienced several redefinitions, being perceived first a question as the colony integration and the coordination of parts within wholes, and, following the expansion of formal biology, as a question of how to explain the existence of apparent altruism in nature. These transformations were intertwined and embedded into the larger narrative of the advent and later hardening of the modern evolutionary synthesis and with changes in the relative appeal of the compositional and formal style within the biological community,

Whereas the first paper reaches an overall *positive* conclusion concerning the explanatory merits of Winther's (2005; 20006) distinction between formal and compositional biology, the second paper ends up having some (although minor) reservations against this theoretical scheme. This paper examines the very disparate attitudes that various scientists has taken towards a classical argument against the evolution of altruism by group selection – the so-called *argument of subversion from within.* Using the related debates on group selection, altruism and the handicap principle as a case study, it argues that different applications of epistemic values played an important role in the disagreements between John Maynard Smith and Amotz Zahavi over a number of important evolutionary issues. These disparate applications were in turn related to other important epistemological and ontological commitments, as the antagonists differed both in the confidence they ascribed to mathematical modeling and over the hereditary basis for altruistic behaviour. Comparing these findings with Winther's original distinction, it concludes that although the distinction of formal and compositional biology also has some explanatory merit in this case, the idiosyncrasies of Zahavi's approach illustrate that the peculiarities of *individual* scientists may play an important role in the shaping of scientific controversies – a role that is not covered adequately by this theoretical scheme.

In conclusion, one might add, that pointing to the inability of the style concept to account for the role of idiosyncrasy might be an unfair critique. After all, it was originally developed at a different scale, as a tool for understanding similarities in epistemic conflicts across different biological communities. But it does tell us that we will need other theoretical tools to understand the interplay between the dominant epistemic values of the collective and role of individual idiosyncrasy. This realization will be the starting point of the analysis of Section III.

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How the problem of division of labour, became a question of kin vs. group selection: a conflict of formal and compositional biology.

Abstract: This paper examines the role of conflicting styles of theorizing in the history of the problem of division of labour within social insects. It argues that that a conflict between adherents of two styles of biological theorizing, formal and compositional biology, played a central role in the transformations of how this problem was perceived and approached by biologists and myrmecologists at different periods during the 20th century – and that these transformations was embedded and intertwined in the larger narrative of the advent and later hardening of the modern evolutionary synthesis. In conjunction with the introduction of new methods, cognitive aims and changes in the relative appeal of the compositional and formal style within the biological community, the problem of division of labour has undergone several transformations in the history of myrmecology. Initially perceived as a problem for Lamarckian inheritance, it has experienced several redefinitions, being perceived first a question as the colony integration and the coordination of parts within wholes, and, following the expansion of formal biology, as a question of how to explain the existence of apparent altruism in nature.

Introduction

This article examines the role of conflicting styles of theorizing in the history of a problem within the domain of myrmecology: the origin and maintenance of division of labour within social insects. It argues that the transformation of the problem of division of labour within social insects into a question of kin vs. group selection was embedded and intertwined into the larger narrative of the advent and later hardening of the Modern Evolutionary Synthesis – and that a conflict between adherents of two styles of biological theorizing, formal and compositional biology, played a central role in this development. Initially being framed as a problem for using the inheritance of acquired characters as explanations for the origin of adaptation, the modern synthesis created a theoretical setting, in which the key evolutionary problem became the question of which level natural selection operates. This shift facilitated a reframing of the problem of division of labour into a question of the origin of altruism – and a shift in style, from compositional to formal biology.

This paper is divided into four major parts. The first part (*Formal and compositional biology: two styles of biological theorizing*) describes Hackings concept of scientific styles of reasoning, and, following Winther, presents two styles of theorizing within biology: formal and compositional biology.[51] The second part (*Darwinian and Lamarckian Myrmecology: the superorganism approach and pre-synthetic instances of compositional biology*) describes the theoretical settings in which the division of labour was discussed before the modern synthesis, focusing primarily on the work of William Morton Wheeler, coiner of the term 'Myrmecology' and perceived founding father of the concept of 'Superorganism'. The third part (*The Modern Synthesis and all that: the 'hardening of the constriction' and the organicism of Alfred E. Emerson*) addresses the relations between the origin of a formal style of theorizing and the modern synthesis. It also addresses some of the tensions these close relations facilitated among an organicist minded evolutionary biologists and myrmecologist such as Alfred E. Emerson. Finally, the fourth part (*Group selection, Kin selection and the hay-stack model*) decribes the impacts of these close relations on the development on the debate on the division of labour among social insects, arguing that the initial success of mathemathically minded population geneticist like Fisher, Haldane and Wright in the 1930's created a normative setting that favorized the arguments of biologists following a formal style of theorizing in the following decades. By historical coincidence this resulted in the temporary ostracizing of the theory of group selection from mainstream evolutionary biology.

Formal and compositional biology: two styles of biological theorizing:

Methodological concerns have been a focal point for philosophical analyses of science for several generations. The search for a universal scientific method was central in the attempts of the Vienna circle, and their notable critic Karl Popper, to establish sharp demarcation criteria between scientific and non-scientific claims. Similar concerns lay behind Merton's formulation of the CUDOS norms as a universal ethos of science.[52]

These universalistic approaches to methodology were criticized by later generations of philosophers, historians and sociologists of science, who claimed that their absolutist perspective did not adequately address the role that contextual elements (institutional, philosophical or otherwise) plays in setting the standards for the scientific investigation. For these scholars, it was the contextual setting of the scientific *collective*

[51] For further explication of these concepts see Hacking 2002; Winther 2005; 2006.
[52] Merton 1942.

that became the focal point of analysis – and theoretical entities like *paradigms, epistemes,* or *moral economies* were appropriated as categorical tools for analyzing the development and transformation of these contextual elements. In turn, this development were criticized by philosophers such as Laudan, who chided Kuhn for embracing contextualism to such an extent that made it impossible to understand the existence of agreement between scientists who adhere to different theoretical background settings. Insisting that paradigms underdetermine theory-choice, Laudan argued that there is a network of shifting and interdependent justificatory relations between methods, factual beliefs and cognitive aims. Thus, not only may aims justify choice of preferred method or theory, but factual beliefs may be relevant at the appraisal of methods (as in the case of the Placebo effect) or may provide constraints on appropriate cognitive goals by deeming certain goals to be impossible to reach. Likewise, considerations about available methods may shape scientists' perceptions about the attainability of a specific cognitive goal, or may even lead to claims that the goal is too ambiguously or imprecisely stated as to be reachable by empirical means at all.[53]

While these considerations may be bad news for universalistic attempts to find *the* scientific method, they do offer a possible way out of a strong contextualist understanding of methodology as being strictly paradigm or community-dependent. While abandoning the hope of *one* scientific method, perhaps there exists a finite *plurality* of general methodologies in science (shaped in part by the adoption of certain cognitive aims and factual beliefs) that pervades across the boundaries of scientific communities?

Such a road has been followed by scholars pursuing the thesis that there exist several, but in numbers finite, "grand" classes or styles of reasoning within science.[54]

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[53] Laudan 1984, p. 50ff.

[54] The concept of styles have been employed in a variety of disparate ways in the literature of science studies. A classical work on this subject was Fleck (1935/1979), who defined a thought style (germain: *denkstil*) as the "directed perception, with corresponding mental and objective assimilation of what has been so perceived" (Fleck 1935/1979, p. 99), noting that a thought style was characterized by common features in the problems of interest to the thought collective, by the judgment which the thought collectives considers evident, and by the methods which it applies its means of cognition. (Fleck 1935/1979, p. 99). Other uses of the style concept includes, for instance Harwoods (1987) *national styles* in science or Maienscheins (1991) *epistemic styles,* and Hackings *styles of reasoning.* The concept of style has caught the attention of a variety of scholars with somewhat disparate theoretical approaches. For a comparison of these, see Vicedo (1995).

Hence, having undertaken the daunting task of delivering a complete account of the western history of science since the early greeks, historian of science A. C. Crombie identified six general styles of thinking", each of which he believed had played a central role in the development of certain scientific areas.[55] Building on the work of Crombie, Hacking has attempted to explicate the content and meaning of this concept and its bearing on our understanding of science. Preferring the term "styles of reasoning" to "styles of thinking" Hacking regards styles to be constitutive of scientific work and embedded in contingent systems of thought that sets the standard both for what is good scientific practice and how to evaluate what truth or falsehood is within a given domain. Futhermore, every new style introduces a range of novelties including new possibilities for investigation, new types of objects; new evidence; new sentences; new laws or modalities; and, on occasion, new types of classification and new types of explanations.[56] To this list Winther adds new ways of unifying, understanding and modeling.[57] As can be seen styles of reasoning represent distinct ways of reasoning, hypothezising, evaluating, investigating, organizing and so on.

Giving this encompassing account of what a style is, it should be noted, perhaps, what a style is *not.* It is not a "theory of the world" that can be verified or falsified, at least not in any trivial sense. Perhaps a style can be shown to be unfruitful, although the complete extinction of a style seems to be much rarer than in the case of paradigms and moral economies.[58] Hacking notes that the six styles originally described by Crombie are still going strong, although the oldest of them originated in Ancient Greece.

According to Hacking the styles of reasoning that we employ determines what counts as objectivity,[59] in the sense that they provide to the frame and criteria that

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[55] The six styles identified by Crombie were the following: 1) a style based on axiomatic postulation and mathematical proof; 2) a experimental style based on designed observation and measurement; 3) a style based on hypothetical modeling as a method of exploring the unknown properties of natural phenomena; 4) a taxonomic style using comparative methods to order the variety in any subject-matter; 5) a probalistic style based on the application statistical analysis; and finally 6) a style of historical derivation seeking to explore the origin and diversification of any subject- matter, whether language or organisms from the common source, and to explain the cause for that diversification (Crombie, 1994, p. xi).
[56] Hacking 2002, p. 189.
[57] Winther 2005, p. 46.
[58] Hacking gives two examples of possible ”dead styles”: Renaissance medicine and withchcraft (Hacking 2002, p 194-195)
[59] Hacking himself avoids directly defining this thorny concept. See Daston and Galison 2007 for an extensive treatment of this subject.

determines which kinds of questions and problems that are scientific legitimate, procedures for how to decide and distinguish between different possible approaches to solving these questions, as well as for deciding which kinds of solutions are scientific acceptable. Thus, every style of reasoning has a strong normative component. Furthermore, there is an element of self-authenticating circularity in styles. By setting the standards for what counts objectivity a style of reasoning determines the procedure by which we find out whether certain sentences are true or false. But the sentences of this kind only become candidates for truth or falsehood in the context of a specific style of reasoning. According to Hacking there are no higher standards to which a style must answer, and it is his contention that this self-authenticating character of styles of reasoning is a first step in understanding what gives science its "quasi-stability".[60]

Winther, building heavily on Hackings styles of reasoning differentiates two scientific styles within biology, alternately denoting them *styles of scientific investigation* or *styles of theorizing*.[61] This differentiation is based on a conceptual distinction (considered by Winther to be pivotal for understanding biological theorizing) between *laws* and *parts.* One of these styles of theorizing, denoted "formal biology" focuses on mathematical laws and models that represent quantitative relations among parameters and variables. Winther regards this style to be dominant in disciplines like theoretical ecology and theoretical population genetics, and notes (in a critique of his fellow philosophers of biology) that this style has received much attention by philophers, who have tended to treat it as if this approach was the only respectable way of doing biology (and perhaps doing science in general). Much biology cannot be accounted within this framework, however.

Winther denotes the other style of theorizing *compositional* biology. Unlike its formal counterpart, compositional biology is based on the notion of organic world as organized in parts and wholes, and focus on revealing their respective functions and capacities. According to Winther, this style tend to be employed in a disparate set of biological disciplines, including comparative morphology, functional morphology,

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[60] Hacking 2002, p. 189-191. He does, however, doubt that the late Crombie would agree with this, noting that if such a disagreement existed, it would have been philosophical in character rather than historical.
[61] Winther 2005; 2006. In the following I will use the latter term.

developmental biology, cellular biology and molecular biology.[62] However, noting that although certain natural domains tend to lend themselves to one style than the other, most if not all natural domains can be explored using either style.[63] At the same time both Hacking and Winther is ready to admit that styles may hybridize and intertwine.[64] Given this, one might ask whether there is any reason to suppose that styles may come into conflict at all? According to Winther, the answer to this question lies in the all-encompassing ambitions of each style:

> "The important differences between compositional and formal styles are neither the scientific disciplines, nor the natural domains to which the styles tend to be applied. Rather, the fundamental differences lie in their respective *methodologies* of theorizing. Often each style can, and does, examine a similar set of phenomena in the same biological system (e.g. development in organisms) in distinct ways, sometimes reaching even conflicting conclusions about the systems processes and entities. Theoretical conflict arise especially since each style *yearns for completeness* – that is, each style employs its own methods to develop a coherent and general theory, which it then takes to be necessary and sufficient to explain *all* the data in question." (Winther 2006, p. 472)

Within a given domain of inquiry, we may thus expect that, at a given period of time, one style of theorizing may be dominant, while at other times, another style may be dominant; or styles may be competing for hegemony; or perhaps even (for a time) coexist peacefully in a division-of-labour kind of fashion. As we shall see, the history of myrmecology offers instances of all four situations.

Darwinian and Lamarckian Myrmecology: The superorganism approach and pre-synthetic instances of compositional biology

In the 19th century that gave birth to evolutionary biology, the behaviour of social insects was considered to be one of the major biological problems for which any theory of evolution had to account. In his chapter on this subject in the *Origin of Species* Darwin

[62] Winther 2006, p. 471.
[63] Winther mentions cellular and developmental phenoma as examples of natural domains that tend to lend themselves to one style (in this case compositional biology). "Tend" should, of course not be understood in an imperative fashion. Thus, important contribution to the understanding developmental processes has also been given by scientist employing a formal style analysis. Prominent examples of this can for instance be found in the writings of Stuart Kauffman (Winther 2006, p. 472; Kauffman 1993).
[64] Hacking 2002 p. 183; Winther 2005, p. 46.

aimed to show that the apparently complex instincts of slave making among ants and the cell-making of the bee hive were the result of gradual variation and selection.[65]

The doctrine of transmutation of species itself was of course far from unknown at the time of the publication of the *Origin of Species*, having been imported from revolutionary France to Victorian England in the beginning of the 19th century by political radicals.[66] The proposed mechanism for this transmutation, however, was Lamarckian inheritance of acquired characters. Advocating natural selection over Lamarckian inheritance, Darwin argued that the reproductive division of labour among social insects could not be maintained by the inheritance of acquired characters.

> "…no amounts of exercise, or habit, or volition, in the utterly sterile members of a community could possibly have affected the structure or instincts of the fertile member which alone leave descendants. I am surprised that no one has advanced this demonstrative case of neuter insects, against the well-known doctrine of Lamarck." (Darwin 1859, p. 242).

Darwin's alternative solution to the persistence of sterile workers among social insects, natural selection, were of course itself not without problems, as the struggle of existence presupposed the reproduction of heritable variations. Darwin's solution to this was to argue that the relevant unit of selection in this case was not the individual worker or queen but the higher collective level of the colony:

> "… with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how it is possible to reconcile this case with natural selection? … This difficulty, though appearing insuperable is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end." (Darwin 1859, p. 237).

As can be seen from this, the problem of caste specialization and the reproductive division labour was, right from the inception of evolutionary biology, conceived as a battlefield for competing claims about the causal mechanism of evolution. This was to become of increasing importance towards the end of the 19th century. By the 1870's the

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[65] Darwin 1859.
[66] Desmond 1989.

doctrine of common descent was securely established, although few believed that the theory of natural selection provided a complete explanation of how the process worked. The disagreements concerning this question became the focal point of evolutionary discussion as a diversity of competing evolutionary schools emerged during the 1880's and in the decades around 1900. In this period August Weismann rose to be the dominant defender of narrow selectionism; two schools of neo-lamarckism rose on either side of the Atlantic; and a saltational mutation theory for the origin of species became coupled with a set of genetic laws that were ascribed to the genius of a dead bohemian monk.[67] Added to this landscape of controversy concerning the causal mechanisms of evolution were the Spencer-Weismann controversy over inheritance of acquired somatic characters[68] and two important intellectual trends, both of them contributing to the diversity of theoretical directions that was a central feature of this era of biological thinking. One was the recapitulationist thinking that had informed Ernst Haeckel's formulation of the biogenetic law and the phylogenetic speculations that had been part of his *Entwicklungsgeschichte.* The other was the neo-vitalist revival that was facilitated by development within the experimental embryological field of *Entwicklungsmechanik* (developmental mechanics), and the famous experiments on the embryos of sea urchins by Hans Driesch. It was within this context that the reproductive division of labour of social insects was to be discussed and understood within this period of time. The most influential contribution to this topic in the beginning of the 20th century came from William Morton Wheeler, coiner of the term "myrmecology" and, by a later generation, credited as the founding father of the "Superorganism" approach to insect colonies.[69] The source that is most often cited as being the origin of superorganism concept within myrmecology is Wheeler's famous paper "The Ant-colony as an organism" from 1911.

[67] Bowler 1984; 2004, p. 52. The extent to which Mendel himself could be held to be a "Mendelian" has been a topic of discussion. See for, instance Olby 1979 and Sapp 1991.
[68] See Churchill 1978; Griesemer and Wimsatt, 1989, Winther 2001 as well as the original polemic between Spencer and Weismann in *Contemporary Review* (Spencer 1893a; 1893b; 1893c; 1893d; 1893e; 1894; 1895; Weismann 1893a; 1893b; 1895). As described by Winther, the views of Weismann concerning inheritance and variation were complex and changed several times during his career, and did not always correspond to the position that was later constructed as "Weismanissm".
[69] Sleigh 2007.

Curiously though, this paper does not feature the word “superorganism” at all. Instead Wheeler pictures the colony not as a “superorganism”, but as an organism *per se.*[70]

> “The most general organismal character of the ant colony is its individuality. Like the cell or the person, it behaves as a unitary whole, maintaining its identity in space, resisting dissolution and, as a general rule, any fusion with other colonies of the same or alien species. This resistance is very strongly manifested in the fierce defensive and offensive cooporation of the colonial personnel.” (Wheeler 1911, p. 310).

The philosophical position that lay behind the arguments in “The Ant-colony as an organism” saw the organism was the central metaphor for understanding the organizational aspects of life. This did not mean that the focus of Wheeler’s studies of social insects lay on the ant as a single organism. On the contrary Wheeler saw the most interesting questions in myrmecology as lying not so much in the qualities of the individual ant, as in the formic society as a whole. In order to appreciate the ontological implications of the claim that the colony was an organism *per se,* it is necessary to take into account that Wheeler, throughout his career, retained a metaphysical skepticism toward the integrity of the organism.[71] For Wheeler the organism was a social entity in two senses: both as *part* of a collective aggregate of organisms that itself consitituted a higher level organism; and as a collective aggregated *whole* constituted as an emergent entity by organisms at a lower level. In the 1911 paper Wheeler envisaged a nested hierarchical ordering of organisms at different levels organized in after this principle of parts and wholes. The lowest level mentioned by Wheeler was the level of the hypothetical “biophore” - a theoretical entity postulated by Weismann that supposedly aggregated to form the first cells. The next levels in this ordering were filled by unicellular “Protozoon” or “Protophyte”; then with multicellular lifeforms of different stages in cellular differentiation; and proceeding through the colony level of organization to coenobioses which he defined as “more or less definite consociations of animals and

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[70] The oldest direct reference to the superorganism concept that this author has found in Wheeler’s writings stem from the lecture ”Termitodoxa, or Biology and Society”, read by Wheeler at the Symposium of the American Society of Naturalist, Princeton Meeting, December 1919, and published the *Scientific Monthly,* February the following years. This satirical text tells a humorous account of the history of the evolution of termite society as seen from the perspective of a certain “King Wee-Wee” who is presented as “43rd Neotenic King of the 8429th Dynasty of the Bellicose Termites.” (Wheeler 1920). According to “Termitodoxa” it was apparently King Wee-Wee who introduced Wheeler to the superorganism concept!
[71] Sleigh 2004, 2007.

plants of different species”. Finally Wheeler even speculated that the entire biosphere of the Earth could be claimed to be an organism.[72] Spelling out the implications of this ontology, Wheeler argued that:

> "If the cell is a colony of lower physiological units, or biophores, as some cytologists believe, we must face the fact that all organisms are colonial or social and that one of the fundamental tendencies of life is sociogenic. Every organisms manifests a strong predilection for seeking out other organisms and either assimilating them or cooperating with them to form a more comprehensive and efficient individual." (Wheeler 1911, p. 324).

A consequence of this perception of the organism of a social entity (and the colony as an organism) was that the question of coherence became a central problem not only for understanding the colony integration but at all levels in Wheeler’s nested organismal hierarchy.

Throughout Wheeler’s career, food sharing or (as Wheeler was to call it) ‘trophallaxis’ was seen as the kit that knitted the colony together, though the later Wheeler believed he had somewhat underestimated the importance of olfactorial factors and chemical communication. Introducing the term in 1918, Wheeler had argued that care of the brood was not simply a one-way affair as the larvae produce substances which are fed back to the workers. Wheeler saw trophallaxis as a self-regulating system of stimulus and response that completed the circuit between the colony’s inner world of the nest inhabitants and the outer world, and the concept of trophallaxis became central for Wheeler's emerging view of the colony as a ‘superorganism’. When the superorganism and its environment were considered to be the product of trophallactic interactions, the metaphysical distinction became increasingly difficult to specify. Right from 1918 he considered trophallaxis to be an elastic social phenomen that covered interspecific, parasitic and even animal-plant relationship.[73] The functionalist approach that Wheeler took to mutual feeding led him to propose a hierarchy of trophallactic interactions that were arranged in accordance with their position of importance for the nest. The most

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[72] Wheeler 1911, p. 308-309.

[73] One of the reasons Wheeler preferred his own ‘trophallaxis’ compared with Emile Roubauds competing ‘oecotrophobiosis’ was on the grounds that Robaud’s term implied intraspecific relations only (Wheeler 1918, p. 322).

important form of trophallaxis (and the primary form in evolutionary terms) occurred between the queen and larvae and between workers and larvae. On Wheeler's second level became food exchange between adults; on the third exchange with symphiles, then between ants of different species (in the case of slave-making ants) and finally with other insects and plants outside the nest.[74]

Wheeler perceived this nested hierarchy of parts and whole as functioning under a set of premises that was idiosyncratic to the theoretical context in which he was navigating. Among these premises were a fascination with certain strains of neo-vitalist thought; a Lamarckian belief in the inheritance of acquired characters; a functionalist account of instinct and behaviour, and a commitment to a quasi-Haeckellian monism and the biogenetic law.

At the time of the publication of the 1911 paper, Wheeler was greatly influenced by the prominent neo-vitalist Henri Bergson.[75] It was especially Bergson's processual view of the organism as an entity of becoming that appealed to Wheeler and fitted well with his metaphysical skepticism towards the integrity of the organism. Wheeler described the organism was a "continual flux or process, and hence therefore forever and never completed"[76], and he credited the neo-vitalist school for jolting the biological community out of the delusion that they were "seriously studying biology" when they were scrutinizing paraffine sections of plants and animals or dried specimens on mounted on pins.

Wheeler was fighting on all fronts in order to defend this position. 'All fronts' also included the philosophical and epistemological front, where he took exception to classical Comtean positivism and the perceived excesses of the writings of Bergson's neo-vitalist collegue Hans Driesch, as well as of physical materialism. As to the writings of Hans Driesch, Wheeler used his concept of entelechy as an example of a scientific unfruitful concept of which he believed that "we ought not to let it play about in our labouratories".[77] And arguing against reductive materialism as the philosophical basis for biological studies (and the study of insect colonies in particular) Wheeler stated that:

[74] Wheeler 1918, p. 322; 326.
[75] Sleigh 2004.
[76] Wheeler 1911, p. 308.
[77] Wheeler 1911, p. 324.

"…I have acquired the conviction that our biological theories must remain inadequate so long as we confine ourselves to the study of cells and persons and leave out the psychologists, sociologists and metaphysicians to deal with the more complex organisms. Indeed our failure to cooperate with these investigators in the study of animal and plant societies has blinded us to many aspects of the cellular and personal activities with which we are constantly dealing. This failure, moreover, is largely responsible for our fear of the psychological and the metaphysical, a fear which becomes the ludicrous from the fact that even our so-called 'exact' sciences smell to heaven with the rankest kind of materialistic metaphysics." (Wheeler 1911, p. 309-310).

Like other myrmecologists of Lamarckian inclinations, Wheeler had to struggle with the fact that Darwin had attempted to use the example of infertile worker ants to 'disprove' the Lamarckian inheritance of acquired character in ants in the *Origin*. Wheeler's strategy against Darwin's argument of worker sterility was to point out that there were significantly more fertile ants than was generally supposed. When a queen was removed from a colony, enough fertile workers were likely to appear as to make significant contribution to the germ-plasm of the next generation possible. There was thus no need to uphold a strong Weissmannian segregation between the soma and the germ plasm:

"If we grant the possibility of a periodical influx of the worker germ plasm into that of the species, the transmission of characters acquired by this caste is no more impossible than it is in other animals, and the social insects should no longer be considered as furnishing conclusive proof for Weismannism." (Wheeler 1910, p. 116).

Throughout his career Wheeler's retained an affinity for Lamarckian inheritance, although the theoretical lenses through which he understood the inheritance of acquired characters undertook several intellectual transformations. Apart from a fascination of Bergson's processual understanding of life as something "becoming" rather than "being", the early Wheeler's[78] perception of the Lamarckian inheritance were also based on the recapitulationist thinking of Ernst Haeckel and the biogenetic law. For Haeckel phylogeny was the "mechanical" cause of ontogeny in the sense that the inheritance of acquired adaptations was processed by way of an ontogenetic addition to the terminal

[78] Apparently Wheeler outgrew Bergson around 1917, though he still retained an affinity for the basic processual view of life as "becoming" that was part of Bergson's thinking (Sleigh 2004, p. 160).

adult stage through succeeding generations. Apart from the principle of terminal addition, it was necessary that the repetition of ancestral adult stages were condensed during ontogeny, or else the time span of development would be prolonged indefinitely. A result of this process was supposedly that an organism's phylogenetic history could be derived from a studying of its development.

The early Wheeler's commitment to Haeckel's biogenetic law went so far that he, already having committed himself to an ontology of nested hierarchies of organisms at different levels, was willing to extend Haeckel's biogenetic law to the colony level. Comparing the role of the fecundated queen with the fertilized egg, Wheeler claimed that the formation of an ant colony to be a process comparable to the ontogeny of a multi-cellular organism, and he saw the production of different castes during the development of a colony as a process akind to cell differentiation. After describing what Wheeler considers to be the typical life history cycle of a colony he stated that

> "It is so similar to the phylogenetic history derived from the sources mentioned above that we have no hesitation in affirming that it conforms in the most striking manner to the biogenetic law. The very ancient behaviour of the solitary female Hymenopteron is still reproduced during the incipient stage of colony formation, just as the unicellular phase of the Metazoon is represented by the egg. A further correspondence of the ontogeny and phylogeny is indicated by the fact that the most archaic and primitive of living ants form small colonies of monomorphic workers closely resembling the queen, whereas the more recent and most highly specialized ants produce large colonies of workers not only very unlike the queen but unlike one another." (Wheeler 1911, p. 313-314)

The intellectual road from Haeckel to Wheeler went via the swiss psychiatrist Auguste Forel, who was a committed monist, something that led him to a firm belief in the identity theory of mind and brain.[79]

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[79] Forel's conviction that mind and brain were one and the same was viewed by him as a validation of his reeducation of alcoholics, hysterics and other patients - a reeducation through which he literally (so he believed) reconstructed the brain. As Forel believed ants to be a simpler model of the same processes. He saw a functional discussion of insect anatomy (especially in its connection with sensation) was therefore the key to understanding the "insect mind", and the senses and nerves were a physical reflection of the evolved adaptive aspects of the insects psyche. Though Forel's habits of making psychological comparisons between insects and human was certainly not shared by all his peers or successors, his use of the insect behaviour as an exemplary model of instincts where shared by a large number of entomologists at the time. Hence, Forel's psychological conception of instinct as "organic memory" was at the heart of the myrmecological science that Wheeler inherited. (Sleigh 2004, p. 156-158; 2007, p. 70).

In the views of Forel, the behaviour of ants should be regarded as the results of adjustment to changing conditions that had since become engraved in the heritable structures of their nervous system. Forel's theories on this process drew on a theory of "organic memory", according to which the associative behaviours of long term repeated stimuli could be fixed as innate instincts. Forel's prime example of this psychophysical complementarity was the soldier termites that blocked the entrance to the nest from intruders with their immense armoured heads. These species had gradually ceased the practice of blocking the entrance with gathered or secreted materials, a task that was now accomplished with a specialized caste. For Forel it made no sense to ask whether changes in the behaviour or the anatomy came first, as they were useless without each other. The behaviour and anatomy of the soldier caste were acquired in tandem, anatomy following behavioural changes.

With the general decline of Haeckels biogenetic law during the first decades of the 20th century,[80] Wheeler found a final bastion for his Lamarckism in the writings of the Italian sociologist Vilfredo Pareto. Pareto's sociology revolved around the assumption that most people did not live by logical thought but by irrational atavistic residues. These residues were emotional responses and non-logical forms of reasoning, themselves the result of the hardening of adaptive human behaviours into innate habits equivalent to the instincts of ants. This view corresponded to Forel's opinion on instincts, though Paretan instincts, of course, carried a much more negative connotation, being a metaphor for the mass collectivization of humanity.

But Pareto’s collectivistic approach to instincts were in line with Wheeler’s belief that life were an inherently social phenomenon, and with the metaphysical skepticism towards the integrity of the organism that had been part of his thinking from the time he took up the study of ants. The skepticism that Wheeler’s professed toward selectionist

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[80] See Gould (1977, p.167ff) for a description of the theoretical developments that led to the eventual demise of the biogenetic law. Though recapitulationist thinking did not disappear from Wheeler’s writings entirely, the growing general skepticism towards the biogenetic law did have an effect on Wheeler. In his 1917 lecture to the Royce club 'On Instincts' Wheeler was considerably more cautious towards its use than in 1911, stating that

“In nothing is the courage of the psychoanalysts better seen than in their use of the biogenetic law. They certainly employ that great slogan of the nineteen century with a fearlessness that makes the timid twentieth century biologist gasp.” (Wheeler 1921, p. 317).

explanations was an important corollary of this. Wheeler saw the competitive struggle for resources as being essentially anti-social, and therefore believed that Darwinian evolution could never be more than half the story, if life was inherently a social phenomenon, the other being cooporation. Wheeler's own studies of the complex relations in nature persuaded him that things were the other way around – that cooporation was the norm and selfish individualism the exception.

The Modern Synthesis and all that: The "hardening of the constriction" and the organicism of Alfred E. Emerson

With the exception of the events leading to the publication of the Origin of Species, the emergence of the modern synthesis is probably *the* event in the history of biology that has received the most thorough scholarly treatment. Numerous accounts and interpretations of has been published both by participants in the events that took place; from biologists having a stake in later evolutionary discussion, and from scholars approaching the issues with the perspective of science or cultural studies.[81] One of the prominent claims about the history of the synthesis has been that it suffered a "hardening" during the 1950's and 1960's – a hardening in which an initial plurality of claims were decimated to a selectionist core.[82] Gould's initial claim of a hardening of the synthesis was made with the case of paleontology, but the idea was later taken up Provine who preferred the term 'evolutionary constriction' to denote the cut-down of variables considered important in the evolutionary process:

> "The term 'evolutionary constriction' helps us to understand that evolutionists after 1930 might disagree intensely with each other about effective population size, population structure, random genetic drift, level of heterozygosity, mutation rates, migration rates etc., but all could agree that these variables were or could be important in evolution in nature, and that purposive forces played no role at all. So the agreement was on the set of variables, and the disagreement concerned differences in evaluating relative influences of the agreed-upon variables. I agree with Gould that evolutionary biology 'hardened' toward a selectionist interpretation during the late 1940's and 1950's. I see this as a further constriction (but I like the sound of 'hardening of the constriction')." (Provine 1992, p. 61)

[81] A full treatment of the vast amount of literature on this subject is far beyond the scope of this paper. But see Mayr and Provine 1980; and Smocovitis 1996 and the references therein.
[82] Gould 1980, p. 153ff.

What guided this "evolutionary constriction"? Most obviously, of course, was the ambition to build an evolutionary biology that based its theoretical understanding on the various causal factors mentioned by Provine in this quote, and to rid it of the "purposive forces" that had been prominent in Lamarckian or vitalist thinkers. But another important element of the developments that led to the modern synthesis was the import of mathemathical methods of formalization and axiomatization into evolutionary biology.[83] This import was part of a larger trend within the period of 1915-1935 – a period during which the formal style originated and expanded as a style of theorizing within the domain of biology. Apart from evolutionary biology, examples of the innovative employment of such methods during this period include method D'Arcy Thompsons *On Growth and Form,* a foundational work within theoretical morphology; and the equations of Lotka and Volterra on prey-predator ratio within ecology – a line of research that has become equally foundational for theoretical ecology.[84] Within evolutionary biology this trend was spearheaded by the works of population geneticists such as J. B. S. Haldane (1932), Sewall Wright and R. A. Fisher, who in the preface to the *The Genetical Theory of Natural Selection* would state that:

> "It seems impossible that full justice could be done to the subject in this way, until there is built up a tradition of mathemathical work devoted to biological problems, comparable to the researches upon which a mathematical physicist can draw in the resolution of special difficulties." (Fisher 1930, p. x)

Although the successful formalizations of these scientists were a central factor in the development of the modern synthesis, they were also met with reservations by organicist minded biologists, even from people who shared the same unifying ambitions that prompted this development. Thus, Theodosius Dobzhansky, although in general positive towards these efforts, ironically remarked that the significance of these changes in methods

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[83] These two trends undoubtedly worked in tandem on several occasions.
[84] Thompson 1917; Lotka 1925; Volterra 1926. I am indebted to Rasmus Winther for this point.

"…has been stressed in the writings of many authors, some of whom went to length on ascribing to the quantitative and experimental methods almost magical virtues." (Dobzhansky 1937, p. 6).

The most prominent of these critics, of course, was Ernst Mayr, who lashed out against the perceived excesses of "bean-bag" genetics,[85] and questioned the importance of the contributions of mathematics to evolutionary theory. On this, he was answered by Haldane, who stated that one of the important functions of beanbag genetic laid in showing biologist which numerical data are needed.[86] But Haldane himself was equally cautious when defending the applications of mathematics to evolutionary theory, and ended the introduction of his major synthetic work, *The Causes of Evolution* with the following disclaimer:

"I can write of natural selection with authority because I am one of the three people who know most about its mathematical theory. But many of my readers know enough about evolution to justify them in passing value judgments upon it which may be different from, and even wholly opposed to, my own." (Haldane 1932, p. 33)

These tensions also affected myrmecology. It was within this context of a 'hardening of the constriction' that the rise of the conflict between formal and compositional biology within the domain of social insects study took place. This conflict ended with the problem of the division of labour among social insects transformed into a question of group vs. kin selection, and what for some time appeared to be the hegemony of formal biology over the domain of caste specialization in social insects.

A leading transitory figure in this process was Alfred E. Emerson. Emerson was a member of the "Ecology Group" of the University of Chicago, a scientific community

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[85] Mayr 1959, p. 2; 1963, p. 263. Mayr's polemic against beanbag genetics deserves to be quoted in length: "The emphasis in early population genetics was on the frequency of genes and on the control of this frequency by mutation, selection, and random events. Each gene was essentially treated as an independent unit favored or discriminated against by various causal factors. In order to permit mathematical treatment, numerous simplifying assumptions had to be made, such as that of an absolute selective value to a given gene. The great contribution of this period was that it restored the prestige of natural selection, which had been rather low among the geneticists active in the early decades of the century, and that it prepared the ground for treatment of quantitative characters. Yet this period was one of gross simplification. Evolutionary change was essentially presented as an input or output of genes, as in the adding of certain beans to a beanbag and the withdrawing of others." (Mayr 1959 p. 2).

[86] Haldane 1964.

that spurred the leading proponents of ecological organicism in American biology after Wheeler.[87] This scientific community was used by Winther (2005, pp. 53-73) as exemplary of a group of scientists with a research program employing the compositional style, describing another member of that group, Thomas Park, as a hybrid figure between compositional and formal biology.[88] Furthermore, together with Mayr and other leading figures in the events that led to (what has been called) the 'formation' of the modern synthesis, Emerson was also a cofounder of the Society for the Study of Evolution in 1946 – the Society that launched the journal *Evolution* and became the central institution for the collective efforts of evolutionists in the years to come. This double identity of Emerson as a prominent figure in the establishment of the Society for the Study of Evolution; and as a prominent figure in the ecological organicism of the Ecology Group at the University of Chicago; allows us to explore the relation between the general theoretical developments within biology under synthetic rule (including the tensions between formal and compositional styles of theorizing that resulted from this) and the fate and transformation of the division of labour-problem from being perceived to be a question of the credibility of Lamarckian inheritance to a question of kin vs. group selection.

While still retaining a superorganismic approach to the colony (though slightly changing the terminology describing the colony as a 'supra-organism'), the context in which Emerson approached this problem was both organicist and selectionist. This double identity is exposed in *Principles of Animal Ecology* – a major result of the collabourations of the Chicago ecologists.[89] Though being the result of a collective effort, Emerson was responsible for the chapters on social insects and evolution - having, among others, Sewall Wright and Ernst Mayr as consultary readers.[90] Being grounded in a synthetic framework, Emerson regarded hereditary variation, reproductive isolation and natural selection to be the main factors influencing evolution and Lamarckian inheritance

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[87] Worster 1994, p. 326.
[88] Winther 2005, pp. 53-73. Park, whose primary interest laid in the biology of populations, combined a compositional view of nature as organized in nested hierarchies with a strong interest in the applications of mathematics and statistics to biological problems. Together with Sewall Wright he was on the phd. committee of Michael Wade, whose formal work on group selection was pivotal in the developments that led evolutionary to reconsider it as a viable alternative. See Winther 2005, p. 70-72 and Wade 1978.
[89] Allee *et al.* 1949.
[90] Allee *et al*. 1949, p. viii-ix.

to be “unlikely”, referring Darwin’s example of “neuter insects” as the most prominent case of evidence against the inheritance of acquired characters as a universal mechanism for adaptation.[91]

The theoretical foundations on which Emerson based his evolutionary views, had other connotations however. Like Wheeler, Emerson envisaged life as being organized in a nested hierarchical ordering. In a defense of the use of organismal analogies at the super/supra-organismal level, Emerson took an emergentist position, at the same time arguing for a pragmatic approach to the study of wholes and parts in biology:

> “The theory of emergent evolution has been applied to the concept of organismic levels. This theory recognizes that new or novel properties and characteristics emerge from new combinations. Complex associations have properties that are not merely the sum of its constituent parts ... Some proponents of the theory of emergent evolution state that the novel properties arising from interaction are fundamentally unpredictable from a knowledge of the unassociated parts. This philosophical aspect of the theory is beyond our field of enquiry. In essence, emergent evolution emphasizes the basic necessity for the study of wholes, as contrasted to the study of parts, and adds a certain dignity to synthetic sciences. Biology is the study of whole systems as well as parts, and ecology, among the various subsciences of biology, tends to be holistic in its approach.” (Emerson, p. 693)

In line with this, Emerson argued that both the individual organism as well as the population as a whole could function as unit of selection, and that the colony served as such a unit. In the process of evolving homeostatic mechanisms it developed adaptations closely analogous to those seen in the behaviour of individual organisms. Among these were a well-defined division of labour that Emerson saw as a defining characteristic of animals integration into sociality:

> “A well-defined division of labour is characteristic of the strictly social animals. Separated functions of the parts make coordination necessary. Division of labour and integration advance as reciprocal manifestations in both ontogeny and phylogeny of the social population, parallelling similar manifestations in the organism. This parallellism between the organism and the society is included in the concept of the supra-organism,” (Emerson 1949, p. 420)

[91] Emerson 1949, p. 599.

Emerson saw division of labour and the coordinated integration of parts as associated principles, and stated that specialization of function could not occur unless the specialized parts were coordinated. Emerson regarded efficient homeostasis to be the result of an increase in the special functions of integrated parts. He believed these principles applied to every level of organization from the cell to the ecosystem, but were particularly well exhibited by colonies of social insects.[92] He also warned that the analogies between individual organisms and colonies could not be lightly dismissed by pointing out differences in mechanisms and functions.

> "The refusal to accept analogical comparisons as a part of a scientific method would eliminate the comparative study of convergent social systems in insects - for example, that of ants and termites. In opposition to this attitude against analogical reasoning, we hold that the synthesis growing out of the comparison of organism and supra-organism helps to elucidate fundamental principles and is a challenge leading to further analysis and understanding of biological mechanisms." (Emerson 1949, p. 435)

The research program envisaged by Emerson thus approached social insects, and hence the problem of division of labour, from a compositional perspective of life as being nested hierarchical ordering and posed its question as the integration and coordination of parts within wholes. As to the future of this endeavor Emerson stated that while still being in an early state of comprehension concerning the details of the functions and integration that make any organism an organism, we knew enough to see that the social insect colony had a pattern significantly similar to that of a lowly multi-cellular organism.[93]

Group selection, Kin selection and the hay-stack model.

As noted Emerson envisaged the problem of division of labour within social insects as a question of how to explain the coordinated integration of parts within wholes – a question that could only be solved by empirical investigations of the nature of the actions and interactions of ants within the context of a colony.

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[92] Emerson 1949, p. 426-427; p. 683.
[93] Emerson 1949, p. 426-427.

During the next decades, the majority of biologists were to pursue a different path on this topic, however. According to Worster the Chicago ecology group "fell silent" and was disbanded after Warder Allees retirement in 1950, leaving ecological organicism with no important professional voice in the postwar period. He furthermore notes that organismic approaches dropped out of the mainstream of the discipline of ecology after this period.[94]

Worster, however, gives no satisfactory account for this development. Under ordinary circumstances, one might expect that a new generation of scientists would be ready to take over and continue the intellectual pursuits of their predecessors. Instead it appears that problem of division of labour was "high-jacked" by a bunch of evolutionary biologist with more reductionist leanings than the Chicago school of ecology. Whereas Emerson had envisaged the problem of division of labour within social insects as a question of how to explain the coordinated integration of parts within whole, they would envisage it as a question of how to explain the existence of apparent altruistic behaviour. And their method to solve this question was by the use of the tradition of mathemathical modeling that had been introduced into evolutionary biology by Fisher, Haldane and Wright.[95]

During the 1960's the hypothesis of group selection, which had been central in selectionist accounts of the division of labour within social insects when faced with Lamarckian alternatives fell victim to a seemingly devastating critique – a critique that resulted in the idea becoming ostracized from mainstream[96] evolutionary biology during the next decades. The attack on group selection in the 1960's were first and foremost directed against the writings of Wynne-Edwards, a British ornithologist who, in 1959 formulated a theory of group selection according to which population density could be

[94] Worster 1994, p. 331.

[95] In fact, Wright himself was the first to propose a simple formalized model of group selection wherein he reasoned that altruism could be established in a few groups (which could then outcompete selfish groups) as a result of genetic drift, despite being initially disadvantageous. He remained however, doubtful of the effectiveness of such a scenario. See Wright 1945.

[96] The term 'mainstream' is used here as a lack of better terms, since it begs questions such as exactly what constitutes a mainstream position, and who decides what is mainstream and what is not. But the fact that the dominant attitude towards group selection during this period was a negative one has been amply documented. See for instance Dawkins 2006; Borello (2003; 2004; 2005) Wilson and Sober 1998 and the references therein.

controlled by altruistic food sharing and dispersion. This theory that was later explored in depth in the book *Animal Dispersion and Mutual Aid.*[97]

Much has been said about this debate, and a full treatment of this subject is beyond the scope of this paper.[98] However, as described by Sober and Wilson, the development that led to the temporary ostracizing of group selection in the 1960's was marked by several notable "rebuttals" of group selection.[99] These included the book *Adaptation and Natural Selection* by the philosopher George Williams; two influential papers by Bill Hamilton on the genetical evolution of sexual behaviour in the *Journal of Theoretical Biology*; and John Maynard Smiths paper on the "Haystack model" of group selection.[100]

As pointed out by Winther (2005, p. 64), the development of the levels of selection debate took place partly as a *reaction* to the works of the Chicago ecology group.[101] This is illustrated by a later statement by Williams, who, recounting a lecture by Emerson that interpreted all of the nature on the model of a termite colony, expressed that:

> "If this was evolutionary biology, I wanted to do something else – like car insurance." (quote taken from Sober and Wilson 1998, p. 36).

As hinted by this quote, the attack on group selection was not only an attack on a specific position within evolutionary biology, although this was also certainly the case. What was at stake was also the manner in which *evolutionary questions were posed and how to solve them.* One of the perceived problems of both the works of the Chicago Ecology group and Wynne-Edwards, and a focal point for critique from these mathematically minded biologists, were their lack of mathematical formalization. Like Emerson, Wynne-Edwards approached from a compositional perspective, claiming the regulation of the population density (the *whole*) came about by the altruistic acts by the population's *parts* – the individuals. Thus, Wynne-Edwards asserted, by virtue of their power of movement, most animal have a predominant role in regulating their own

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[97] Wynne-Edwards 1959; 1962.
[98] But see Wilson and Sober 1998; Keller 1999; and Borello 2003; 2004; 2005.
[99] Sober and Wilson, 2000.
[100] Hamilton 1964a; 1964b; Maynard Smith 1964; Williams 1966.
[101] Winther 2005, p. 64.

population densities. As to his own area of expertise, avians, he maintained that although food was almost always the critical limiting factor, birds were largely able to regulate their own population densities through social conventions connected to territory system and pecking order.

As a response to this situation both Hamilton and Maynard Smith took it upon themselves the task of formulating mathematical models that explored the relations between social behaviour and Darwinian fitness. Making use of Sewall Wright's Coefficient of Relationship, Hamilton proposed a mathematical model of *inclusive fitness* (or, as Maynard Smith relabeled it, *kin selection*), arguing that many instances of apparent altruistic behaviour, for instance among social insects workers, were in fact evolutionary selfish as they contributed to the propagation of offspring by relatives.[102]

Maynard Smith's haystack model supplied what appeared to be another nail in the coffin. The haystack model is built around a fictitious species of mice that lives entirely in haystacks. The population of each haystack is founded by a single fertilized female, whose progeny mate within the haystack entirely among themselves for a number of generations. The presence of evolutionary altruists in a haystack benefit the colony in such a way that the whole group breeds faster but within the group the altruists themselves breed less than evolutionary selfish individuals in the same group. At the end of the year the haystack colonies break up and all the individuals mate randomly in a single large population before repeating the cycle. Based on this model Maynards Smith concluded that while group selection would be possible under such circumstance, it was a necessary condition that the presence of altruist had been previously established in the population, something Maynard Smith considered to be highly improbable.[103].

This "implausibility" of group selection became an established truth that were to enter the textbooks of behavoural biology, and Maynards Smith's haystack model became the basis for the most common argument against group selection – that it is susceptible to *subversion from within.* This argument was later popularized by Richard Dawkins in *The Selfish Gene* who gave the following account:

[102] Hamilton 1964a, 1964b.
[103] Maynard Smith 1964.

"Even in the group of altruists, there will almost certainly be a dissenting minority who refuse to make any sacrifice. If there is just one selfish rebel, prepared to exploit the altruism of the rest, then he, by definition, is more likely than they are to survive and have children, Each of these children will tend to inherit his selfish traits After several generations of this natural selection, the 'altruistic group' will be over-run by selfish individuals, and will be indistinguishable from the selfish group." (Dawkins 2006, p 7-8),

There are subtle but important differences between this account and the conclusions based on the model presented in the haystack paper. Notable in Dawkins account is that the disappearance of altruists only occurs *after several generations.* But as noted by Sober and Wilson, Maynards Smith's haystack model was not equally as generous towards group selection:

"…Maynard Smith added a simplifying assumption to the haystack model that amounts to a worst case scenario for group selection. He assumed that the altruistic gene not only declines in frequency but goes completely extinct in all groups that are initially mixed! Altruists survive only in haystacks established by altruistic females who have mated with altruistic males. Given such powerful within-group selection, Maynard Smith conclude that altruism could not plausible evolve by group selection." (Sober and Wilson 1998, p. 1970)

Indeed, as a reply to the *subversion of within* argument against group selection Wilson and Sober have responded by the challenging the basic assumptions of its modeling conditions. Their task has been to work out the theoretical conditions where group selection may be active despite the subversion from within of altruistic groups by selfish individuals. The result of these efforts are by now well known and has been published in a series of papers.[104] A major conclusion of theirs is that group selection is theoretically possible if the rate of group splitting and extinction are higher than fitness advantage of selfish individuals within groups.[105]

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[104] See for example Sober 1991 and Wilson and Sober 1994.

[105] See also Wade (1978) for a systematic critique of the assumptions behind the haystack model and similar models of group selection. An interesting side story to the subversion of within argument is the way Amotz Zahavi – founder of the handicap principle and an adherent of strict individual selection – has turned it against those who, like Dawkins and others, promote a genes-eye view of evolution, and claim that all apparent altruistic behaviour can be explained as inherently selfish mechanisms such as reciprocal altruism or kin selection. Zahavi argues that these kinds of "indirect selection" suffers from the same weakness as group selection, and that they are equally susceptible to subversion from within (Zahavi 1995). Subversion from within is therefore not only a problem for group selection, but for *all*

Given this rather obvious problem with the haystack model, one might ask why it came to play such a consensus-creating role in the development that led to the temporary ostracizing of group selection from mainstream evolutionary biology. Why did the haystack paper become hailed as canonic in the demise of group selection, whereas the works of Wynne-Edwards came to play the role as an example of how evolutionary biology ought *not* to proceed?

The analysis here suggests that part of the explanation to this question is to be sought in the pressures that the apparent success of a formal style of theorizing during the emergence of the modern synthesis exercised on the domain of evolutionary biology for this period. The efforts of mathematicians and mathematically oriented biologists to expand these methods towards new biological problems contributed to the creation of a normative atmosphere that favorized a formal style of theorizing, and played a continuing role in the following years of the 'hardening of the constriction' where group selection was ostracized. On the surface this development might appear to be the logical result of the efforts of the architects of the synthesis to cut-down the number of variables considered important in the evolutionary process, and to rid evolutionary biology of all purposive forces, creating a 'true' Darwinian evolutionary biology. However, as already noted, this doesn't fit with the fact that Darwin himself embraced group selection and that one of the leading proponents of this idea, Alfred E. Emerson, played a very active role in establishing the Society for the Study of Evolution in 1946 – the Society that became the central institution for the collective efforts of evolutionists in the development of the modern synthesis. Nor does the fact that adherents of group selection is now given more respect than in the 1970's lead us to conclude that group selection *per se* is inherently in conflict with the basic propositions in the modern synthesis.[106] Instead it seems that part of the perceived problem with group selection in the 1960's was the compositional manner in which it was put forward. Unlike his adversaries, Wynne-Edwards did not attempt to make a formalized model of group selection. In fact, as noted by Borello,[107] it was only by the mid 1970's and onward, that we find the first instances of succesful

kinds of "indirect selection" – including kin selection and reciprocal altruism.

[106] Although one may argue, as Borello (2005, p. 45) have done, that this was in fact the case with the way it was presented by Wynne-Edwards.

[107] Borello 2004, p. 28; 2005, p. 46.

attempts to model group selection mathematically within a strictly selectionist framework.[108] But by this time, group selection had already fallen from grace, and it took several decades, and the stubbornness and most of the careers of a select few, to convince evolutionary biologists to reconsider this conclusion.[109]

Conclusion

By the beginning of the 1970's, the unifying ambitions of the modern synthesis had reached its full momentum within the study of social insects. In the book *Insect Societies,* Edward O. Wilson, later hailed (and attacked) as the founder of sociobiology, described the history of the study of social insects as a progressive development in three stages leading to the establishment of insect sociology as a "mature science". While the first stage included the discovery and description of social insects and the evolutionary interpretation of their behaviour and ecology, the second included the experimental analysis of social systems and their physiological bases. Although Wilson regarded these two stages to be the necessary and logical precursors to other kinds of investigations, the ultimate goal, however was the third stage; the construction of mathematical models and predictions in the fashion of the "hypothetically-deductive method of any mature science", and the account of social phenomena in the terms of the "first principles" of population genetics and population ecology.[110] For Wilson, the aim of the book was to provide "a modern synthesis of insect sociology"[111] and in a reiteration of the unifying ambitions behind the development of the modern synthesis, he confidently stated that:

> "In time all of this information will be assembled in the framework of population biology and form an important branch of that larger science. A principal theme of this book is, therefore, the expression of insect sociology as population biology." (Wilson 1971, p. 3)

Is Wilson's prophecy coming true? Almost forty years later the road to it seems bumpy indeed. Undoubtedly the works of Hamilton and other biologists following a

[108] Wilson 1975.
[109] It should be noted of course, that the fact that group selection has now reentered evolutionary discourse as a viable theory, does not mean, that it is generally endorsed. Dawkins, for example, remain as equally unconvinced today as he did in the 1970's (Dawkins 2006, p. 297-298).
[110] Wilson 1971, p. 7-8.
[111] Wilson 1971, p. 2.

formal style of theorizing has had a profound effect on the study of social insects. Large textbooks now exist that in their chosen content and manner of presenting the subject exclusively follow a formal style of theorizing.[112] However, the introduction of approaches based on self-organization into the study of social insects have given rise to instances of interesting intertwinements between these two styles and some of these instances challenge the selectionist[113] perspective prevalent in Wilsons vision of the future of "insect sociology" and dominant in most synthetic and post-synthetic works on the division of labour problem. Both within a selectionist and a non-selectionist perspective, the problem is approached with attempts to construct formal models of the part-whole relations between the cohesion of the colony and individual ant interaction.

Within a selectionist perspective, such an attempt has been made from a kin selection perspective within the framework of tug-of-war theory.[114] Tug-of-war theory has been used to understand evolutionary stable situations of reproductive portioning, in instances when the dominant members of a group have incomplete control over the behaviour of subordinates, and when group members have such a limited outside reproductive options that they will not receive reproductive payments to remain in that group. In a tug-of-war, the members of a group selfishly invest a fraction of the groups output in order to increase their share of that output. Each group member's share depends on the magnitude of its selfish investment relative to the selfish investment of other group members. Based on this assumption (equal to the situation in a tug-of-war, where to outcome depends on the relative magnitude of forces invested on each end of the rope) Kern Reeve & Hölldolber has constructed a model that predict the cooperative investment of group members to increase when within-group relatedness increases; decrease as group size increases (when the number of competing groups is held constant); increase as the number of competing groups increases, decrease as between-group

[112] An example of this is F. R. Bourke and Nigel Franks *Social Evolution in Ants* (1996).
[113] I use the term 'selectionist perspective' here simply to denote any theoretical framework that seeks to explain biological phenomena by referring natural selection, regardless of whether this explanation is based on gene- individual, group or even species selection (or a comination of these approaches). A 'non-selectionist' perspective takes an explanatory approach based on something else than a theory of natural selction – for instance – in this case – on notions of self-organisation.
[114] See Keern Reeve and Hölldobler 2007.

relatedness increases, and (finally) to increase as the intensity of between-group competition increases relative to the intensity of within-group competition.[115]

A non-selectionist approach has been pursued by Fewell and colleagues who have argued that division of labour in social insects may arise as a self-organic feature of large group size. Using an adaptive network approach, Fewell explains the emergence of division a labour as a result of intrinsic variation in worker response tresholds. In order to explain her theory Fewell's uses the analogy of a family living in a home where the same person always end up doing the dish-washing because that person has the lowest threshold of patience for a messy kitchen. If different persons the household have the lowest threshold of patience for other menial tasks, this itself may be enough to create a situation of divided labour. Whether this threshold variation arises by genetic, developmental, or environmental means is of no consequence for Fewell's theory, but, together with other properties of the network, like group size and connectivity this may have a profound influence on the adaptive function of the social group. Likewise, the network interactions of the social group have a profound influence on the fitness of its individuals, and in some systems, self-organization can actually generate conflicting fitness effects at the individual and the group level.[116]

As these recent examples illustrates, the problem of division of labour remains an interesting challenge to contemporary myrmecologists and entomologists studying social insects. In conjunction with the introduction of new methods, cognitive aims and changes in the relative appeal of the compositional and formal style within the biological community, the problem of division of labour has undergone several transformations in the history of myrmecology. Initially perceived as a problem for Lamarckian inheritance, the problem has experienced several redefinitions, being perceived first a question as the colony integration and the coordination of parts within wholes, and, following the expansion of formal biology, as a question of how to explain the existence of apparent altruism in nature. These historical legacies continue to play a role even as newly developed hybrid perspectives (such as tug-of-war theory and self-organizing network

[115] Kern Reeve and Hôlldobler, 2007.
[116] Fewell 2003, p. 1869.

approaches) are advanced to study the problem, ensuring ample room for a plurality of constructive combinations of approaches.

Acknowledgements: Thanks to the employees and associates at the Center for Social Evolution at the University of Copenhagen (especially J. Koos Boomsma and Jes Søe-Pedersen) for giving me access to the daily life of myrmecologists; to Andrew Hamilton and Manfred Laubichler for the encouragement to make this paper, and to Rasmus G. Winther for constructive critique. The Center for Biology and Society at the Arizona State University were the kind hosts during a three months stay in Tempe, Arizona, during which I also had the chance to encounter local myrmecologists. And finally thanks to employees and associates at Center for Philosophy of Nature and Science Studies at the University of Copenhagen for moral support. The responsibility for any shortcomings of this paper is, of course, mine alone.

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The Handicap Principle and the Argument of Subversion from Within

Abstract: This paper discusses the role of epistemic values in scientific discussions in the context of a cluster of debates within behavioural ecology. Based on Rasmus Winther's distinction between two styles of biological theorizing, formal and compositional biology, it examines the very disparate attitudes that various actors takes towards the *argument of subversion from within* (a classical argument against the evolution of altruism by group selection) in a set of related debates on group selection, altruism and the handicap principle. Using this set of debates as a case study, the paper argues that different applications of epistemic values was one of the factors behind the disagreements between John Maynard Smith and Amotz Zahavi over a number of important evolutionary issues. It also argues that these different applications were connected to important epistemological differences related in part (but not solely) to their disciplinary background. Apart from conflicting evolutionary views, these antagonists both differed in the confidence they ascribed to mathematical modeling and over the hereditary basis for altruistic behaviour. And finally, comparing these findings with Winther's original distinction, it concludes that although the division of biological theorizing into formal and compositional biology has some explanatory merit, the idiosyncrasies of *individual* scientists may play a pivotal role in the shaping of scientific controversies that is not captured within this theoretical scheme.

Introduction

How are epistemic values implemented in scientific discussions? The question of the role of epistemic values has been a focal point for the analysis of scientific practice for more than sixty years. Epistemic values are criteria for "good" scientific conduct, i.e. the criteria by which they distinguish good science from bad science, or "pseudo-science", and by which they evaluate the scientific quality of specific explanations, investigations or factual claims. As such, they purportedly serve an important function in the thinking and decision-making of scientist and permeate every aspect of the scientific process.

Most attempts to capture the role of epistemic values in science, has taken the scientific *collective* as its focal point of analysis. From this perspective philosophers, historians and sociologists of sciences has constructed a diversity of theoretical entities all designed in order to capture the normative properties of scientific communities. The theoretical entities designed with this purpose includes as diverse constructs as Merton's *CUDOS* norms; Kuhn's *disciplinary matrix*; Daston's *moral economies*, the *styles of* *reasoning* of Hacking, or even Ziman's descriptions of the *PLACE norms* for post-academic science.[117]

As to the role of individual choice in the establishment and application of preferred epistemic values within a scientific community, this tradition has in general been silent, although this does not mean that there has been no recognition of a level of individual idiosyncrasy in the application of epistemic values. Perhaps the most important of these recognitions came from Kuhn in his 1969 *Postscript* to the *Structure of Scientific Revolutions.* Here, Kuhn warned against believing that the application of epistemic values was a trivial affair. Although certain kinds of scientific judgments concerning, for instance accuracy might be relatively (though not entirely) stable from one time to another and among members of a scientific community, Kuhn noted that

> "… judgments of simplicity, consistency, plausibility, and so on often vary greatly from individual to individual. What was for Einstein an insupportable inconsistency, one that rendered the pursuit of normal science impossible, was for Bohr and others a difficulty that could be expected to work itself out by normal means." (Kuhn 1969, p. 184).

Although recognizing that collectivist approaches have delivered important contributions to our understanding of the dynamics of epistemic values in scientific practice, this paper's main analytical perspective is the relation between a collective's shared epistemic values and the idiosyncrasies of the individuals who apply them as means to various ends. The focal point of analysis is on two problems of behavioural ecology: the topic of altruism and the debate on the handicap principle. Taking its departure in the the analysis of styles of theorizing given by Winther (2005, 2006) and Baron (*in review*), as well as in the *argument of subversion from within* (a classical argument against the evolution of altruism by group selection), it examines the interplay between epistemic values, and other contextual factors such as scientific prestige, disciplinary background, factual beliefs and ontological commitments in a situation where a discipline is under the hegemony of a formal style of theorizing. The paper consists of six parts. The first part (*Two styles of biological theorizing: compositional and*

[117] A far from exhaustive list of important texts on this subject include Merton (1942); Kuhn (1969; 1977); Laudan (1984); Daston (1995) and Ziman (2000).

formal biology) describes Hacking's (2002) concept of scientific styles of reasoning, and, following Winther (2005; 2006), presents compositional and formal biology as two styles of theorizing within biology. The second part (*The Argument of Subversion from Within*) presents the argument of subversion from within and relates it to the classic discussion on group selection, at the same time pointing shortly to one of its important background assumptions. The third part (*The Handicap Principle*) introduces the handicap hypothesis and recounts the scientific controversy over its validity. The fourth part (*The controversy of "Indirect Selection": The Argument of Subversion from Within is subverted from within*) recounts Zahavi's development of the handicap hypothesis into a general attack on explanations of altruistic behaviour based upon reciprocal altruism, kin selection and group selection. Finally the fifth (*Now it's valid, now its not: the disparate attitudes towards the Argument of Subersion from Within*) and the sixth parts (*The idiosyncratic "style" of Amotz Zahavi*) seeks to extract the conflicting epistemic ideals employed by some of the key players engaged in these scientific discussions, and, based on this informative example, discusses how the application of epistemic values is connected to other contextual elements as mentioned above.

Two styles of biological theorizing: compositional and formal biology:

The concept of style has been employed in a variety of ways in the literature of science studies having caught the attention of scholars with somewhat disparate theoretical approaches. A classical work in this tradition was Fleck's *The Genesis of a Scientific Fact* (1935/1979). Here Fleck defined a thought style (German: *Denkstil*) as the "directed perception, with corresponding mental and objective assimilation of what has been so perceived" (Fleck 1935/1979, p. 99), noting that a thought style was characterized by common features in the problems of interest to the thought collective, by the judgment which the thought collectives considers evident, and by the methods which it applies its means of cognition. (Fleck 1935/1979, p. 99). Other uses of the style concept include Harwood's (1987) *national styles* in science or Maienschein's (1991) *epistemic styles.*[118]

[118] For a comparison of different approaches to scientific styles, see Vicedo (1995).

In recent years the style concept has been employed by scholars pursuing the idea that it is possible to identify a finite plurality of general methodologies in science that pervades across the boundaries of scientific communities. In a pioneering work, historian of science A. C. Crombie, undertook the daunting task of delivering a complete account of the western history of science since the early greeks, and identified six general "styles of thinking" - each of which he believed had played a central role in the development of certain scientific areas: 1) a style based on axiomatic postulation and mathematical proof; 2) a experimental style based on designed observation and measurement; 3) a style based on hypothetical modeling as a method of exploring the unknown properties of natural phenomena; 4) a taxonomic style using comparative methods to order the variety in any subject-matter; 5) a probalistic style based on the application statistical analysis; and finally 6) a style of historical derivation seeking to explore the origin and diversification of any subject- matter, whether language or organisms from the common source, and to explain the cause for that diversification (Crombie 1994, p. xi).

Building on the work of Crombie, philosopher of science Ian Hacking has attempted to explicate the content and meaning of the style concept and its bearing on our understanding of science. Preferring the term "styles of reasoning" to "styles of thinking" Hacking has argued that styles are constitutive of scientific work and embedded in contingent systems of thought that, within a given domain, sets the standard both for what is good scientific practice and how to evaluate the truth or falsehood of knowledge claims. According to Hacking the styles of reasoning that we employ determine what counts as objectivity, in the sense that they provide the frame and criteria that determine which kinds of questions and problems that are scientific legitimate, procedures for how to decide and distinguish between different possible approaches to solving these questions, as well as for deciding which kinds of solutions are scientific acceptable.

There is thus a strong normative component to every style of reasoning. But apart from adhering to a specific set of epistemic values or ideals, every style also contain a range of other component including specific possibilities for investigation, types of objects; new evidence; a vocabulary; laws or modalities; and, on occasion, new types of classification and new types of explanations (Hacking 2002, p. 189). There is a 'holistic' nature to styles of reasoning in the sense that as a concept it attempts to encompass all relevant components that are part of distinct ways of reasoning, hypothezising, evaluating, investigating, organizing, unifying, understanding, modeling and so on.

With this encompassing account of what a style is, it might be prudent to recount what a style is *not.* It is not a "theory of the world" that can be verified or falsified, at least not in any trivial sense. It might be that a style can be shown to be unfruitful, although the complete extinction of a style seems to be a rare incident.[119] Although the oldest of the six styles originally described by Crombie originated in Ancient Greece, Hacking notes that they are all still going strong.

Building heavily on Hackings styles of reasoning, Winther (2005, 2006) has identified two scientific styles within biology, alternately denoting them *styles of scientific investigation* (2005) or *styles of theorizing* (2006).[120] This identification is based on a conceptual distinction between *parts* and *laws* – a distinction that Winther believes is pivotal for understanding biological theorizing. Hence, much biology follow a style of theorizing that Winther denotes "compositional biology". Compositional biology is based on the notion of organic world as organized in parts and wholes, and focus on revealing their respective functions and capacities. This style tend to be employed in a disparate set of biological disciplines, including comparative morphology, functional morphology, developmental biology, cellular biology and molecular biology (Winther 2006, p. 471)

Although this style of theorizing is prevalent in many biological disciplines, Winther notes that most philosophers of biology has had their eyes focused on another style of theorizing, a style that Winther denotes "formal biology". This style of theorizing focuses on mathematical laws and models that represent quantitative relations among parameters and variables. Winther regards this style to be dominant in disciplines like theoretical ecology and theoretical population genetics.

Although certain natural domains tend to lend themselves to one style than the other, Winther also notes that most if not all natural domains can be explored using either

[119] Hacking gives two examples of possible ”dead styles”: Renaissance medicine and withchcraft (Hacking 2002, p 194-195)
[120] In the following I will use the latter term.

styles.[121] The important differences between different styles are neither the scientific disciplines, nor the natural domains to which they tend to be applied. Rather, it lies in their respective *methodologies* of theorizing. This also means that the prevalence of a specific style of theorizing within a given domain may be the result of historical accident rather than logical necessity. There may be instances where styles may hybridize and intertwine, or even coexist (Hacking 2002, p. 183; Winther 2005, p. 46, Baron *in review*). But the all-encompassing ambitions of each style ensures, along with their normative character, that conflict remains a likely result of encounters between adherents of different styles of theorizing.

With these theoretical tools now made available, we shall now focus on a cluster of evolutionary topics, the study of which has historically been a battlefield of proponents of different styles of theorizing. This cluster of problems is set within the domain of behavioural ecology and includes issues like evolutionary possibility of altruism, group selection and the handicap principle.

The Argument of Subversion from Within

The argument of subversion from within can be found in several versions in the scientific and popular literature. But the version that has been most widely read is probably the one that has been popularized by Richard Dawkins in *The Selfish Gene* (2006, p. 7-8), where it has been used to promote a genes-eye view of evolution, arguing that all apparent altruistic behaviour can be explained as inherently selfish mechanisms such as reciprocal altruism or kin selection. The argument has been hailed as detrimental to the group selection theory of Wynne-Edwards, which is interesting, since (as we shall shortly see) its validity is questionable. In the version popularized by Dawkins, the argument goes something like this: imagine a population consisting of individuals with two heritable evolutionary strategies A (altruism) and S (selfishness). In strategy A the individual allocates resources on order to help the reproductive success of other

[121] Cellular and developmental phenoma are mentioned as examples of natural domains that tend to lend themselves to one style (in this case compositional biology). However it is important to note that this should not be understood in an imperative fashion. Thus, important contribution to the understanding developmental processes has also been given by scientist employing a formal style analysis. Prominent examples of this can for instance be found in the writings of Stuart Kauffman (Winther 2006, p. 472; Kauffman 1993).

individuals even to the point where it may do it at its own expense. In strategy S, the individual always act in order to enhance its own reproductive success.

Now suppose that groups consisting of relatively more individuals with strategy A may be selectively superior to groups where strategy S is more frequent. At the same time individuals with strategy S are individually competitive superior to individuals with strategy A, because of the fact that in strategy S the individual allocates all resources in order to enhance its own reproductive success, whereas in strategy A, part of the resources is allocated for helping others. If there is just one selfish rebel prepared to exploit the altruism of the rest, then this individual has a comparative greater chance of having surviving offspring even in groups where strategy A is the predominating. After several generations of natural selection, the 'altruistic group' will therefore overrun by individuals with the selfish strategy. Dawkins notes that:

> "Even in groups of altruists there will almost certainly be a dissenting minority who refuse to make any sacrifice. If there is just one selfish rebel, prepared to exploit the altruism of the rest, then he, by definition, is more likely than they are to survive and have children. Each of these children will tend to inherit his selfish traits. After several generations of this natural selection, the 'altruistic group' will be overrun by selfish individuals, and will be indistinguishable from the selfish group" (Dawkins 2006, p. 7-8)

Although popularized by Dawkins the argument of subversion from within has a history dating back at least to Maynard Smith's famous "haystack paper" (1964) that was long considered canonical in establishing the apparent implausibility of group selection. Maynard Smith's haystack model was built around a fictitious species of mice that lives their entire lives in haystacks. According to this model, each haystack population is founded by a single fertilized female, the progeny of which mate within the haystack entirely among themselves for a number of generations. The colony of the haystack benefits from the presence of evolutionary altruists in such a way that the whole group breeds faster – but within the group the altruist themselves breed less than evolutionary selfish individuals in the same group. At the end of each year the colonies break up and all individuals mate randomly in a single large population before repeating the cycle. Based on these premises, Maynard Smith concluded that group selection might work under such circumstance. But in order for it to work, it was a necessary condition that a genetic component for altruistic behaviour had been previously established in the population. The problem, however, was to explain how such a situation could occur:

> "It cannot be pictured as spreading to all members of a group by natural selection, because if it could do that, it could equally well spread in a large population – either by individual selection or kin selection – and there is no need to invoke a special mechanism of group selection to explain it. Hence, the only way in which such a characteristic could spread to all members of a group would be by genetic drift. (There is also the possibility that it might spread through a group by cultural transmission, but this is unlikely to occur in any other species than man.) If this were to happen at all often, then the groups must be small (or else commonly re-established by single fertilized females or single pairs), the disadvantage of the characteristic to the individual slight, and the gene flow between groups small, because every time a group possessing the sociably desirable characteristic is 'infected' by a gene for anti-social behaviour, that gene is likely to spread through the group." Maynard Smith 1964, p. 1145)

Although Maynard Smith granted that these conditions may sometimes be satisfied, he also described them as "severe". Thus, the paper carried the general implication (or, in any case was received as carrying the general implication) that such a situation was unlikely and that group selection was therefore relatively unimportant for the general evolutionary picture.

A comparison between Maynard Smith's haystack model and Dawkin's account of the argument of subversion from within shows a subtle but vital difference that was to be exploited by a later generation of adherents of group selection. In Dawkin's account, the disappearance of altruists only occurs *after several generations.* But, as has been pointed out Sober and Wilson (1998), the altruists of Maynard Smith's haystack model was eliminated at a must faster rate:

> "…Maynard Smith added a simplifying assumption to the haystack model that amounts to a worst case scenario for group selection. He assumed that the altruistic gene not only declines in frequency but goes completely extinct in all groups that are initially mixed! Altruists survive only in haystacks established by altruistic females who have mated with altruistic males. Given such powerful within-group selection, Maynard Smith conclude that altruism could not plausible evolve by group selection." (Sober and Wilson 1998, p. 1970)

Given this, Sober and Wilson's response to the subversion of within argument against group selection have been to challenge the premises of its modeling conditions, and to work out the theoretical conditions, where group selection may be active despite the subversion from within of altruistic groups by selfish individuals. The result of these efforts has been published in a series of papers (see for example Sober 1991; Wilson and Sober 1994), and a major conclusion of theirs is that group selection is theoretically possible if the rate of group splitting and extinction are higher than fitness advantage of selfish individuals within groups. From a temporary position as ostracized from evolutionary biology, group selection has by now reentered evolutionary theory as a position that appears viable, although this, of course, doesn't mean that it is generally endorsed.

The premises for this development are themselves interesting. As described by Baron (*in review*) it reflects the rise of formal biology to a position of being a dominating style of theorizing within evolutionary biology – a position gained at the expense of a compositional style of theorizing.[122] Unlike his adversaries, Wynne-Edwards did not attempt to make a formalized model of group selection, and part of the perceived problem with group selection in the 1960's was the compositional manner in which it was put forward.[123] Only by accepting the hegemony of a formal style of theorizing as "the way to do it" did adherents of group selection convince evolutionary biologists to reconsider its viability, and it formed an integral part of the efforts taken by people such Michael Wade, David Sloan Wilson and Elliott Sober.

Of course, giving prevalence to a specific scientific style within a given scientific community is not without its dangers. While the formal style of theorizing may confer certain epistemic advantages to a scientific theory it also has weaknesses that may become straightjackets if not handled carefully. Perhaps a major weakness of the formal

[122] For further explication of these two biological styles of theorizing, see Winther 2005; 2006 as well as Baron (*in review*).

[123] As described by Baron (*in review*) Wynne-Edwards compositional perspective is expressed in his claim that the regulation of the population density (the *whole*) came about by the altruistic acts by the population's *parts* – the individuals. By virtue of their power of movement, he asserted, most animal have a predominant role in regulating their own population densities. Applying these principles to his own area of expertise, avians, he maintained that although food was almost always the critical limiting factor, birds were largely able to regulate their own population densities through social conventions connected to territory system and pecking order.

style lies in its indifference towards the complex properties of the entities whose activities it attempts to model. This indifference towards the ontology of the modeled entities, makes basic ontological inconsistencies harder to discover, since they are usually not addressed during the investigation process.[124] But this indifference does not mean that no ontological commitments are made. Within this area of behavioural ecology this is most clearly addressed in the "Phenotypic Gambit" of Alan Grafen:

> "The phenotypic gambit is to examine the evolutionary basis of a character as if the very simplest genetic system controlled it: as if there were a haploid loci at which each distinct strategy was represented by a distinct allele, as if the payoff rule gave the number of offspring for each allele, and as enough mutation occurred to allow each strategy the chance to invade." (Grafen 1984 p. 63-64).

As part of the model conditions, this approach assumes that altruistic behaviour is governed by what Ernst Mayr (1961, 1974) has called a "closed genetic program", where the control of the behaviour is entirely laid down in the genotype. This is in contrast with what Mayr has called an "open genetic program" that is constituted in such a way that it can incorporate additional information acquired through learning, conditioning or other expenses (Mayr 1974, p. 103).[125] Although not explicitly stated, this notion of a closed genetic program is a shared assumption of the kind of population genetical models that has been employed by adherents of a formal style of theorizing in this discussion. This may at first seem surprising, as altruism could very easily be conceived as kind of behaviour that could be informed by learning or conditioning. But for the biologist pursuing a formal strategy the modeling certainly becomes much easier when adopting this presumption. One might, of course, wonder, what became lost in the translation. In order to answer this, it may be useful to turn our attention to a biologist who has several times been at conflict with adherents of a formal style of theorizing, and the epistemic ideal that underlies it.

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[124] In fact, as we shall see, they may stay hidden even for people who have been within a field for years (or perhaps precisely because of this).

[125] See Mayr (1961; 1974) for an explication of this distinction. It should be noted that the concept of a genetic program itself is muchly critizised. See Keller (2000); the papers in Oyama, Griffiths and Gray (2001) and Neumann-Held and Rehmann Sutter (2006) – as well as below.

The Handicap Principle

Amotz Zahavi, a strict adherent of individual selection, has long been a staunch defender of the role of "verbal models" in evolutionary biology. The Israeli biologist is best known for his formulation of the *handicap principle* – a somewhat controversial hypothesis on the evolution of biological communication. Originally proposed in 1975[126] it aims to explain how reliable signaling may evolve between animals who could otherwise be thought to have a fitness-based interest in deceptive behavoiur. It is based on Darwin's theory of sexual selection (1871) that explains the existence of apparently detrimental characters (like, for instance the large unhandy tail of the male peacock) among animals to be the historical result of preference in mating choice (in this case in the mating choices of the female peacocks).

The basic premise of this hypothesis is the suggestion that reliable signals must be costly to the signaler, and that this cost of signaling exceeds what individuals not in possession (or in the possession of a weaker state) of the characters related to it, could afford. By being able to take this cost upon themselves, and still survive, high fitness individuals signal their superior quality to potential mates. It is precisely because these signals are costly that receivers of the signal know that the signal indicates high fitness. Otherwise the signaller would not be able to bear the cost of such extravagant signals. In the case of the male peacock the elongated strong-colored tail feathers bears several costs: they demand extra energy to develop and maintain; and does not provide the camouflage that is given to female peacocks (and, hence, give a higher risk of getting eaten by a predator). According to the handicap principle this cost is recognized by the female peacocks and this recognition forms the basis for their preferences for mating with peacocks with the longest and most extravagant tail feathers.

Since its inception the empirical possibility and generality of this explanation has been the subject of disagreement and debate. Early critics of the handicap principle were Maynard Smith (1976) and Davis and O'Donald (1976). Maynard Smith argued that for such a principle to work, it was a necessary condition that the inheritance of the handicap was limited to the sex displaying the handicap, in order to avoid that this fitness cost would be given to offspring of the mate choosing sex. Based on these considerations

[126] See Zahavi (1975, 1977) and Zahavi and Zahavi (1997).

Maynard Smith constructed a diploid 3-locus model, in which sex-limited inheritance of the handicap was a basic premise, and assumed that the handicap had an additive effect on fitness.[127] This model showed no separate increase in offspring fitness that could be ascribed to a handicap effect. In an equal manner Davis and O'Donald constructed a model to test the handicap hypothesis that assumed a selection regime where phenotypes are being selected for an optimum combination of characters. Their conclusion was that the cost of maintaining a handicap was so high that handicapped males could only gain a fitness advantage under extreme conditions of selection that were very unlikely to occur in nature.

Zahavi responded to these criticisms by sending a letter to the editor of *The Journal of Theoretical Biology* – where the critique had originally been published. A longer passage in the opening paragraph of this letter discloses some of his discomfort with a formal style of theorizing:

> "The model of the handicap principle has been disputed by Maynard Smith (1976) and Davis & O'Donald (1976). They claimed on the basis of mathematical models that the handicap principle cannot operate under normal conditions. I believe that in natural populations the need to advertise on the one hand and the need to check the reliability of the advertisement on the other hand result in the evolution of much more sophisticated mechanisms than the simple mathematical models investigated by Maynard Smith and Davis and O'Donald. In the following I shall point to some general considerations which were overlooked in their models. These may be just some of the conditions which allow for the widespread use of handicaps in nature." (Zahavi 1977, p. 693)

One of Zahavis complaints against the models of Maynard Smith and Davis & O'Donald was that they assumed a simple additive value of the handicap and the tested quality. The relationship between them may be more sophisticated however. For instance, one can assume that the handicap (that at the same time is the sexually attracting character) is present in all the population and that phenotypic manifestation of the handicap is adjusted to correlate to the phenotypic quality of the individual. These assumptions are not unreasonable and are probably the case in most sexually attracting

[127] In Maynard Smith's 3-locus model, a gene A caused male, but not female, to have the handicap; a gene B conferred high viability of both males and females, and a third gene C caused females to prefer males with gene A (the handicap).

characters. If such a correlation is kept, the advertisement of the individuals' quality will remain reliable, and should any individual, by mutation or genetic recombination, develop a handicap larger than it should, this genotype will be selected out, as it will be unable to bear the cost that accompanies it. In such a situation, Zahavi argued, the cost of maintaining the handicap would remain reduced thereby ruling out the main objections of Davis and O'Donald. As a final critique of the assumptions behind the mathematical models of Maynard Smith and Davis and O'Donald, Zahavi stated that although these models were not favorable for the evolution of handicaps, it was not difficult to build precise genetic models which would favor it. He went on to give a verbal explication for the premises for such a genetic model:

> "Assume that Aa is of a better quality than AA and aa are inferior to both of them. aa can survive to mate but it is not successful in its reproduction. Hence an individual which mates with aa damage its own reproduction as well. Potential mates should be interested to distinguish between Aa, AA and aa individuals. Assume a marker M which when together with aa kills but lowers slightly the survival of Aa or AA individuals. Such a marker which is a handicap to Aa and AA individuals, is also a good advertisement for them since it ensusres to potential mates that hey are not of the aa genotype. It is obvious that his model can operate in a population which is in a stable equilibrium." (Zahavi 1977, 604-605)

Zahavi's response was followed up by his Israeli colleague Ilan Eshel who came to his defense in another letter to the editor of the *Journal of Theoretical Biology.* Giving a lengthy critique of the assumptions of Davis and O'Donald's model, (and pointing out the problem of generations that were later to reappear in Sober and Wilson's critique of Maynard Smith's haystack model of group selection) he stated that:

> "Unfortunately, Davis & O'Donald considered only that part of the handicap-quality correlation that may develop *within one generation.* Tacitly (but quite crucially for their results), they assumed a permanent *linkage equilibrium* at birth – an assumption which, even in their model, becomes false after one generation. Moreover, presumably for the sake of mathematical convenience, they restricted their analysis to a very special situation in which the deep effect of the handicap is limited to a *linear* exaggeration of the carrier's deficiency in quality. Therefore, what they have shown is that without the cumulative effect of linkage disequilibrium, a linear effect of the handicap on the fitness of its carrier is not sufficient for the evolution of that handicap as a quality-marker." (Eshel 1978, p. 246)

In order to develop a model for a more discriminative effect of the handicap on the fitness of individuals of different quality, Eshel decided to adopt and expand on the 3-locus model of Maynard Smith, since, unlike the model of Davis and O'Donald, it allows for the most general effect of the handicap on various types. Based on the work of Maynard Smith, Eshel constructed a model that assumed that high quality was determined by a single dominant allele A at one locus, and that handicap was determined by a single dominant allele, B, at another non-linked locus (linkage was introduced later in the model). In a manner similar to Davis and O'Donald, Eshel started by investigating the possible advantages of choosing handicapped males concentrating on the choice of a non-handicapped female when the handicapped male was assumed to be heterozygote. Contrary to the findings of Davis and O'Donald, Eshel could conclude that a handicap effect was indeed possible given certain conditions. Thus, two important corrollaries could be extracted from Eshel's model. One was that natural selection will favor the tendency of females to choose handicapped males, from the first appearance of the handicap, even if the handicap expressed in both sexes, if the damage caused by a rare handicap is sufficiently low for high-quality individuals and sufficiently high for low-quality individuals. The other was that there will be a selective advantage for preferring handicapped males providing that the linkage between handicap and the quality-determining locus is tight enough and that the damage inflicted by the handicap on the high quality individuals is small enough. Eshel therefore concluded that the evolutionary significance of the handicap effect was still open to investigation:

> "What remains to be considered is the question of which assumption is qualitatively more relevant to natural situation and, to my judgement, the controversy is not yet settled by the suggested models." (Eshel 1978, p. 250)

Eshel's paper led Maynard Smith to conclude that he had been "overdogmatic" in his original rejection of the handicap hypothesis, although he still stated that he was unconvinced that this mechanism could account for the evolution of secondary fitness-reducing characters. In the wake of this statement a series of papers were published by several authors that attempted to model various aspects of the handicap effect.[128] In a review of these models, Maynard Smith retained a skeptical stance towards Zahavi's handicap hypothesis, but also, implicitly, gave a reason for preferring a formal style of theorizing, when he stated that it had always been difficult to know exactly what Zahavi had in mind, when he proposed the handicap hypothesis, since he did not offer any explicit genetic model of the phenomenon (Maynard Smith 1985, p. 3). In line with this he was later to state that

> "I was cynical about the idea when I first heard it, essentially because it was expressed in words rather than in a mathematical model. This may seem an odd reason, but I remain convinced that formal models are better than verbal ones, because they force the theorist to say precisely what he means." (Maynard Smith 2001)

Indeed it was the development of such formal models of the handicap effect that finally convinced Maynard Smith of its viability, and led to his public retraction of his resistance against it.[129] As described by Maynard Smith and Harper (2003) this process was facilitated by three models (Enquist 1985; Pomiankowski, 1987, Grafen 1990a; 1990b) in which the cost of signaling penalized less needy individuals or individuals with lower quality. But the decisive point was that Alan Grafen was able to bring the handicap effect successfully into the game-theoretic context that he himself had developed (Maynard Smith 1983). For Maynard Smith and adherents of a formal style of theorizing, the development of debate on the handicap principle (and the final acceptance of the handicap effect that was facilitated by the succesful models of Grafen and others) could thus be interpreted as confirming their view that formal and mathematical modeling was the right approach to settle evolutionary questions.[130] Zahavi, however, was to interpret this development quite differently.

The Controversy of "Indirect Selection": The Argument of Subversion from Within is subverted from within.

[128] See Hamilton and Zuk 1982; Eshel & Hamilton 1984, Kirkpartrick 1982; Dominey 1983
[129] This was done with a public announcement at a dinner at a Royal Society discussion meeting in London in 1992.
[130] Although it should be noted that Maynard Smith (according to Harper (2006, p. 204)) subsequently worried that he had single-handedly delayed the acceptance of the handicap principle for over a decade.

Looking back upon the controversy on the handicap hypothesis, a later Zahavi, expressed his gratitude towards Maynard Smith for agreeing to publish Zahavi's original paper, despite the fact he himself didn't believe in verbal models. He would even thank Maynard Smith for publishing his own rejection of the handicap principle along with Zahavis original paper, thereby bringing attention to the subject. However, he also reported being stung by the dismissal of verbal modeling that he had experienced from Maynard Smith and other theoreticians:

> "The simple argument of the handicap principle was considered by theoreticians to be 'intuitive'; they insisted on having mathematical models to show its operation in evolution. For some reason I cannot understand, logical models expressed verbally is often rejected as being 'intuitive'. (Zahavi 2003, p. 860).

The attitude expressed here indicates a deeper epistemological commitment to the importance of verbal reasoning that has been part and parcel of Zahavi's scientific views for several decades. This commitment is partly disclosed in the emphasis Zahavi's skeptical stance places towards the limits of mathematical modeling in his response to Maynard Smith (1976) and Davis 6 O'Donald.(1976). It was explicated more fully in a commentary in the ornithological journal *Auk,* entitled "Some comments on sociobiology", where Zahavi laid out his resistance towards some of the key concepts coming out from the work of biologists adhering to formal style of theorizing, namely "kin selection, reciprocal altruism, and the growing use of models of Evolutionary Stable Strategies." (Zahavi,1981, p. 413). Here, Zahavi contributing to a debate on the relation between avian studies and the sociobiological research program that had earlier been advocated by E. O Wilson (1975), argued that the genetic models that has been applied to social interactions in game-theoretic contexts (for instance dividing behaviour into to strategies: attack or flee) were much too simple. Depending upon the specific circumstances, the same individual might attack, threaten, flee, or avoid interaction altogether, and its reaction (so Zahavi argued) seemed to be determined by information gathered in the situation, rather than by a pre-set program that is activated by simple arbitrary signals (Zahavi 1981, p. 414). He also took the opportunity to speak out against the emphasis these models placed on cheating and manipulation in signaling, arguing that if signals are selected to have a cost that ensures their reliability, there would be little room for signal manipulation.[131]

On his resistance to kin selection, Zahavi remarked, based on his own empirical long term studies of the behaviour of the Arabian Babbler[132] that apparent altruistic behaviour often occurs among non-relatives, and that what look like altruistic activities do not necessarily increase the fitness of the individuals they help. However, it was in his arguments against reciprocal altruism that Zahavi pointed to a problem that apparently had not occurred to Dawkins or others who had used the argument of subversion from within as a rebuttal of group selection, and in favor of their own kin selectionist explanations:

> "The problem of reinforcing reciprocation is no less difficult than that of altruism; in fact it is the same problem in another disguise. Describing reciprocal interactions, even when it can be proved that all collabourators benefit, does not explain why one of the collabourators should not exploit the others" (Zahavi 1981, p. 414).

Originally directed towards reciprocal altruism, this argument would later be turned against *all* kinds of "indirect selection" (i.e. selection that is not directly of benefit to the individual) including not only reciprocal altruism (RA) and group selection (GS) but also kin selection (KS) as well. In an opinion paper from 1995, published in the *Journal of Avian Biology,* Zahavi advocated the handicap hypothesis as a general explanation for the existence of apparent altruism in nature, and at the same time dismissed competing "indirect" explanations, as susceptible to subversion from within. The paper was entitled "Altruism as a handicap – the limitations of kin selection and reciprocity ". Once again Zahavi dismissed game-theoretical models (here in the form of 'prisoner's dilemma) as too simple to account for anything relevant in the biological world (Zahavi 1995, p. 3) After shortly repeating the argument of subversion from within as it had been used against group selection (referring to Maynard Smith 1964), Zahavi

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[131] This is not a point on which Zahavi has gained general acceptance. See Getty 1998.

[132] The Arabian Babbler (*Turdoides squamiceps*) is a group-breeding songbird living in the Negev. It has a life-span of about 30 years.

claimed that both kin selection and reciprocal altruism suffered from the same weakness. As to the model of kin selection, Zahavi gave the following remarks:

"According to KS theory, altruism is based on a model of individual selection in which the gene is the selected unit (Dawkins 1989). The theory claims that the frequency of the gene for altruism increases in the population as a result of the altruistic behaviour, even though it decreases the reproduction of the altruist itself. Is this really so? The best way to expose the fallacy if this claim is to tell a variant of a story attributed to J. B. S. Haldane (1955) who suggested that if one of two brothers walking beside a river, were to fall into it and be in danger of drowning, it would seem reasonable for the other brother to risk his life somewhat to save the drowning brother, since by taking such a risk (i.e. decreasing his fitness), he may save his brother and increase the frequency of genes similar to his own in the following generation.
The instability of the model is clearly apparent if the same story is told with three or more brothers instead of two, walking along the river. It is obvious that if one of them jumps to the rescue, the other sibling (who does not risk himself), gains as much as the one who risks himself, but without any recurring cost. Thus in KS models, as in GS models, the total gain of the selfish brother (the social parasite), is higher than that of the altruist." (Zahavi 1995, p. 1)

As Zahavi had long been struggling to win legitimacy for his handicap hypothesis, it is perhaps not surprising that the extension of the handicap principle as a general explanation for altruism had to await the general acceptance it gained by Grafen's defense in his 1990 papers – a defense that itself ironically was formulated on the very game-theoretical foundations of which Zahavi had expressed his deep skepticism. Whereas others might interpret this development as confirming their adherence to formal and mathematical modeling, Zahavi undoubtedly saw this development as a vindication and victory of his own "verbal approach" against formal minded biologists, for he gave the following account of it:

"In 1990 Grafen formulated a mathematical model for the handicap principle, and thus made it acceptable to mathematically minded biologists and ethologists. However, Grafen also stated that the main biological conclusions of his papers were 'the same as those of Zahavi's original papers on the handicap principle' (Grafen 1990a) and that 'the handicap principle is a strategic principle, properly elucidated by game theory, but actually simple enogh that no formal elucidation is really required' (Grafen 1990b, page 541). Still, for some reason, biologists remained unimpressed by the logic of the verbal model, and accepted the handicap principle only when expressed in a complex mathematical model, which I and probably many other ethologists do not understand." (Zahavi 2003, p. 860).

Of course the 'reason' for preferring formal models, on which Zahavi did not elabourate, was stated repeatedly by Maynard Smith, namely that only formal models were precise enough to enable the scientist to state his argument clearly and without ambiguity. Zahavi, on his part, did not share Maynard Smith's confidence in formal models. Having experienced how unclear modeling assumptions could themselves contribute to confusing the issue[133] Zahavi felt a certain justification for his epistemic preference of "verbal models":

> "One small mistake in the logic of the verbal assumptions forming the basis of explicit mathematical models will create false, and most of those models are wrong not because of their mathematical technique but because of the false assumptions stated in English. The best theoreticians now supporting the handicap principle were building mathematical models that rejected it. Why should we believe in their ability to test theory better than done with verbal logic?" (Zahavi 1999, p. 115)

Thus, while Maynard Smith justified his preference of formal models on alleged precision and clarity, Zahavi would attack them for lacking exactly these features. For Zahavi, the adoption of formal modals meant that the mathematically untrained biologists would be excluded from the discussion. As he did not believe these models conferred any other advantages, this seemed to be an unnecessary price to pay.

Now its valid, now its not: the disparate attitudes towards the Argument of Subversion from Within.

For the reader, who have followed the account and disagreements above, it should be clear that the procedure by which scientists give judgment as to whether a given line of reasoning is deemed convincing is by no means a trivial affair. The most obvious

[133] The most clear illustration of this can be found be found in Parker's (1979) critique of Maynard Smith's (1976) first attempt to model the handicap principle – a paper whose full implication was only realized much later in the debate (Harper, 2003, p. 204). Parker pointed out that Maynard Smith's model was inappropriate because it assumed that the cost of bearing the handicap lowers the fitness of all males in the same proportion, However, the handicap hypothesis assumes that either the costs of signaling or the potential benefits obtained if the receiver response favorably, must be scaled "differentially" for different signalers. In the first case, an individual's high quality can only be signaled reliably, because high-quality individuals will gain a net-benefit, thanks to a lower cost oif signaling. In the second case, the individuals "need" can be reliable signaled because only genuinely needy individuals will gain enough to offset the costs. See also Harper 2006, p. 204.

example is the fact that Maynard Smith was only convinced of the validity of the Handicap hypothesis when it was accounted for within the framework of game-theory – a framework which Zahavi, the founder of the handicap principle, had earlier explicitly rejected. But one might also note how the argument of subversion from within, which had been pivotal in the rejection of Wynne-Edwards theory of group selection among a majority of biologists, did not carry the same convincing force when Zahavi directed it at their own "pet theories" - the theories of kin selection and reciprocal altruism. This is further illustrated by the fact that adherents of group selection such as Wilson and Sober (1994) were as equally quick to point to this similarity between kin and group selection, but instead of Zahavi they drew the *opposite* conclusion, namely that the argument of subversion from within was not decisive enough to reject either.

By now it might be prudent to ask what lies behind such differences in judgment. Now, there is of course an obvious element of scientific prestige that may be involved, as the various actors in this theatre may tend to adopt a line of reasoning that supports the position, they are already holding. Another obvious source of disagreement may be their different conceptions of epistemic values or ideals of what "proper" science is. We find the most prominent examples of this in a comparison of Maynard Smith's defense of formal models and Zahavi's defense of verbal models. As noted, Maynard Smith's defense of formal models rests on the identification of precision as the central epistemic value in his conception of how good science is done. Zahavi, however, did not share Maynard Smith's confidence in the alleged clarity and precision of mathematical models. In fact to the extent that Zahavi has commented on this issue, it would seem that he tend to consider mathematical modeling to be a rather obscure activity that risks muddling the understanding of the biological problem at hand. Precision and clarity are clearly not ubiquitous concepts, nor for that matter are many other epistemic values, upon which scientists base their reasoning.

Thus it is not only in the different priorities of epistemic values but also differences in their perceived implementation that is a source of disagreement here. But the question of how to make this implementation is itself a problem that impinges on a nexus of other factors, including factual claims, disciplinary training, and ontological commitments. Maynard Smith's confidence in the clarity and precision of formal mathemathical models as tools for scientific reasoning is a conviction he shared with his former mentor, J. B. S. Haldane, under whose supervision he was trained in theoretical population genetics.[134] Zahavi's argument that the behaviour of individuals is much to complex as to be captured adequately in ESS models is a conviction that he explicitly relates to his ornithological background and extensive empirical studies of the Arabian Babbler (As comparison, it would be harder to imagine, for instance, Zahavi taking an equally strong stance against kin selection theory, should he defend it in a context of, say, social insects).

As to the role of ontological commitments, it has already been noted that Zahavi did not share the assumption that altruistic behaviour is governed by a closed genetic program – an assumption that is a silent part of the modeling conditions of the models coming out of the phenotypic gambit approach. On the contrary, he explicitly rejected this stance, instead arguing for a high degree of flexibility and individual choice in instances where we observe apparent altruistic behaviour. One may further note that, like many opponents of group selection, Zahavi believed all apparent altruist to be inherently selfish. But unlike Dawkins and other promoters of a gene-eyes view of evolution he believes the individual, and not the gene, to be the basic unit of selfishness.

These differences in belief might help explain the different force the actors in this controversy attribute to Zahavi's argument that kin selection is subverted by selfish defection. For an adherent of a selfish gene's eye of evolution, it would make little sense that siblings should be tempted by defection, since they more or less share the same genes.[135] For Zahavi and other adherents of a strict "selfish individual" eye of evolution, it would of course equally make little sense to claim that this process would be operative in groups, but not in kin groups.

So much for open and closed genetic programs. Of course, the question remains whether the metaphor of a 'genetic program' is an adequate description at all in these situations. In Mayr's explication of a program, he defined it tentatively as "*coded or prearranged information that controls a process (or behaviour) leading it toward a given*

[134] In fact Maynard Smith defense against the attack of the ornithologist Amotz Zahavi resembles in a lot of ways Haldanes (1964) earlier defense of "bean-bags genetics" against the attack of ornithologist Ernst Mayr. (1959; 1963).
[135] Although one might of course argue that the temptation of defection lies in the fact that they do not necessarily share *all* their genes.

end.” (Mayr 1974, p. 102) and characterized a genetic program as containing not only a blueprint but also a set of instructions of how to use the information of the blueprint. With the molecular revolution in biology, and with more knowledge about the cellular machinery this characterization has become increasingly difficult to defend, however. For a number of years, several authors have been attacking not only the way various information metaphors (code, program, blueprint etc.) have been used to describe the role of DNA inheritance and development, but also the ontological claim of causal privilege that has been part of these descriptions as well.[136] A consequence of this critique is that the ambiguity of the gene concept has now been explicated much more clearly than previously, and it has now become clear that it is used in quite distinct different ways when confronting different problems in biology. Hence, one important analysis in this body of literature (Moss 2001) distinguishes between to very different applications of the gene concept: 1) The gene as a developmental resource (Gene-D): here the gene is conceived as a string of DNA coding for a polypeptide (or, in the case of alternative splicing for a set of polypeptides). This is the manner in which the gene concept is most often used by molecular biologists, and when used in this way, the gene’s phenotypic effect is unspecified and context dependent; 2) The gene as the heritable determinant of a specific phenotype (Gene-P): here the gene is conceived instrumentally as if it specified a specific phenotypic trait, even though we may be aware, that the genetic systems that underlies it may be much more complex. It is this conception of genes that underlies its application in the formal models that are common in population genetics and in discussions on altruism and group selection and (to the dismay of Zahavi) the handicap hypothesis. According to Moss, both of these applications can be used productively as explanatory strategies in biological research, albeit nothing good will result from their conflation:

> “The common use of two qualitatively different explanatory strategies, that is, that of Gene-P and that of Gene-D, which yet share the name “gene” predictably lends itself to much easy confusion. The notion that there exist such a thing as a gene that is *simultaneously* a specific nucleic acid template *and* a

[136] See Oyama 1985; 2001; Gray 1992; Giffiths & Gray 1994; Keller 1995; 2000; Moss 2001; and Neumann-Held 1999; 2001; 2006.

preformationistic determinant of an organismic phenotype (i.e. the genetic *blueprint* we hear so much about) is based on exactly this conflation." (Moss 2001, p. 89-90).

Where does this leave the approach of the phenotypic gambit? Although Moss states that Gene-P (which is as close as we get to the way the gene concept is applied in the models based on the phenotypic gambit) works fine, as long as it is used in insulation from claims that a gene corresponds to a particular DNA-string, this instrumental account of the gene concept would probably be less than satisfactory for adherents of the phenotypic gambit approach, many of whom have expressed unifying ambitions on behalf of biology.[137] Indeed, as Grafen noted, when describing the phenotypic gambit:

> "The behavioural ecologist has to hope in his ignorance that his method will work regardless of which particular genetic system underlies the character [he studies]. This raises two questions. First is it justified? Secondly is the assumption so powerful and plausible that a whole research strategy should be based on it?" (Grafen 1984, p. 63]

Writing in 1984, Grafen could, with some confidence, argue in favor of a positive reply to both of these questions. However, as the analysis of Moss and others illustrates, the days are over where such a position could be held without further defense. This is not to say that such a defense is necessarily unfeasible. It remains to be seen whether it is possible to reconciliate the different applications of the gene concepts into a coherent theoretical framework.[138] Although this question is beyond the scope of this paper, it should be noted that the implications of this problem are quite severe for the phenotypic gambit approach. Should this challenge of reconciliation ultimately be met with a negative result, it would entail either that one would have to give up the phenotypic gambit approach or that the explanatory power of this strategy would be restricted considerably.

The idiosyncratic "style" of Amotz Zahavi

[137] The most obvious case of this is of course E. O. Wilson's *Sociobiology: the new synthesis* (1975).
[138] Of course whether one actually *wishes* to reconciliate the different applications of the gene concept into a coherent theoretical framework, is a question that depends on whether one believes the theoretical unification of biology to be desirable at all. This is not a given. See for instance Griesemer (2006) for an attempt to explicate the relations between different theoretical perspectives in biology *without* unification.

Finally, while we have successfully identified John Maynard Smith as a prominent adherent of a formal style of theorizing, what are we to say about the idiosyncrasies of Amotz Zahavi? Can we, following Winther's characterization of styles, identify him as an adherent of a compositional style of theorizing (as he is clearly *not* advocating a formal style)? Is it for instance possible to identify *wholes and parts* in Zahavi's explanatory strategy?

Based on the previous pages, I believe that we *can* identify Zahavi as an adherent of a compositional style of theorizing. But his position also contains a number of unique features that reveal that there are limits to what this theoretical distinction (between formal and compositional biology) is able to account for. As noted earlier, compositional biology is based on the notion of organic world as organized in parts and wholes, and focus on revealing their respective functions and capacities. In an almost trivial sense, the handicap hypothesis is concerned with the feedback relation between a *whole,* the population, and the interaction of its *parts,* the individuals who either signal their quality through their handicaps, or are able to identify the quality of potential partner through the capacity of possessing an apparatus that enables them to interpret these signals in a biological meaningful way. However these features might also be said, say, about Darwin's original theory of natural selection – a theory that concerns itself with the feedback relation between a *whole,* the population, and the interaction of its *parts,* the individuals who compete on various capacities related to their fitness. Zahavi's argument that the behaviour of individuals as being "too complex" to model effectively and his adherence to individual selection *vís a vís* gene selection seems to echo the organicist arguments often been used by Ernst Mayr.[139] But one might also add that the nested hierarchical ordering of biological entities into parts and whole at different scalar levels (a hierachical ordering that one would otherwise expect to be a central feature in a compositional style of theorizing) plays no important role in Zahavi's writings. For Zahavi, the causal primacy is ascribed to the individual alone, and he is vehemently opposed to selectionist explanations based on the group above or the gene below. In this respect the explanatory strategy of Zahavi's equals Dawkins "genic reductionism" in its

[139] Mayr claims himself to be an organicist ("the paradigm that is dominant today" (Mayr 1997, p. 3). Mayr notes that the word organicim in its biological sense was coined by W.W. Ritter in 1919.

own "individualistic reductionism"[140] – and as pointed out by Harper (2003) this feature of Zahavi's writing had a tendency to provoke Maynard Smith whose evolutionary views actually were more pluralistic than his opponent – a fact that also serves as counter-example to the idea that the explanatory strategies of adherents of formal modeling operate with more restricted range of possible causal agents and processes, than biologists with a background in natural history.[141] As this example show, this is not necessarily the case.

Hence, the case of Amotz Zahavi shows that the theoretical scheme that divides biological theorizing into formal and compositional biology, although having some explanatory merit, is certainly not the whole story: The attitudes and idiosyncrasies of *individual* scientists may play an important role in the shaping of scientific controversies – a role that is not captured within these categories.

Acknowledgements: This paper was inspired primarily by talk and conversations with staff and associates of the Centre for Social Evolution at the University of Copenhagen. The Centre also provided a setting that gave me the opportunity to meet or attend to the talks of several prominent biologists that has been concerned with evolutionary altruism, group selection, the handicap principle and/or biological signaling. These include David Harper, Robert Trivers and Amotz Zahavi himself. I would also like to thank Claus Emmeche for giving an early critique of this paper, and Andrew Hamilton for leading me on the trail to the problems of Maynard Smith's original haystack model.

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[140] I call both of these explanatory strategies reductionist because they both insist that causal primacy must be ascribed to *one* type of biological entities (although the differ on *which* entity it is that deserves this honour) rather than several..

[141] Again, the most prominent example of this kind of organicist critique of formal modeling is Mayr's attack on "bean-bag" genetics.

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Section III: Paleontology

How do scientific controversies interact? Traditionally, this question has received little attention in the history, philosophy and sociology of science. The theoretical accounts of scientific collectives that were treated in Section I all had a tendency to treat the scientist as relating to a single scientific community, only.[142] For the student of scientific controversies, however, this delineation may seem rather strange. The recognition that 1) many complicated controversies are concerned with *clusters* of apparently unrelated (but in fact often deeply entangled) scientific problems; and 2) that many discussions take place in semi-independent communities which themselves are parts of larger epistemic collectives that transgress the boundaries of several disciplines, begs the question of what bearing this structure of 'semi-porosity' has on how various scientific claims are received and evaluated. What happens when a scientist (who, as we learned in Section II, may have his *own* individual idiosyncrasies in his applications of certain epistemic values) has to promote a certain line of reasoning convincingly in accord with the epistemic standards of several thought collectives, in a situation where these standards themselves may be subject to critique and unstable transformation?

It is questions such as these that are the focal point of the investigations of Section III. The set of related problems that are the subject of investigations here are connected with a debate (or rather, a set of related debates) related to the evolutionary interpretation and significance of the Cambrian fossils of the Burgess Shale fauna. Discovered in 1909, these fossils have been named as one of the 20th century's biggest paleontological discoveries. Being the first discovery of Cambrian fossils with their soft body parts preserved, they represent a window to life in Cambrian oceans from a time "shortly" (in geological time scales) after the first major radiation of multicellular animals (i.e. metazoans). Within the wider domain of evolutionary biology, it was Stephen Jay Gould, who was the first to bring them to widespread scientific and public attention. Basing his claims on the morphological reconstructions and systematic analyses of these animals done by Anglo-Saxon paleontogists in the 1970's and 1980's, Gould argued that the early

[142] This even goes for Fleck's original analysis of thought styles – although, as mentioned, it does open up the possibility that individuals are member of more than one thought collective.

Cambrian represented an unprecedented period of vast morphological diversity in animal evolution – and that this diversity was later decimated by a major extinction, never to return again. At the same time taking a skeptical view on the possibility for giving a satisfying adaptive explanation for this development, Gould argued that this scenario of early diversity and later decimation illustrated the major role of contingency in the shaping of life's evolutionary history.

This rather complicated evolutionary argument spawned a major interest in the significance of these fossils. However, it also spawned several scientific controversies, as the different elements of Gould's evolutionary claims were taken apart and subjected to scrutiny. It is this nexus of related problems that are the subject of the investigations in Section III. The primary problems included in this nexus are the role of contingency in evolution and the empirical claims of greater Cambrian disparity. But other scientific questions are entangled in this nexus as well. Thus, developments within systematics play an important part in the understanding the dynamics of these controversies, and so do other more "theoretical" evolutionary debate concerning punctuated equilibria, species selection, and adaptation.

In fact, by entering the domain of paleontology, we enter an area where some of the more skeptical views have been expressed concerning the merits of adaptive explanations. Among the reasons for this is no doubt that Gould, as the most famous practitioner of the field in the last part of the 20th century, himself was a prominent campaigner against the perceived excesses of orthodox adaptationism. But it may also pertain to the fact that the disciplinary training of most paleontologists has a strong geological component at the expense of many biological disciplines like, say, physiology, and behavioural ecology – were the emphasis on adaptive explanations has traditionally been stronger. One might speculate whether this lack of exposure to 'adaptationist' thinking has inclined some paleontologists to be less enthusiastic about the explanatory merit of such an approach.[143] In any case, Gould is not the only paleontologist who has taken a somewhat relaxed approach to the merits of adaptive explanations. Other

[143] Depending on the choice of perspective, such a situation may, of course, either be regarded as a weakness ('paleontologists lack the knowledge and insight necessary for fully appreciating the role of adaptation in evolution') or a strength ('paleontologist are free from the adaptionist indoctrination that has affected the minds of the majority of biologists').

prominent paleontologists with a similar relaxed attitude to adaptation include, for instance, the dinosaur specialist Jack Horner, who has been advancing the thesis that the feeding strategy of *Tyrannosaurus Rex* (by many regarded as *the* top predator of the late Cretaceous) primarily was that of a scavenger (Horner 1994).[144]

This situation makes the domain of paleontology a good candidate for a comparative study that can be contrasted with the domain of behavioural ecology. Although both of these areas of inquiry fall within what we may call "natural history", the theoretical settings in which they are embedded are very disparate. This become all the more clearer when we regard the two 'problem clusters' that are under scrutiny. As described earlier the cluster of problems that were under investigation in Section II includes the topics of altruism, group selection and the validity of the handicap hypothesis. The clusters investigated in Section III includes the topics of contingency (and, hence, adaptaption), morphological disparity, as well as considerations on the tempo of evolution (punctuated equilibria) and systematics. Taken together these two clusters encompass a number of scientific problems that impinges on a very wide range of important disciplines in evolutionary biology.[145]

Like Section II, the main part of Section III consists of two papers. The first paper (*Epistemic values in the Burgess Shale debate*) can to some extent be regarded as a sort of 'twin paper' to the second paper in Section II (*The Handicap Principle and the Argument of Subversion from Within*). Like this paper, it explores the role of individual idiosyncrasy in this application of epistemic values – this time in the context of a discipline (paleontology) seeking to establish scientific authority within the larger domain of evolutionary biology. Focusing on the repeated claims of paleontologists that the study of fossils provides their discipline a 'privileged historical perspective', not shared with students of the extant biosphere, the first part of the paper explores how paleontologists, in their attempt to implement this perspective, has shifted between two stratetegies that employ opposing views on the classical positivist and physicalist ideal of science. The

[144] I would like to emphasize, that I am not hereby claiming that all, or even most, paleontologists are taking this attitude toward adaptive explanations. On the contrary, I believe that many paleontologists are quite happy with 'orthodox adaptationism.' This is certainly the case for Simon Conway Morris, who will appear shortly as Gould's main adversary in the debate on contingency.

[145] Included here is not only behavioural ecology and paleontology but also e.g. population genetics (who provided the models top discuss the handicap hypothesis), and systematics (whose methods are pivotal for the taxononomic interpretion hat led to the claims of higher Cambrian disparity).

second part of the paper addresses this claim of privileged access to the historical dimension of evolution in a situation where an independent theoretical upheaval (in this case within systematics) completely shifts the standards for evaluating the legitimacy of various knowledge claims within the epistemic problem at hand. The paper concludes that although the various strategies employed to defend this claim of privileged access have themselves been disparate (and to some extent even contradictory), they all have in common, that each strategy impinge on the acceptance of a specific epistemic ideal or set of values - and that the success of failure of this strategy depends on the compability of this epistemic ideal with the surrounding community of scientists.

Exploring this last point, the second paper (*A web of controversies: complexity in the Burgess Shale debate*) argues that controversies within different domains may interact as to create a situation of "complicated intricacies", where the practicing scientist has to navigate through the standards of multiple scientific thought collectives. Each of these collectives may to some extents have its own epistemic dynamic - complete with a specific set of theoretical background assumptions; certain peculiarities of practice and some fairly negotiated standards for investigation and explanation. But occasionally, the intellectual development in one of these collectives may "spill over" with far reaching consequences for the treatment of apparently independent epistemic problems that are under scrutiny in other scientific thought collectives. This analysis demonstrates that the traditional encapsulated approach, where the practicing scientist are treated as members of a single enclosed thought collective that stands intellectually isolated from other similar entities (unless the discipline is in a state of paradigmatic crisis) are inadequate in explaining the complicated relations and interaction between different domains of intellectual inquiry.

As noted in the introduction of this thesis, the case-study of the Burgess Shale debates presented here is based on an earlier publication in Danish (Baron 2004). It should be noted though, that the theoretical stance defended in the two papers of Section III is somewhat different than the one defended by Baron (2004). The original analysis was based primarily on an elabouration of Kuhn's theory of paradigms, and Daston's concept of the moral economies of science. In recent years, however, I have come to doubt whether I, by emplying this theoretical scheme, has in fact been stretching its analytical tools to the extent where they are no longer recognizable. By explicating the multifold and disparate ways Kuhn's theory of paradigms has been applied in the study of a variety of academic disciplines, a recent Danish anthology (Andersen and Faye 2006) has cast serious doubt in the mind of this author, on how many transformations and stretchings this theory (and the concepts connected to it) can undergo, without losing its explanatory power.[146] Add to this the fact that a closer analysis of the moral economy concept reveals several tensions (as described in Section I) that gives us reason to doubt its coherency, I have been compelled to a certain skepticism: do we *really* need the bulk of these theoretical perspectives in order to understand what is going on in the Burgess Shale debates?

With these considerations in mind I have adopted a somewhat minimalistic approach to the choice of theoretical perspectives: include only what is absolutely necessary.for understanding the pivotal points of the case study. Accordingly the "theoretical" perspective adopted in the first paper of this section is limited to include Kuhn's claim (made as part of his explication of the *disciplinary matrix*), that there may be a strong element of idiosyncrasy in the individual application of epistemic values. As to the second paper, I have adopted an approach based primarily on an elabouration of Fleck's concept of thought collective (where it is extended to include the possibility that an individual may be a member (or has to navigate through the standards of) several *scientific* thought collectives. These approaches may appear unsatisfying as theoretical accounts of the role of epistemic values in scientific controversies, but I believe that they are adequate enough to help uncovering their role in this specific case-study.

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[146] Ironically the most elabourate account of the 'sloppiness' by which Kuhnian concepts have been applied in science studies (Emmeche 2006) is actually quite sympathetic towards the approach adopted in Baron (2004) – citing it as an example of how Kuhn's theory of paradigms has been used constructively to uncover underlying background presumptions in evolutionary biology (Emmeche 2006, p. 114).

Horner, J.R. 1994. Steak knives, beady eyes, and tiny little arms (a portrait of *Tyrannosaurus* as a scavenger). *The Paleontological Society Special Publication* 7: 157–164.

Studies in History and Philosophy of Biological and Biomedical Sciences 40 (2009) 286–295

Contents lists available at ScienceDirect

Studies in History and Philosophy of Biological and Biomedical Sciences

journal homepage: www.elsevier.com/locate/shpsc

Epistemic values in the Burgess Shale debate

Christian Baron

Center for the Philosophy of Nature and Science Studies, University of Copenhagen, Blegdamsvej 17, 2100 København Ø, Denmark

ARTICLE INFO

Article history:
Received 29 November 2008
Received in revised form 16 March 2009

Keywords:
Epistemic values
Paleontology
Burgess Shale
Historical dimension

ABSTRACT

Focusing primarily on papers and books discussing the evolutionary and systematic interpretation of the Cambrian animal fossils from the Burgess Shale fauna, this paper explores the role of epistemic values in the context of a discipline (paleontology) striving to establish scientific authority within a larger domain of epistemic problems and issues (evolutionary biology). The focal point of this analysis is the repeated claims by paleontologists that the study of fossils gives their discipline a unique 'historical dimension' that makes it possible for them to unravel important aspects of evolution invisible to scientists who study the extant biosphere. The first part of the paper explores the shifting of emphasis in the writings of paleontologists between two strategies that employ opposing views on the classical positivist and physicalist ideal of science. The second part analyzes paleontologists' claims of privileged access to life's historical dimension in a situation where a theoretical upheaval occurring independent of the epistemical problem at hand completely shifts the standards for evaluating the legitimacy of various knowledge claims. Though the various strategies employed in defending the privileged historical perspective of paleontology have been disparate and, to an extent contradictory, each impinges on the acceptance of a specific epistemic ideal or set of values and success or failure of each depends on the compatibility of this ideal with the surrounding community of scientists.

When citing this paper, please use the full journal title *Studies in History and Philosophy of Biological and Biomedical Sciences*

1. Introduction

What role do epistemic values play in science? This question has been a focal point for analyzing scientific practice for more than sixty years. Epistemic values are the criteria by which scientists evaluate whether their findings may be considered to have a sound basis, and to distinguish good science from pseudo-science. As criteria for good scientific conduct, epistemic values purportedly serve an important function in the thinking and actions of scientists and permeate every aspect of the scientific process. Analyses of these normative aspects of science have typically been based on an understanding of epistemic values as being a property of scientific *collectives*.[1] The theoretical framework that has been proposed based on this community level perspective includes such diverse constructs as the *CUDOS*; the *Disciplinary Matrix*; Daston's *Moral economies* or even Ziman's descriptions of the *PLACE norms* for post-academic science.

This is not to say that there has been no recognition of a level of individual choice in the establishment of preferred epistemic value within a scientific community. Perhaps the most important came from Kuhn in his 1969 *Postscript* to the *Structure of scientific revolutions*. Here Kuhn argued for a strong element of individual idiosyncracy in the application of epistemic values when he noted that values such as accuracy or consistency could be understood, applied or prioritized differently among the members of a scientific community. However, defending himself against charges that his position led to a completely relativist and irrational view of science, Kuhn also argued that because these values were shared by the scientific collective, they still had a significant function as guiding principles even when they were not used in a unanimous way. The fact that epistemic values could be applied in various ways did not mean that they could be applied in any manner chosen by the applicant.

E-mail address: baron@nbi.dk

[1] A far from exhaustive list of important texts on this subject include Merton (1942); Kuhn (1996 [1969], 1977); Laudan (1984); Daston (1995); Ziman (2000).

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doi:10.1016/j.shpsc.2009.09.008

Though recognizing the important contributions of collectivist approaches to the understanding of the dynamics of epistemic values in scientific practice, this paper takes its departure in the relation between a collective's shared epistemic values and the idiosyncrasies of the individuals who apply them as means to various ends. It explores the role of epistemic values in the context of a discipline (paleontology) striving to establish scientific authority within a larger domain of epistemic problems and issues (evolutionary biology). This analysis focuses on the repeated claim by paleontologists that the study of fossils gives their discipline a unique 'historical dimension' that makes it possible for them to unravel important aspects of evolution invisible to scientists who study the extant biosphere. Focusing primarily on papers and books discussing the evolutionary and systematic interpretation of the Cambrian animal fossils from the Burgess Shale fauna, various strategies of implanting this historical perspective will be explored. As will be clear the strategies employed in defending the privileged historical perspective of paleontology are disparate, and to some extent contradictory. However, these strategies share a common thread: each of them impinges on the acceptance of a specific epistemic ideal or set of values, and their success or failure depends on the compatibility of this ideal with those of the surrounding community of scientists.

This paper is divided in two major parts. The first part ('Paleobiology between nomothetic physicalism and idiographic independence') explores the shift in emphasis within the writings of paleontologists between two strategies that employ opposing views on the classical positivist and physicalist ideal of science. One of them follows an 'appeasement policy' towards this ideal, and attempts to demonstrate that palaeontology has its own set of general 'historical' principles and laws. The other strategy outright reject this ideal, arguing instead the special 'historical perspective' of paleontology lies in its focus on unique historical coincidence.

The second part of this paper ('Neontology and the historical dimension in systematic crossfire') analyzes a polemic related to paleontologist's claim of privileged access to life's historical dimension in a situation, where a theoretical upheaval (in this case within systematics), occurring independently of the epistemic problem at hand, completely shifts the standards for evaluating the legitimacy of various knowledge claims.

2. Paleobiology between nomothetic physicalism and idiographic independence

The discipline of paleontology has traditionally led a difficult life in evolutionary biology. Darwin saw the virtual absence of intermediate forms as a problem for his theory of descent and he dedicated an entire chapter in *On the origin of species* to this problem, arguing that the available fossil remains were too insufficient to provide a reasonably accurate picture of biological evolution. Since then, this view has troubled palaeontologists who attempted to join discussions in evolutionary theory.[2]

Another stumbling block for paleontogists wishing to enter evolutionary debates has been the classic positivist ideal of science, which played an important role in the unification attempts within biology that ultimately led to the establishment of the modern synthesis.[3] There are several historical sources for this ideal, which can be found more or less explicitly in papers and other forms of public statements from scientists and philosophers of science in the nineteenth and twentieth centuries. It forms in part the attempts of Auguste Comte to create the framework for a unified science, where the common goal (whether in physics or sociology) is the creation of general laws, and his famous hierarchy of the sciences, where physics was hailed as a discipline generating the highest degree of certain knowledge. Perhaps the clearest articulation of this ideal came from Kant, for whom the physicist Isaac Newton epitomized the exemplary model for how science should be performed, and accordingly declared that any doctrine about the natural world only contains true and valuable science to the extent that is contains mathematics. Similar claims can be found in the writings of physicists, perhaps most notoriously in the famous remark by the physicist Ernest Rutherford that there exists but one kind of science, this being physics, while the rest is 'stamp collecting'.[4]

In the classical positivist conception of the hierarchy of sciences disciplines paleontology and geology are hardly mentioned at all.[5] But there is hardly any doubt that, if asked, the proponents of this view of science would place paleontology (and perhaps geology[6]) far down the list and definitely below biology. In the controversy over the great mass extinction at the Cretaceous–Tertiary boundary, the physicist Louis Alvarez, founder of the meteorite impact theory, took every opportunity to use this hierarchy against his paleontologist opponents. In an interview with the New York Times he accordingly characterized them as 'stamp collectors', obviously hinting that their arguments were not truly 'scientific'.[7]

Lacking a prominent status as a biological discipline in its own right, palaeontologists have been compelled to view themselves as belonging to a sub-discipline of geology. Here paleontology has especially contributed to the development of methods for correlating stratigraphical layers at different localities.[8]

Since the late 1960s, a growing dissatisfaction with this situation has emerged amongst paleontologists. Several were involved in attempts to establish a stronger platform for their discipline within evolutionary biology.[9] These efforts came primarily from Anglo-Saxon palaeontologists—initially American, but later also British scientists—and they correlate in time both with a number of rather successful attempts to make palaeontology more visible in the eyes of the general public (such as dinosaur research) and with the financial cuts that hit American science under the Nixon administration in the 1970s and British natural science under Thatcher in the 1980s.[10] Being already placed at the lower end of the scientific hierarchy and, before the blooming 'dinosaur industry', with very limited commercial assets, the threat of cutting positions and funds must have been most strongly felt in paleontology and must accordingly have been a motivating factor in trying to change the status of the discipline.[11]

From a sociological perspective, these efforts can be seen as political strategies to counter the threat of budget cuts. Central in these efforts has been the claim that the study of fossils gave paleontologists a unique 'historical perspective' on life that makes it possible for them to discover important aspects of evolution that were otherwise invisible to scientists focusing on the extant biosphere. As will be clear from the following however, very different

2 Darwin (1859), pp. 279 ff.; Stanley (1979), p. 4.

3 See Smocovitis (1995), pp. 97–171, for a thorough analysis of the relationship between the positivistic ideal of science and the establishment of the modern synthesis.

4 Comte (1971 [1865]), p. 24; Kant (1988 [1790]); Zammito (1992), p. 191, p. 207. Rutherford's quote about stamp collecting can be found in Blackett (1962), p. 108.

5 In fact, in Comte's own version of this hierarchy the sequence is physics, chemistry, biology, sociology (Comte, 1972).

6 This characterization of geology as a 'soft science' may be somewhat misleading, as geology also contains the 'harder' subdisciplines of sedimentology and petrology.

7 Gould (1989), p. 281.

8 Stanley (1979), p. 5.

9 See Gould (1992), pp. 54–84, for an elaboration of this point.

10 See Walsh (1970) for a comment on the US budget cuts during the Nixon administration and Turney (1987) for a comment on the UK budget cuts during the Thatcher administration.

11 See Kesling (2009) for an example of the impact of budget cuts during this period for the Museum of Paleontology at the University of Michigan.

and, with respect to the epistemic ideals utilized, internally opposed strategies have been employed by various paleontologists in their attempt to implement this historical perspective, even at times by the same author. Thus one strategy has been to attempt to demonstrate that palaeontology follows and lives up to the classical positivist ideal of sciences and that, like physics, it strives for general principles and laws. Another strategy has been to reject this ideal as a universal measure for science instead arguing for the autonomy of palaeontology in being an 'idiographic discipline'.

2.1. A preliminary investigation: Gould and the Models in paleobiology

The revival of the debate on the tempo of evolution within paleontology (and its subsequent hype into what for some time seemed to be a full-fledged attack on the modern synthesis) became the first prominent result of Anglo-Saxon paleontologists' efforts to establish a stronger platform for their discipline within evolutionary biology—or perhaps initially it was more an attempt to establish a stronger platform for biological and evolutionary research *within paleontology*. The pace of evolution had been a focal point of disagreement within evolutionary biology in the decades around 1900,[12] but with the advent of the modern synthesis it seemed to be a somewhat dead issue in Anglo-Saxon paleontology by the end of the 1960s, with the last major contributions coming from the works of G. G. Simpson.[13]

This was about to change with the model of evolution that was explicated under the name 'punctuated equilibria' in a paper by Eldredge & Gould in the 1972 anthology *Models in paleobiology*. The model itself originated as an extension of Ernst Mayr's idea of speciation as being the result of genetic revolutions within small peripheral isolated populations. Spelling out the logical consequences of this model Eldredge and Gould argued that the existence of gaps in the fossil record was the natural result of speciation being a process of rapid transformations of small isolated populations, and that traditional perceptions of the ideal record as consisting of a set infinitely graded forms was a chimera.[14]

Even though the original articulation of the punctuational model had appeared already in an earlier paper by Eldredge,[15] it was Eldredge & Gould's explication that gave the theory the publicity that made it a focal point. In the introduction, the editor, Thomas Schopf, stated that *Models in paleobiology* was an attempt to demonstrate the relevance of models in paleontological work in order to counter a traditional empiricist tendency merely to collect and organize fossils into taxonomic groups without also involving more general theoretical considerations. The centrality of a *model* based approach in the anthology formed part of this attempt to 'biologize' paleontology and liberate it from being only a technical method or subdiscipline of geology—thus revealing an underlying commitment to the positivist unity of the sciences and to a law-based ideal of science.[16] This vision which sought to establish paleontology as a nomothetic[17] discipline was later explored during a meeting at the Marine Biological Laboratory at Woods Hole, Massachusetts in late 1972 which, apart from the participation of Gould and Schopf, also benefited from the participation of several prominent American palaeontologists (and one ecologist) with an interest in the application of quantitative methods and techniques on evolutionary questions, including David Raup, Daniel Simberloff and (on the last day) Jack Sepkoski. Among the results of these collaborative efforts was the founding of the journal *Paleobiology*, and several papers attempting to put these quantitative principles into practice.[18]

The building of the punctuated equilibria debate from being a 'strictly' paleontological concern into a controversy with stakes in evolutionary biology only took place in the mid 1970s.[19] That development was primarily facilitated by the advent of the theory of species selection though attempts to criticize the punctuational model on empirical grounds also played a role. The theory of species selection takes its departure in the idea of speciation as being a fairly 'stochastic' event—the result of random drift and adaptation to the local conditions of small isolated population. In such a case, long term trends in the evolution of a lineage might display epiphenomena quite independent of the immediate adaptive needs of individual species—showing for instance an overall trend towards reduced size, despite adaptive pressure toward increased size within each individual species. Such a scenario could function if some branches within a lineage had higher speciation or extinction rates than others.[20]

By the end of the 1970s the notion of a 'decoupling' of different levels in evolution entailed in this idea became a focal point for paleontologists arguing that their discipline had a privileged epistemic access to important factors in evolution which were not readily accessible by studying the extant biosphere. Implicated in this claim was the contention that 'microevolutionary' processes (that is, processes *within* populations, including natural selections, genetic drift, migrations and so on) were unable to explain the higher course of evolution, and that higher level 'macro-evolutionary processes' like species selection were needed in order to understand the origin and extinction of major lineages. Among the most prominent proponents of this contention was Gould, who by 1980 was arguing that the modern synthesis was giving way to a new and general theory of evolution that was based on a hierarchical framework and recognized different levels of evolutionary processes which were epistemically and ontologically decoupled from each other. Embedded within this theoretical framework was the promise and ambition of a macroevolutionary research program that would turn paleontology (or rather *paleobiology*) into a model based nomothetic discipline.[21]

2.2. Contingency and the nature of history

In 1980 Gould was preoccupied with the explication of general principles for a hierarchical theory of evolution; by 1990 he had clearly shifted emphasis. This was most clearly reflected in the 1989 book *Wonderful life: The Burgess Shale and the nature of history*, where Gould described the systematic investigations of Cambrian metazoans from the Burgess Shale—a fossil locality situated in the Yoho National park in British Columbia in the Canadian Rocky Mountains. In *Wonderful life* (a bestseller which introduced Cambrian fossils to scientific audiences and to the public) Gould argued

[12] See Bowler (1983) for a thorough analysis of the situation in evolutionary biology around 1900.
[13] See Simpson (1944, 1953).
[14] Schopf (1972), pp. 3–7; Eldredge & Gould (1972), pp. 82–98.
[15] Eldredge (1971), pp. 156–167.
[16] See the Introduction in Schopf (1972), pp. 3–7, for an elaboration of this agenda.
[17] 'Nomothetic' simply means 'law-producing'.
[18] Sepkoski (2005), p. 226. For an example of an attempt to apply quantitative methods (in the form stochastic models) to evolutionary problems in paleontology, see Raup & Gould (1974).
[19] See Ruse (2000), pp. 234–237, for an account of this development.
[20] For the most prominent empirically based critique of the punctuated eqilibria model at the time came, see Gingerich (1974, 1976). The theory of species selection was first fully articulated by Stanley (1975, 1979). For a defence and outline of the philosophical implications of species selection, see Lloyd & Gould (1993).
[21] Gould (1980a,b).

that these fossils had a special significance for our understanding of impact of history on the major evolutionary course of life on Earth. Taking the fossil reconstructions of the so called 'Cambridge team' that began in the middle of the 1960s under the leadership of the trilobite paleontologist Harry B. Whittington as his point of departure, Gould contended that the early Cambrian had been a period of 'evolutionary experimentation' in body plans leading to the radiation of a fauna of 'weird wonders'—many of which went extinct at the end of the Cambrian. Though believing that the conventional explanation of the Cambrian radiation as a filling of empty niches does capture important processes in this event, Gould found this to be inadequate to explain the origin of the allegedly extraordinary range of anatomical disparity found in the Burgess Shale material. Although advocating this principle of early disparity and later decimation to be a general macroevolutionary principle he also believed that a unique sequence of the events led to the Cambrian radiation, and that part of the explanation behind the apparent explosion was a greater evolutionary potential of Cambrian metazoans as compared to later periods.[22]

According to Gould this Cambrian scenario reveals (and this is the main evolutionary point in *Wonderful life*) the decisive role of contingency in the major course of evolution. In the last chapter of *Wonderful life* Gould presents a series of counter-factuals to the history of life on Earth. In a series of thought-experiments Gould tries to give an illustration of what life on Earth might have looked like, if the history of life was reset at various historical periods and ran again with different outcomes. By presenting scenarios based on questions like 'what if the eukaryot cell had never evolved?' or 'what if the Dinosaur fauna hadn't become extinct?' Gould attempted to illustrate the potential impact of contingency on evolution, arguing that 'replaying the tape of life', life on Earth could have been radically different if particular historical events had slightly different outcomes.

Whereas the early Gould of the 1970s was arguing that the special 'historical dimension' of paleontology lay in the ability to discover general macroevolutionary processes like species selection, the Gould of *Wonderful life* argued that the special 'historical dimension' of paleontology lies in the ability to disclose the importance of the unique historical coincidences that he believes are essential for the historical course of life's evolution on Earth. This development is facilitated by a shift from an appeasement policy towards a physicalist ideal of science, to outright rejection. Criticizing the physicalist ideal as a 'stereotypical' conception of natural science, the later Gould argues that a law based ideal of science becomes inadequate when it comes to understanding complex historical developments. To reach such an understanding, general laws or processes must be complemented with the narrative reconstruction of unique past events, and the Gould of *Wonderful life* commits himself to an understanding of science that gives legitimacy to idiographic as well as nomothetic approaches to explanation.[23]

The intellectual developments behind this shift of emphasis is interesting in itself, as it is an exemplary demonstration of the use of various polemical means to further specific scientific agendas within the paleontological community. It is connected to the famous 1979 'Spandrels' paper that was jointly authored by Gould and the population geneticist Richard Lewontin. Here, the authors attacked what they perceived to be the ubiquitous adaptationism of the scientific practice of their fellow biologists, claiming that they often unreflectively ascribed particular adaptive properties to the origin of every single part of an organism.[24]

There is probably every reason to suggest that Gould conceived his adaptationist critique as a support for the macroevolutionary research program he helped formulate in the 1970s. A conception of organisms as suboptimally adapted helps solve some of the logical problems left by the punctuated equilibria model and the theory of species selection with respect to traditional Darwinian thinking. If species were optimally (or close to optimally[25]) adapted to their environment, then it would make little sense to imagine (as is inherent in the punctuationalist model) that an ancestor-species could be outcompeted in its homerange by a descendant-species that originated as a small peripheral population that was geographically isolated. However, this problem disappears if we grant the possibility that species may be suboptimally adapted, with ample room left for adaptive improvement. Likewise it is difficult to imagine an independent macroevolutionary level of species selection if organisms are optimally adapted. In such a case, it would be difficult to argue for any causal decoupling between within-population processes and higher level trends. These would then presumably be an extension of within-population selection towards optimal fitness.

However, the adaptationist critique by Gould was soon to be hijacked in a polemical attack on the same macroevolutionary research program which it was constructed to support. Simon Conway Morris, who was responsible for the non-arthopod invertebrates during the early reconstructions of the Cambridge team in the 1970s, was by the 1980s ready to turn his attention to the ecology and origin of the Cambrian fauna revealed in the Burgess Shale type faunas. Though subscribing to a similar interpretation of the Cambrian as a period of 'experimentation' in new metazoan body plans that was later reduced by extinctions, Conway Morris's explanation of these events was, in contrast to Gould's in *Wonderful life*, based on a traditional ecological neo-Darwinian framework. The Cambrian radiation was explained as an ecological filling of empty niche space—a claim Conway Morris based on a functional analysis that concluded that the trophic structures were more complex in Cambrian ecosystems, having a relatively sharp niche division with the presence of carnivores, detritivores and suspension feeders, than was the case in older Precambrian systems.[26]

Thus, the agenda of Conway Morris's writings in the 1980s was not primarily to show that Cambrian life-forms were widely different from extant biotas, but to show that despite its alien appearance Cambrian life was remarkably similar to ours, filling out the same ecological roles and having similar trophic structures. Although defending a traditional ecological Darwinian position, Conway Morris was not untouched by the critique of adaptationism that was put forward a decade earlier by Gould and Lewontin. In a comparison of the adaptive potential of the extinct Cambrian invertebrate *Wiwaxia* and mollusks, Conway Morris (introducing the 'replaying life's tape' metaphor later hijacked by Gould) concludes that if life's tape were to be rerun, it seems possible that the former would survive at the expense of the latter.[27]

In a *Science* paper from October 1989 (published almost synchronically with the publication of Stephen Jay Gould's *Wonderful life*) this position was sharpened considerably. In a polemical

[22] Gould (1989), p. 304. 'Idiographic' comes from *idios* which means private or personal and *graphikos*, which pertains to writing or painting. It denotes efforts to understand contingent, particular and accidental phenomena.

[23] Gould (1989), pp. 278, 284.

[24] Gould & Lewontin (1979).

[25] Of course, as pointed out by one reviewer, abiotic changes aside, if organisms really were perfectly optimally adapted, there is no reason to think evolutionary change would happen at all.

[26] Conway Morris (1985), pp. 570–573; (1986), pp. 435–436.

[27] Ibid., p. 572.

attack on the macroevolutionary research program promoted by Gould and his associates during the punctuated equilibria controversy in the 1970s, Conway Morris argued that the ecological filling of niches (driven by adaptation by natural selection) was an adequate explanation for the Cambrian radiation and the resulting anatomical disparity of that process. There was therefore no need to postulate extra macro-evolutionary processes, such as species selection, in order to explain the Cambrian radiation.[28]

This traditional ecological neo-Darwinian perspective also informed Conway Morris's use of the contingency concept. Addressing the 'replaying life's tape' thought experiment, Conway Morris believed that life in such a scenario would, at a distance, look much the same with different species occupying recognizable ecological roles. The actors in this ecological theater might themselves be (phylogenetically and morphologically) totally different, however, and Conway Morris concluded that 'a process of contingent diversification might produce a biota worthy of the finest science fiction'.[29]

Despite the use of common metaphors (i.e. *contingency*; *experimentation* (in body plans); *replaying life's tape*), and despite the fact that both Gould and Conway Morris initially[30] shared the image of the Burgess Shale fossil as a collection of weird wonders and were striving to promote the Burgess Shale as a fossil fauna with a special significance for our understanding of evolution, they had (as can be seen from the above) substantial disagreements at the end of the 1980s as to the evolutionary interpretation of the life in the Cambrian. It is clear these disagreements were primarily theoretical. They reflected different perceptions of the robustness of traditional Darwinian explanatory approaches as well different ideals of scientific explanation. Where Gould perceived his adaptationist critique as part and parcel for a hierarchical theory of evolution, with the existence of a independent 'decoupled' level of macroevolutionary processes, Conway Morris instead interpreted Gould and Lewontin's critique of strong adaptationism as an argument for the adequacy of traditional Darwinian explanations. Likewise, where Conway Morris perceived contingency as an addendum to the general processes that he regards as the *explanans* of evolutionary biology, Gould believed that unique historical coincidences are essential causal agents in life's evolutionary history and perceived contingency to be the decisive factor in evolution. But that implies that these causes are *particular* with respect to the historical sequence in question and that general processes—or law based explanations—are inadequate to understand the higher course of evolution. Although both of them actively promoted the Burgess Shale fossils as 'weird wonders' and as exemplary of what paleontology's 'historical perspective' could contribute to our understanding of evolution, their visions of the significance of this historical perspective were informed by different conceptions of the goal of scientific explanation. For Conway Morris the focus was on general processes, backed by a nomothetic vision of what constitutes scientific explanations—a vision that was retained both before and after the cladistic revolution and the systematic revisions of the Burgess Shale arthropods during the 1990s.[31] Gould, however, made a point of emphasizing the idiographic aspects of evolution in *Wonderful life*, focusing on the role of particulars.

3. Neontology and the historical dimension in systematic crossfire

Though there was ample disagreement concerning the evolutionary significance of the Burgess Shale fossils Gould and Conway Morris both shared (as a common presumption) the evolutionary scenario of the origin of Cambrian metazoans that had been unfolded by Whittington's research team (see below) at Cambridge, of which Conway Morris was a member. When Whittington's research team began their investigations of the Burgess Shale fossils in the 1960s and 1970s, Anglo-Saxon arthropod research was dominated by the so called *British School*, whose leading figure was Sidnie Milana Manton (1902–1979) and their initial interpretations were to a very high degree based on Manton's ideas on the origin and evolution of arthropods.

3.1. Manton, the polyphyletic theory of arthropod origin and the bauplan concept

The thinking of Manton contained a number of idiosyncracies connected to the fact that her academic maturation process took place before the establishment of the modern synthesis. Originally, Manton was a student of Herbert Graham Cannon (1897–1963). Together with the third dominating figure within the British School, William Thomas Calman (1871–1952), they all belonged to an intellectual tradition stemming from the rational morphologist D'Arcy Thompson, whose ontological assumptions included an idealist belief in the existence of archetypical baupläne in the animal kingdom.[32]

This intellectual background was expressed in Manton's theory of the polyphyletic origin of the arthropods—a theory that became dominant among Anglo-Saxon arthropod researchers during her career. As a consequence of her investigations of arthropod anatomy and locomotive functions, Manton came to the conclusion that the *Arthropoda* could be segregated into four major groups (*Crustacea*, *Chelicerata*, *Uniramia* and *Trilobita*) each of which had arisen separately from an annelid-like life form. Typical arthropod characters, including a calcified exoskeleton and segmented limbs had therefore originated several times from a soft bodied stemform.[33]

The main argument for this interpretation was based on the notion that each of the four major groups were bound together by a set of characters, that could be identified as a separate and distinct bauplan and that they were so distinct from one another that transformation between them was 'impossible'. Behind this claim was the implicit presumption that each of these body plans possessed a *functional closure* that made it impossible for a lineage

[28] Conway Morris (1989), p. 345.

[29] Ibid., p. 346.

[30] In the light of developments connected to the cladistic revolution within arthropod systematics described below (and new, more conventional reconstructions of some of the most 'bizarre' Burgess Shale animals including *Hallucigenia sparsa*), Conway Morris was later to change his view, arguing that the 'weird wonders' of the Burgess Shale were, in fact, not so weird, and that the role of contingency in evolution had been overstated by Gould. See Conway Morris (1998); Brysse (2008).

[31] I disagree here with the contention (given by Fortey, 1998) that Conway Morris initially shared the same position as Gould concerning the evolutionary role of contingency and that he completely reversed his views on this subject in *The crucible of creation*. It is, of course, true that it was originally Conway Morris who introduced the metaphor of 'replaying life's tape'. But such a contention seems blind to the fact that Conway Morris, at least in writing, has not at any time abandoned either the basic ecological Darwinism, or the general process- or law-based approach to evolutionary explanations that has all along been the primary premise for his interpretations of the Burgess Shale fossils. Both against the early Gould's claim that the higher course of evolution is governed by special macro-evolutionary processes like species selection, and against the later Gould's claim that the higher course of evolution is governed by contingency, Conway Morris has tried to accommodate the Burgess Shale fossils into a traditional Darwinian interpretation and to demonstrate that the Cambrian biota, despite its alien appearance, has a number of properties in common with extant ecosystems.

[32] Schram (1993), pp. 321, 323.

[33] Manton (1977), pp. 1, 487–488.

to make the shifts that, according to proponents of evolutionary systematics, were vital if a lineage was to enter a new adaptive zone.[34] As a consequence Manton placed each of the four major arthropod groups in separate phyla and claimed that the 'fundamental' difference between them was to be explained by four separate and independent origins.[35]

The Cambridge team took on Manton's ideas on the origin of arthropods as well as her belief in distinct and 'fundamental' baupläne for each of the major arthropod groups. When studies of the Burgess Shale arthropods revealed that these organisms often were in possession of characters that could not be accommodated into one of these four well defined groups, the assumption of functional closure resulted in an interpretation that assigned each of the animals a separate and independent origin from a segmented and soft bodied annelid-like form—and with the implication at they each represented new and hithertho 'unknown' bauplan.[36]

This interpretive practice was not confined to the arthropods. In a series of papers published in 1976 and 1977, Conway Morris, who had been given the responsibility for the remaining invertebrates, described no less than five very different animals as taxonomic problematica and, following the same logic, implied that they were all in possession of unique anatomical designs that would be very hard to fit into extant groups. Thus the most exotic of these reconstructions, *Hallucigenia sparsa*, showed the animal to be walking on seven pairs of stilt-like spines and having seven tentacles protruding upwars. This animal became the emblem for the 'weirdness' of the Burgess Shale fauna.[37]

It was through these studies that the idea of Burgess Shale fossils being the result of explosion in body plans were given form. The idea was launched in *Scientific American* by Conway Morris and Whittington in 1979.[38] Here they claimed that the Burgess Shale contained, apart from a series of arthropods with very unfamiliar morphologies, ten or more representatives from hitherto unknown phyla.

But the most extreme consequence of the Mantonian framework drawn by members of the Cambridge team was Whittington's suggestion that the apparent explosion in anatomical diversity in the Cambrian was to be explained as the result of parallel evolution in many independent lineages, and that metazoans in general had a polyphyletic origin.[39] This claim made Manton's theory of the polyphyletic origin of arthropods a general principle for metazoan origin, and was taken up both by Gould and Conway Morris in their evolutionary interpretations of the Burgess Shale in the 1980s.[40]

3.2. The cladistic revolution, its epistemic ideals and their relation to the fate of the bauplan concept

The theoretical framework that had been a shared presumption of Gould and the Cambridge team's interpretations of the Burgess Shale fauna was by this time getting into trouble, however. Since the 1970s, controversy had been going on within the systematic community concerning the principles of classification.[41] Three major schools had been involved in this conflict. These were the school of evolutionary systematics (also known as the Mayr–Simpson school) which sought a classification based both on phylogenetic relations and on ecological and morphological similarities. The school of numerical taxonomy (also known as the phenetic school) which sought to base their classification on similarity measures alone. And finally, the school of phylogenetic systematics (also known as the cladist school) which sought to base their classification on phylogenetic relations alone, using parsimony and monophyly as their primary guiding principles in systematic analysis.

By the mid 1980s the cladist school itself had bifurcated into two branches, with conflicting views on the epistemological foundation for recognizing homologies, the relations between theory and empirical investigations and also, to a certain extent, the cognitive goal of doing phylogenetic analyses.

The branch known as the Hennigian[42] cladists seeks to base their recognition of homologies in the functional analysis of characters and believes evolutionary theory to be a basic foundation for doing phylogenetic systematics. Accordingly, they regard interpretation and skill to be a natural part of the process of collecting scientific information, and the scientific practice of this community is founded on a strong realistic interpretation of the relations between nature and scientific representations, that is, they seek to make their scientific representations as accurate or 'true' as possible. In contrast, the views of the transformed cladists or pattern cladists are founded upon an epistemic ideal that seeks to restrain human urges to judge, interpret, anthropormophize, aesthetizise or in any other way violate the raw facts of nature in the process of data collecting. The transformed cladist regards homologies to be identical to synapomorfies, and believes it to be possible to recognize them without making any assumptions concerning evolution, merely by preferring the best supported cladogram.[43] Accordingly they reject evolutionary theory to be necessary as a foundation for cladistics, and see the use of computer based methods in cladistic analyses as a way of automatizing data collecting and of doing a pure 'theory-free' systematics.[44]

Despite this heterogeneity, by the end of the 1980s it was increasingly clear that the cladistic school was going to emerge victorious from the controversy within the systematic community. This development turned out to have dramatic consequences for the Burgess Shale debate.[45] Manton's position that adopted the construing of phyla as being defined by having distinct body plans had, to a certain degree, been able to coexist with the evolutionary school, whose systematic practice was based on the idea that major taxonomic groups shared 'adaptive zones'.[46] In contrast several of the prominent philosophical trends in the cladist school are in direct opposition to the most salient feature of Manton's thinking. This is most obvious in the case of the polyphyletic theory of arthropod origin and the essentialist notion of phyla being defined by the common possession of distinct body plans. The polyphyletic theory of arthropod origin is in direct conflict with the principle of parsimony,

[34] Apparently this functional closure was only to be assigned to the arthropods (where Manton was a specialist herself). As should be clear from the precedent, Manton was ready to give other groups (in this case annelids) the kind of evolutionary flexibility that she denied the arthropods.
[35] Manton (1977), p. 1; Conway Morris (1998), p. 172.
[36] Whittington (1979), p. 263.
[37] Conway Morris (1976a), p. 707; (1976b), p. 213; (1977a), p. 271; (1977b), p. 626; (1977c), p. 834.
[38] Conway Morris & Whittington (1979), pp. 110, 116.
[39] Whittington (1980), pp. 145–146.
[40] See, however, n. 31.
[41] The historical development of this controversy and the epistemological issues involved are in themselves fascinating but beyond the scope of this paper. For extensive treatments of this subject, see Hull (1988); Schuh (2000); Williams & Forey (2004).
[42] After Hennig (1966), the founding father of this school.
[43] The best supported cladogram is in this case the one where there are the fewest possible instances of character reversal and instances of convergence.
[44] See also Suárez-Díaz & Anaya-Muñoz (2008).
[45] See Brysse (2008) for an account of this development.
[46] This coexistence must, of course, be based on the extra assumption that shared adaptive zones implies shared body plans.

which is a primary norm in cladistic practice. The principle of parsimony prescribes that the simplest phylogenetic tree (i.e. the one with the *least* possible evolutionary character changes) should be preferred among possible alternatives, and is therefore much more in accord with a monophyletic theory of arthropod origin (where typical characters like exoskeleton, segmented limbs, etc. have a common phylogenetic origin) than a polyphyletic theory.[47]

The essentialist notion of phyla being defined by the common possession of distinct body plans (and the underlying presumption that the taxonomic status of a group reflects a level of organization with an extraordinary biological or evolutionary significance) is in conflict with the epistemic ideals of both the Hennigian and the transformed cladists, though the reasons for this is very different among the two groups.

For the Hennigian cladist it is a primary epistemic value that biological classification reflects relations of descent as accurately as possible. The only relevant units in such an analysis are monophyletic groups, and the absolute taxonomic rank of these groups has no bearing on these analyses whatsoever. Thus modern analysis seems to have shown decisively that the class *Aves* is a subtaxon of the order *Dinosauria*. Hennigian cladists faced with this taxonomic mess often adopt a skeptical attitude towards claims that absolute taxonomic categories like phyla, class, order, and so on should be anything more than useful epistemic tools for ordering nature. Eschewing the talk of body plans some of them instead operate with a concept of 'ground pattern' (germ: *Grundmuster*) as a term for all character states that are ascribed to a monophyletic stem form.[48]

The epistemic ideals of the transformed cladists, however, prescribe that it should be as free from a priori assumptions about which characters are phylogenetically significant. On the contrary this is something to be decided by the analysis a posteriori. As a consequence the transformed cladist rejects the possibility of making prior decisions about which characters are defining a taxons 'body plan'.[49]

3.3. The pivotal role of momentum: unconvincing arguments, good polemics

This development within systematics facilitated a situation where the majority of scientists who were preoccupied with the Burgess Shale fossils distanced themselves from the school of evolutionary systematic, instead embracing cladistics. With this change of premises, it was clear that the new systematic tides in 1990s spelled trouble for the Mantonian research program. Derek Briggs, the third core member of the Cambridge Group, became the leading antagonist in these attacks. Briggs's skepticism towards Manton's polyphyletic theory of arthropod origin can be traced back to 1978 to a symposium on early invertebrate evolution—a symposium where Whittington, Manton and her associate D. T. Anderson presented their argument for a common polyphyletic scenario for the origin of the Metazoan. Despite the fact that both of his mentors, Whittington and Manton had put their scientific prestige on line, defending a polyphyletic origin of the metazoan, Briggs declared himself ready still to take a monophyletic origin of crustaceans, trilobites and chelicerates under consideration in the closing discussion of the symposium.[50]

A preliminary attempt to analyze the phylogenetic relations of the Burgess Shale arthropods can be found in the first volume of *Crustacean issues*, itself the product of that symposium. In this volume Briggs argues for a possible monophyletic origin of the crustaceans and several of the Burgess Shale arthropods.[51]

But we have to move forward to the year 1989 to find an Anglo-Saxon cladistic-based phylogenetic analysis that includes representatives of three of Mantons four major arthropod groups (*Uniramia* excepted). This is done in a paper in the 13 October 1989 issue of *Science* by Briggs and his associate Richard Fortey—just a week before Conway Morris hit the front page of the same journal with *Wiwaxia*. In the paper Briggs & Fortey argue against Manton's polyphyletic origin of the arthropod origin, and for the view that the Cambrian arthropods should be regarded as morphological links between the major arthropod groups.[52]

This monophyletic position is expanded by Briggs in a paper of 1990.[53] The paper can be regarded as an attack on Gould's view of the role of the arthropods in the Cambrian radiation, and especially on the assumption that the Cambrian arthropods should be representative of separate phyla with distinct body plans. Together with the paper of Briggs & Fortey this paper became part of a larger attack that had a significant effect on the development of the debate on Cambrian disparity. Gould afterwards abandoned his previous attempts to justify his claims of greater Cambrian disparity on Manton's taxonomic underpinnings (and indeed denied that he had ever intended to do so), now arguing that cladistic analyses were irrelevant to the question of higher Cambrian disparity, and that the question could only be solved by comparing the morphological Cambrian and extant arthropod in a quantified morphological space.[54]

The argument of Briggs's paper is an example of how a scientist may call on various rhetorical resources to further a specific scientific agenda, and in this case a specific research policy as well. In the introduction Briggs discussed the question of the origin of the arthropods as a conflict between two different basic perspectives.

The first of these Briggs call the 'neontological' perspective. According to Briggs this is the perspective defended by Manton and Gould. In this approach one begins by ignoring the fossil data, focusing only on the morphological character of recent arthropod groups. Cambrian arthropods classified by this approach will,

[47] It should be noted though, that Manton herself actually perceived her theory to be in accord with the principle of parsimony. Confronted with claims to the contrary, Manton argued that her polyphyletic theory was 'parsimonious' in the sense that it did not require the 'invention' of 'non-functional' intermediates (in contrast with Schram). This interpretation of the principle of parsimony was (obviously) not accepted by her adversaries.

[48] The ground pattern concept can be found in Wägele (2001), p. 90 ff., and Ax (1995), p. 18 ff. The latter gives a very articulate statement of his antagonism towards the idea that absolute taxonomic rank should reflect anything biologically significant.

[49] An example of this position can be found in Wilson (1996), p. 143, who attacks Wägeles use of the ground pattern concept, precisely because Wägele polarizes a subset of characters as being plesiomorphic prior to the cladistic analysis.

[50] Whittington (1979), p. 262; Manton & Anderson (1979), p. 269; House (1979), p. 485.

[51] Briggs (1983), p. 1.

[52] Briggs & Fortey (1989), p. 242.

[53] Briggs (1990), pp. 24–43.

[54] Gould (1991). I am inclined not to buy Gould's later denial (1991, p. 412) of the interpretation that his claim in *Wonderful life* of greater Cambrian disparity was based on claims of higher taxonomic diversity (that again were initiated by the interpretive practice based on Manton's theoretical framework). Although Gould, as earlier noted, had been a prominent advocate of quantitative approaches in paleontology in the 1970s, his argument for higher Cambrian disparity in *Wonderful life* was not developed along these lines. Instead he based it precisely on a logic facilitated by (and extended from) Manton's claim of the existence distinct bauplans for each of her four major arthropod groups. This is apparent both in the section 'The classification and anatomy of arthropods' (pp.102–106), that is based directly on Manton's division of arthropods, and in the section 'Summary statement on the bestiary of the Burgess Shale' (pp. 207–218), where the practice of interpreting taxonomically problematic Burgess Shale fossils as having 'uniquely' anatomical designs is unfolded. Only after it became apparent that these taxonomic arguments were made on shaky grounds did Gould resort to a quantitative approach.

according to Briggs, be placed in a taxonomical vacuum. This vacuum arises because the characteristics Manton considered diagnostic for the four major groups (the number of cephalic limbs and the level of cephalic tagmosis) are fundamental to the classification of Cambrian arthropods. However, these characteristics may seem stable and reliable from a neontological perspective, but are exactly the ones that vary the most in Cambrian arthropods. This is not surprising since they are from a period when these characteristics were still evolving.[55] An interpretation based on a neontological perspective will therefore result in a view of the Cambrian arthropods as belonging to a variety of higher taxa, each with a low diversity, often consisting of a single species or genus. According to Briggs, such an approach will almost invariably lead to a polyphyletic view on arthropod origin.[56]

The description of this perspective as 'neontological' is a scarcely hidden attempt to attack Gould on his own home field. Within the paleontogical community it is often used as part of a critique of people that ignore the insights that can be extracted from considerations based on fossil data. This application of 'neontological' is closely connected with a view that a paleontological approach gives a special and unique perspective on evolution qua its status as *historical* discipline. By far the most prominent defender of that position is, of course, Gould. By describing Gould's view on the origin of arthropods as 'neontological', Briggs tries to score rhetorical points by implying that Gould has committed one of the sins he so often warns against himself—not taking a historical perspective and evidence into account in the analysis.

This is emphasized by the fact that Briggs chooses the term 'Cambrian' to denote his own alternative perspective. This Cambrian perspective takes as a working hypothesis that extant and Cambrian arthropods have a common monophyletic origin. In this perspective Cambrian arthropods are regarded as missing links between the major arthropod groups. Accordingly, it comes as no surprise that the majority of the Cambrian arthropods lack several of the characteristics that today have become defining for the four major groups, since they presumably were still evolving at the time. Briggs regards this approach as more constructive than beginning by imposing an interpretative straightjacket based on the classification of extant arthropods. To claim that each of the Cambrian arthropods should be placed in a separate taxon with an independent evolutionary origin from an annelid ancestor is, for Briggs, equal to accepting in advance that no information concerning the phylogenetic relations of arthropods can be derived from fossils at all.

Briggs's equation of 'neontological' with 'polyphyletic' and 'Cambrian' with 'monophyletic' is, in my opinion, directly misleading. Firstly because, of the four major arthropod taxa, one of them, *Trilobita*, consists of extinct forms only. Manton's polyphyletic theory on arthropod origin is not more 'neontological' than incorporating a very important part of the fossil documentation of this group's evolutionary history. It is also unfair to the fact that the polyphyletic theory on arthropod origin has a fairly clear 'Cambrian dimension' in the evolutionary scenario of Conway Morris & Whittington's paper in *Scientific American*.

Secondly, nothing hinders a pure 'neontological' analysis from taking a monophyletic perspective on arthropod evolution. The decisive criteria for this is not whether the analysis incorporates fossil data or not, but the principles upon which the systematic analysis is founded. Hence, it comes as no surprise that Briggs's primary reason for preferring a monophyletic working hypothesis is that it is 'more parsimonious'.

That Briggs succeeds in conveying his message of arthropod monophyly, despite these argumentative inadequacies, is probably to be ascribed to two factors. Contrary to his opponents, Briggs is arguing from a cladistic perspective and is gaining the benefit of being in line with the current general intellectual trends within the systematic community. Secondly, Briggs's critique of the way the number of segmented limbs and the degree of tagmosis constitute diagnostic criteria for arthropods gives him the opportunity to win rhetorical points in a cladistic community that would regard the strong essentialist claims regarding body plans as one of the most problematic elements in Manton's thinking. It is thus from the contextual setting that Briggs gains his momentum, rather than from the quality of his arguments.

4. Discussion

The fact that the outcome of scientific debates depends on more than just a matter of the content and quality of arguments should come as no surprise to the scholar who has followed the developments within the history, philosophy and sociology of science during the last five decades.[57] However, the relation between a collective's shared epistemic values and the indiosyncrasies of the individuals who apply them as means to various ends is still a subject needing further exploration. Exploring the role of epistemic values in the context of paleontology, the analysis above reveals a complex situation where the fate and evaluation of various claims and arguments within a scientific community depends on the ability to live up to certain expectations connected to the practitioners' understanding of their own discipline, as well as a conglomerate of epistemic norms with a changing and unstable internal balance.

The first of these elements is illustrated by the central role of the 'historical dimension' in paleontologists' attempts to establish scientific authority within the larger domain of evolutionary biology. Thus the actors in this analysis seemed obliged to pay homage to the contention that the study of fossils gives palaeontology a unique 'historical perspective' by making it possible to unravel important aspects of evolution invisible to scientists studying the extant biosphere. This commitment to a privileged historical perspective of paleontology was shared by the actors, even though the strategies they employed in defending this perspective have been disparate and a subject for disagreement. Although both Gould and Conway Morris actively promoted the Burgess Shale fossils as 'weird wonders' and exemplary of what paleontology's 'historical perspective' could contribute to our understanding of evolution, their visions of the significance of this historical perspective were informed by disparate conceptions of the goal of scientific explanation. For Conway Morris the focus was on general processes, backed by a nomothetic vision of what constitutes scientific explanations—a vision which was retained both before and after the cladistic revolution and the systematic revisions of the Burgess Shale arthropods during the 1990s. Gould, however, made a point of emphasizing the idiographic aspects of evolution in *Wonderful life*, focusing on the role of particulars. The underlying epistemic ideals of these two approaches were likewise embedded in opposing attitudes toward a classical law based ideal of science.

The second of these elements is illustrated by the way in which the contextual climate for discussing Cambrian metazoans was

[55] According to Briggs this is demonstrated by studying two of the Burgess Shale arthropods, *Sanctacaris* and *Canadaspis*. Contrary to most Cambrian arthropods, both of them can be clearly classified within the confines of Manton's four main groups (in this case *Chelicerata* and *Crustacea* respectively), but neither of them is in possession of all the diagnostic characteristics that today would be considered to define these groups.
[56] Briggs (1990), pp. 24, 29–30.
[57] See, for instance, McMullin (1987) for a systematic analysis of possible ways of reaching closure in scientific controversies.

affected by intellectual developments within systematics—developments that were unrelated to the epistemic problem at hand. The theoretical upheaval facilitated by the wide acceptance of cladistic approaches by the end of 1980s created a balancing of epistemic values where the adherence to the principle of parsimony effectively discredited polyphyletic approaches to arthropod and metazoan origins—a situation that was (by means of an effective rhetoric playing on paleontology's 'privileged historical perspective') used by Briggs to promote a monophyletic research program. The momentum that Briggs gained for this agenda illustrates the advantage of being in line with the current balance of epistemic values in surrounding community of scientists. Despite the fact that Briggs's initial critique of Gould's account of Cambrian arthopods may seem inconsistent and unconvincing from a purely analytical perspective, the compatibility between his proposed research program and the rise of Ockham's razor (known locally as the principle of parsimony) as the dominating epistemic value within the systematic community, gave Briggs the advantage of being on the side of the angels—an advantage he used effectively by implicitly chiding his opponents for taking a 'neontological perspective'.

The success or failure of a rhetorical strategy thus depends (at least to some extent) on the acceptance of the specific epistemic ideal or set of values to which the surrounding community of scientists adheres. But if this is the case, then how would we expect otherwise logically and epistemically sound arguments to be treated in an environment hostile towards their normative foundation? Might they fall on deaf ears?

It would be tempting to claim so, but as shown by the cases presented here, it is more complicated than that. A scientist might choose to directly address and criticise the normative foundation for a scientific practice, in which case the ideals themselves become a part of the discussion. This was done effectively by Gould in *Wonderful life*—a book that itself drew considerable attention to the contingency thesis and a debate about what constitutes an evolutionary biology. However the diverse reactions to the message of this book also illustrate the difficulty of convincing a sceptical audience about such a message. Whereas the contingency thesis has received considerable attention among philosophers of biology and humanist scholars,[58] its validity and relevance has been strongly contested by paleontologists such as Conway Morris, and has generated even less attention among practitioners in the wider field of evolutionary biology, where the positivistic vision of a unified science based on natural laws has played an important historical role in the establishment of the modern evolutionary synthesis.[59]

The answer probably lies in the possibilities for providing new and alternative research programs. The epistemic values that are dominant within a scientific thought collective are embedded within the scientific practice and habits of that collective. Arguments for changing values, must at the same time address the fruitfulness of that practice.

Acknowledgements

Thanks to Jens Høeg and Claus Emmeche for help and encouragement and constructive critique during the entire process of the making of this paper. Keynyn Brysse provided an inspiring talk and constructive discussions at the ISHPSSB meeting in Exeter 2007. An early draft of this paper was read and commented on by Andrew Hamilton and Jane Maienschein, and the Center for Biology and Society at Arizona State University were the kind hosts during a three months stay in Tempe, Arizona. And finally thanks to the employees and associates at the Zoological Museum, the Biological Institute and Center for Philosophy of Nature and Science Studies at the University of Copenhagen for moral support and helpful critique. The responsibility for any shortcomings of this paper is, of course, mine alone.

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[58] See for instance Sterelny & Griffiths (1999); Beatty (1995).

[59] There are, however a few notable exceptions, the most prominent one being the study of contingency in replicated adaptive radiations of island lizards by Losos et al. (1998).

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A web of controversies: complexity in the Burgess Shale debate

Abstract: Using the Burgess Shale controversies as a case-study, this paper argues that controversies within different domains may interact as to create a situation of "complicated intricacies", where the practicing scientist has to navigate through a context of multiple thought collectives. To some extent each of these collectives has its own dynamic complete with fairly negotiated standards for investigation and explanation, theoretical background assumptions and certain peculiarities of practice. But the intellectual development in one of these collectives may "spill over" having far reaching consequences for the treatment of apparently independent epistemic problems that are subject of investigation in other thought collectives. For the practicing scientist it is necessary to take this complex web of interactions into account in order to be able to navigate in such a situation. So far most studies of academic science have had a tendency to treat the practicing scientist as members of a single (enclosed) thought collective that stands intellectually isolated from other similar entities unless the discipline was in a state of crisis of paradigmatic proportions. The richness and complexity of Burgess Shale debate shows that this encapsulated kind of analysis is not enough.

Introduction: The web of controversies

How do different scientific controversies affect each other? This topic has received little attention within science studies. Though it has long been recognized that contextual elements (institutional, philosophical or otherwise) play a crucial role in the shaping of scientific discussions, the dynamics of interactions between scientific controversies over time is as yet largely unexplored territory. Most theoretical accounts of scientific collectives tend to treat the scientist as relating only to one scientific community, and most empirical studies of controversy tend to handle one controversy at a time.[1] This may seem strange considering that many scientific discussions take place in fairly small, idiosyncratic communities which themselves are parts of larger thought collectives that transgress several disciplinary boundaries.[2]

[1] Examples of the former include Kuhn (1962), Foucault (1964) Daston (1995), and Hacking (2002). Examples of the latter include Rudwick (1985); Shapin and Shaffer (1985); Engelhardt and Caplan (1987) and Collins and Pinch (1993).

[2] I am using the term 'thought collective' (ger: *denkkollektiv*) here in a sense fairly similar to Fleck (1935, p. 45) who defined it as a community of persons mutually exchanging ideas or maintaining intellectual interactionism, and who designated this entity the role of 'carrier' for the historical development of a field of thought as well as the given stock of knowledge and cultural habits that were part of the collective belief system. While this fairly vague characterization may be unsatisfying as an account of scientific collective, it has the advantage *vis-a´-vis* competing concepts (like Kuhn's (1962) *paradigms* or Daston's (1995) *moral economies*, that an individual may be a member of serveral thought collectives at once (although

Evolutionary biology may be considered to be such a larger thought collective. Evolutionary biology itself is a heterogeneous field spanning disciplines as diverse as, for instance, ecology, genetics, developmental biology and paleontology. The paleontologist interested in evolutionary questions has to navigate within these different intellectual landscapes and must be able to address a diverse set of challenges including the dating of fossils and reconstruction of extinct species; methodological conventions of systematics; as well as general problems in evolutionary theory. Add to this, say, a sociological dimension where questions of authority, legitimacy and cultural hegemony come into focus as do fiscal issues related to funding, and what emerges is a quite complex image of the scientific process.

The richness and complexity of what I will here call the “Burgess Shale debate” makes this set of skirmishes ideal for a study of how scientific controversies interact. Named as one of the 20th century’s biggest paleontological discoveries, the Burgess Shale fossils represent a window to Cambrian animal life during the time “shortly” (in geological time scales) after the apparent event of the Cambrian Explosion. Since its discovery in 1909 by the American paleontologist Charles D. Walcott (1850-1927), more than 30 fossil localities of the same type have been found - all from lower or Middle Cambrian, and the Burgess Shale has given name to a special fauna type, characterizing fossil faunas consisting of compressed fossils of Cambrian metazoans with soft body parts beautifully preserved in shale.

The Cambrian fossils excavated from these localities were first brought to widespread scientific public attention with the publication of Stephen Jay Gould’s 1989 bestseller *Wonderful Life: The Burgess Shale and the nature of history.* In this publication Gould described two phases in the treatment of the Burgess Shale fossils. Referring to the first phase as ‘Walcott’s shoehorn’ Gould argued that Walcott had been biased by his adherence to a gradualist world view that forced an interpretation of these fossils as the primitive representatives of modern groups. This view was later overturned during a second phase of systematic investigations and reconstructions that began in the middle of the 1960’s by the so-called ‘Cambridge team’ under the leadership of the trilobite

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Fleck never addressed the possibility that an individual may be a member (or has to navigate through the standards of) several *scientific* thought collectives – something that is a salient feature of the analysis presented here).

paleontologist Harry B. Whittington. In this phase the vast majority of the Burgess Shale fossils were reinterpreted as "weird wonders," many of which could not be classified into known taxa. For Gould this scenario served as evidence for the existence of a major extinction at the end of the Cambrian – an extinction that illustrated the major role of contingency in the shaping of life's evolutionary history.

Wonderful Life sparked a major interest in the evolutionary significance of Cambrian fossils but it also spawned controversy, since several of its claims were contested even by people, who had been participants in the very events described by the book. During the 1990's the Cambrian became the focal point of several controversies, the most prominent of these being the debates on the relative disparity of the morphology of Cambrian and extant metazoans; and the role of contingency in evolution. Focusing on the systematic aspects of this debate, historian of science Keynyn Brysse identified this period as a third phase, characterizing it as a second reclassification of the Burgess Shale fauna (based on cladistic principles), with the fossils no longer being regarded as weird wonders but as representatives of the stem lineages of extant groups.[3]

The systematic perspective is just one of several important dimensions in this web of disagreements, however. In fact, the final incorporation of these morphologically weird organisms into a phylogeny of life was not merely the solution to a taxonomic problem. As the title of this paper implies, there is in fact not one, but several scientific controversies connected with the interpretation of the Burgess Shale type faunas and the debates about the Cambrian Explosion; solving that taxonomic problem has larger and more interesting consequences, particularly for sociologists and historians of science. Contextualizing the Burgess Shale debate is a complex task as it is embedded not only in specific institutional and geographical settings, but also in the nexus of several important scientific discussions – some of which have been the center of attention in paleontology and evolutionary biology during the last two decades. The debates about the interpretations of the Burgess Shale type faunas is connected with several "theoretical" discussions concerning punctuated equilibria, species selection, adaptation, evolutionary progression, contingency as well as the principles of systematics. But it is also connected with more "empirical" discussions concerning the nature and causes of the Cambrian

[3] See Brysse 2008, p. 298.

Explosion; discussions on the phylogenetic relationships of the animals that were found in the fossil beds; geological controversies concerning the dating of the Burgess Shale fauna and other fossil faunas from Middle Cambrian, and by discussions of the reconstruction of specific Burgess Shale fossils as living, three-dimensional organisms.

Using the Burgess Shale controversies as a case-study this paper will argue that all these issues are interrelated and that their interaction creates a situation of "complicated intricacies," — a set of theoretical, methodological and empirical constraints originating in different parts of biology that converge in a controversy, forcing the practicing scientist working at their intersection to contend with parts of multiple overlapping thought collectives. It also argues that none of the theoretical accounts of scientific practice, that have so far been proposed, gives an adequate description of this situation.[4]

The paper is divided in to major parts. The first part (*Situating the Burgess Shale Debate*) situates the conflict concerning the interpretations of the Burgess Shale fossils historically in the intellectual and institutional landscape of Anglo-Saxon invertebrate paleontology and carcinology. It briefly describes the origin of the Cambridge team, the peculiarities of that group's practice and its commitment to an essentialist understanding of organismal body plans. The second part of this paper (*Contingency and the Cambrian Disparity Debate*) focuses on the conflict between Stephen Jay Gould and fellow invertebrate paleontologist Simon Conway Morris concerning the role of contingency in evolution, and the actions and intellectual navigations of these two antagonists during a transformative period in the history of zoology and paleontology through which scientists faced budget cuts and shifting standards of evaluation for competing claims concerning the phylogeny and evolution of arthropods.

Part I: Situating the Burgess Shale Debate

Our story begins with a rebellion against modesty. In the late 1960's there was a growing dissatisfaction among a group of paleontologists, who believed that their discipline possessed an unexplored potential as a resource for understanding evolution. Being located in the nexus between biology and geology, paleontology had, for many of its practitioners, first and foremost remained a sub-discipline of geology, where it had

[4] I am referring here to the literature mentioned in note 1.

justified its own existence by contributing to the development of methods to correlate stratigraphical layers at different localities.[5]

As a result of this dissatisfaction, several of these paleontologists, together with other students of extinct organisms, like Daniel Simberloff, that were not necessarily trained as paleontologists, became involved in attempts to establish a stronger platform for their discipline in evolutionary biology. From a sociological perspective, these efforts, which came initially from American palaeontologists, but later also included British scientists, can be seen as political strategies to counter the threat of budget cuts, as they correlate in time with the financial cuts that hit American Science under the Nixon administration in the 1970's and British natural science under Thatcher in the 1980's.[6] A more substantial product of these efforts was an attempt to engage with pressing theoretical problems recognized by evolutionary biology at large. As a result, the intellectual landscape of paleontology in the 1970's came to be dominated by several prominent theoretical debates. Most notable among them were the debates about the theory of punctuated equilibria and the possible role of species selection as the cause of higher trends of evolution. But other debates on adaptation and the methodology of systematics helped structure the context and development of the Burgess Shale discussions as well.

The tempo and mode of evolution: the theory of punctuated equilibria and the role of macroevolution in evolution.

As noted by Baron (2009), the first prominent result of the efforts to establish a stronger platform for their discipline within evolutionary biology was a revival of the debate on the tempo of evolution. This issue had been a focal point of disagreement among the disparate conflicting theoretical positions that dominated evolutionary biology in the decades around 1900.[7] By the end of the 1960's, the Modern Synthesis had established itself as *the* major trend in evolutionary thinking, and the pace of evolution was regarded to be a somewhat solved issue in Anglo-Saxon paleontology, with the last major contributions coming from George Gaylord Simpson in the form of the books *The*

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[5] Stanley, 1979, p. 4.

[6] Baron 2009, p. 287, as well as Walsh, 1970 and Turney 1987 for comments on the US budget cuts during the Nixon administration and the UK budgets cuts under the Thatcher government.

[7] Baron 2009, p. 288. See Bowler 1984 for an overview of the landscape of evolutionary theories during this period.

Tempo and Mode of Evoution (1944) and *The Major Features of Evolution* (1953), which was a revised version of his 1944 book.[8]

This was all about to change, when two young American paleontologists, Niles Eldredge and Stephen Jay Gould, went public with a punctuational model of evolution which was presented under the name "punctuated equilibria".[9] Their model originated as an attempt to spell out the logical consequences of Ernst Mayr's idea of speciation as the consequence of genetic revolutions within small peripheral isolated populations – and as an attempt to address an old problem in paleontology.[10] Since the publication of Darwin's *Origin of Species*, paleontologists had been plagued by the existence of morphological gaps in the fossil record. For Darwin, the virtual absence of intermediate forms remained the most troublesome problem to his theory of descent and accordingly he dedicated a whole chapter in *On the Origin of Species* to this it, arguing that the available fossil remains were insufficient to give a full, accurate picture of biological evolution. However contrary to Darwin's apology concerning the state of the fossil record, Eldredge and Gould argued that it (or at least parts of the invertebrate record) was by now complete enough to make sound inferences about the tempo and mode of evolution, and that patterns in the fossil record had to be considered and even accommodated by any credible theory of evolution. In fact, gaps in the fossil record were to be expected in accordance with Mayr's model, being the natural result of speciation being a process of rapid transformations of small isolated populations. Traditional perceptions of the ideal fossil record as consisting of a set infinitely graded forms was therefore a chimera.

Although the original articulation of the theory had appeared already in an earlier paper by Eldredge,[11] it was clearly Eldredge and Gould's explication of it that gave the theory of punctuated equilibria[12] the kind of publicity that made it the center of so much attention. The paper was published in an anthology entitled *Models in Paleobiology* – an anthology which itself was an attempt to give the newly coined discipline of 'Paleobiology' a stronger connection to general evolutionary problems. The centrality of

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[8] Simpson 1944; 1953. See Bowler, 1983, for a thorough analysis of the situation in evolutionary biology around 1900.
[9] Schopf 1972a; Eldredge and Gould 1972.
[10] See Mayr 1954; 1963.
[11] Eldredge 1971; p. 156ff.
[12] It was later termed *punctuated equilibrium,* but I will stick to the theory's original name in this paper in order to avoid unnecessary confusion.

a *model*-based approach in the anthology formed part of this attempt to "biologize" paleontology and liberate it from being only a technical method or subdiscipline of geology. This vision, which sought to establish a nomothetic basis for paleontology, and to counter a perceived 'traditional paleontological practice' which merely sought to collect and organize fossils into taxonomic groups without regard for more general theoretical considerations, was later explored during a meeting at the Marine Biological Labouratory at Woods hole, Massachusetts in late 1972. This fruitful meeting benefited from the participation of Gould and Schopf, also benefited from the participation of several prominent American paleontologists (as well as one ecologist) – all having a profound interest in the application of quantitative methods and techniques on questions with relevance to evolutionary biology.[13] The journal *Paleobiology* was founded as a result of the collabourative efforts that spurred from this meeting, and several papers were later published that attempted to put these quantitative principles into practice.[14]

By the mid-1970's, the debate on the theory punctuated equilibria underwent a transformation from being a "strictly" paleontological concern into a controversy with stakes in evolutionary biology at large.[15] Although attempts to criticize the theory of punctuated equilibria on empirical grounds also played a role, the primary facilitator of this development was the theory of species selection that was formulated by the American paleontologist Steven Stanley in 1975.[16] Like the theory of punctuated equilibria, this theory takes its departure in the Mayr's speciation model where the evolution of a new species (being the result of random drift and adaptation to the local conditions of small isolated populations) is an event having a strong stochastic component. Based on this model of speciation, Stanley argued that in a situation where some branches within a lineage had higher speciation or extinction rates than others, long term morphological trends in a lineage's evolution might display phenomena that were quite independent of the immediate adaptive needs of the individual species (for instance, by showing an overall trend towards increased size, despite adaptive pressure toward

[13] Among the prominent participants in this meeting we find Stephen Jay Gould, Thomas J. Schopf (the editor of *Models in Paleobiology*), David Raup, Daniel Simberloff and (on the last day) Jack Sepkoski. Sepkoski 2005, p. 226.
[14] Sepkoski 2005, p. 226. For an example of an attempt to apply this approach (in the form of stochastic form of stochastic models) to evolutionary problems in paleontology, see Raup and Gould 1974.
[15] An analysis of development (based on the science citation index) can be found in Ruse 2000, p. 234f.
[16] Stanley 1975.

reduced size within each individual species).[17] In the closing paragraph of the paper Stanley spelled out the epistemological consequences of this claim, arguing that "microevolutionary" processes (i.e. processes *within* populations, including natural selections, genetic drift, migrations etc.) were unable to explain the higher course of evolution and that a higher "macroevolutionary" process, like species selection, were needed in order to understanding the origin and extinction of major lineages:

> "The recognition of a process of macroevolution analogous to, but differing from, the process of natural selection in microevolution is of great consequence for population biology. Contrary to prevailing belief, natural selection seems to provide little more than the raw material and fine adjustment of large-scale evolution. The reductionist view that evolution can ultimately be understood in terms of genetics and molecular biology is clearly in error. We must not turn to population genetics studies of established species, but to studies of speciation and extinction in order to decipher the higher-level process that govern the general course of evolution." (Stanley 1975, p. 650).

This notion of a "decoupling" of different levels in evolution that was entailed in this idea, would soon to be appropriated by other paleontologists who were arguing that their discipline gave a privileged epistemic access to important factors in evolution which were not revealed by any extant studies of the biosphere. By the end of the 1970's this claim had been accommodated by Gould and Eldredge in their defense of the punctuated equilibrium model.[18] And by 1980, Gould was arguing that the Modern Synthesis was now giving way to a new and general theory of evolution that was to be based on a hierarchical framework and recognized different levels of evolutionary processes which were epistemically and ontologically decoupled from each other. Embedded within this theoretical framework was the promise and ambition of a macroevolutionary research program that would turn the study of fossils into a model-based nomothetic discipline in exactly the way that modern positivism demands.[19]

[17] Stanley 1975. For the most prominent empirically ground critique of punctuated equilibria at the time, see Gingerich 1974; 1976. For a defense and lineout of the philosophical implications of species selection, see Lloyd and Gould, 1993.
[18] Gould and Eldredge 1977, p. 132f; p. 139ff.
[19] Gould 1980a; 1980b.

Critique of adaptationism as a punctuationalist spin-off

The macroevolutionary research program described above was not the only spin-off of the punctuated equilibra debates of the 1970's, however. An equally interesting, and much more influential spin-off, was the jointly authored "Spandrels" paper by Gould and population geneticist Richard Lewontin. Here the authors attacked what they considered to be the ubiquitus "adaptationism" of the scientific practice of their fellow biologists and claimed that they too often unreflectively ascribed particular adaptive explanations to the origin of every single part of an organism.[20]

The contextual background for Gould's and Lewontin's critique of the "adaptationist programme" has been described by several authors.[21] The most thorough analysis of that event has been given by the sociologist Ullica Segerstråle who describes several motivations behind this publication. Perhaps the most prominent of these motivations was a wish to attack and undermine the scientific presumptions behind the research program of Edward O. Wilson's book *Sociobiology,* where especially the last chapter on human nature were perceived by the authors of the Spandrel both as politically dangerous and epistemically flawed.[22]

As noted by Segerstråle, however, a closer analysis of the context surrounding the publication of the Spandrels paper reveals other agendas as well. On a sociological level the attack on adaptationism (which was launched on a symposium on adaptation held by *The Royal Society* – the most esteemed scientific institution in Britain) can be regarded as an attack by *Americans* on a century-long *British* tradition of preferring functionalist explanations – a tradition that goes back to a pre-Darwinian occupation with design of the times of William Paley.[23]

With respect to the scope of this paper, the most interesting aspect of Segerstråle's analysis is her notion of the Spandrels paper as a 'trojan horse' that serves not only to further political agendas, but also (and most importantly) scientific agendas as well. By 1979, Lewontin was already known for his electrophoretic investigations of genetic variation, and for his neutralist claim that there is much more variation in natural

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[20] Gould and Lewontin 1979.
[21] See e.g. Ruse 2000; Segerstråle 2000.
[22] Wilson 1975; Segerstråle 2000, p. 14; p. 101; p. 108ff.
[23] Segerstråle 2000, p. 109-110.

populations than can be accounted for by natural selection. Having already put scientific prestige into attacking Theodosius Dobzhansky's balance hypothesis concerning superiority of heterozygotes (which gives a selectionist account of the existence of genetic variation in natural populations), Lewontin only had to expand this line of thinking to realize that his theoretical views as a population geneticist would not go well with ubiquitus adaptationism.[24]

For Gould the critique of adaptations served as an attempt to solve some of the logical problems left by the punctuated equilibria model and the theory of species selection with respect to traditional Darwinian thinking complete with the obligation to explain examples of genuinely adaptive morphological characters. It would make little sense to claim (as it is done in the theory of punctuated equilibria) that an ancestor-species could be outcompeted in it home range by a descendant-species that originated as a small, geographically isolated, peripheral population, if species are optimally (or close to optimally) adapted to their environment. Should such a contest occur, the ancestor-species (being optimally adapted to its habitat) would presumably hold the competitive advantage. However, if we grant the possibility that *all* species may be suboptimally adapted, with ample room for improvement, this problem disappears.

Likewise, if organisms *are* optimally adapted to their environment, it would be difficult to imagine an independent macroevolutionary level of species selection. In such a case, it would be difficult to argue for any causal decoupling between within-population processes and higher level trends, precisely because optimized individuals and collections of them in the form of homogeneous, optimized species would be indistinguishable with respect to selection. Species selection, then, would then presumable just be an extension of within-population selection towards optimal fitness.

The adaptationist critique presented by Gould and Lewontin could thus be perceived as a support for a hierarchical and level-based view of evolution that itself owed much to the model of punctuated equilibria. Indeed, there is every reason to suggest that it was this way Gould perceived these ideas, as he was to defend them as a coherent whole during his entire career up to and including his final work on evolutionary theory.[25]

[24] Lewontin 1974, p. 25, p. 267; Segerstråle 2000, p. 118.
[25] Gould 2001.

But, as will be clear in the second part of this paper, other paleontologists were to interpret the relation between these ideas very differently.

Manton, Anglo-Saxon Arthropod Systematics, and the Reconstructions of the Cambridge Team

These theoretical discussions were yet to begin when the Geological Survey of Canada (GSC) organized an expedition to the Burgess Shale in the mid-1960's. The purpose of that field work was to generate a Canadian-owned collection of fossils, but this new round of collecting almost a half-century after Walcott's work began the second phase of the controversy. When Harry B. Whittington, a renowned trilobite paleontologist, accepted GSC's invitation to lead the investigations of the ecology and biology of the Burgess Shale animals, his prime scientific motivation was a dissatisfaction with the methodological inadequacy of earlier studies of these fossils, rather than considerations connected to evolutionary theory.[26]

Whereas earlier investigators had treated the fossils as flat imprints on the surface of the shale slabs, it was Whittington's intention to analyse them as three-dimensional structures, whose layers were in principle discernible, though strongly compressed. In order to do this, it was necessary to develop an approach that made it possible to recognize and document these fine layers, and use that information on the three-dimensional structure of the fossils to make a credible reconstruction. The development and application of these methods turned out to be much more comprehensive than Whittington initially had considered, and it took him four and a half years to finish the first monograph on *Marrella splendens* – a small arthropod (less than 2 cm) whose most salient features is the existence of to long rearward directed spikes on its headshield. Whittington therefore decided to hire two doctoral students in the beginning of 1972. One of them, Derek Briggs, was assigned the task of (together with Whittington) reconstructing the arthropod specimens which were by far the most abundant group of organisms in the fossil material. The other, Simon Conway Morris, was put in charge of the remaining invertebrates, at the time then categorized (by Walcott) as "worms."[27]

[26] Whittington 1985, p. xiv; p. 17; 46; Briggs *et al.* 1994, p. 10-11.
[27] Gould 1989, p. 116; Briggs *et al*., 1994, p. 13. 195.

When the Cambridge team began their investigations the Burgess Shale fossils was dominated by the so-called *British School of Carcinology,*[28] which by the 1960's and 1970's had achieved scientific hegemony in Anglo-Saxon arthropod research – and whose leading figure, Sidnie Milana Manton (1902-1979), like Whittington and most of his associates working on the Burgess Shale material, was connected to Cambridge. Manton was known primarily as a functional morphologist, her claim to fame coming from her comprehensive work on the locomotive functions of arthropods, where she was considered the field's leading expert. According to Schram (1993) few zoologists and paleontologists published anything in that field without consulting her. This was also the case for Whittington's team of paleontologists working with the Burgess Shale "arthropods", where Manton was used as a consultant on the later monographs.[29]

The influence of Manton went beyond the level of functional reconstruction, however. The Cambridge team's systematic and evolutionary interpretation of the Burgess Shale material was initially to a very high degree based on Manton's ideas about the origin and evolution of arthropods.[30] Except in very general terms, Manton did not relate the criteria for her taxonomic and evolutionary position on arthropods to the theoretical debate on systematic principles that took hold during the 1960's and 1970's. But should we construct her position in relation to the three major systematic schools (the evolutionary, the phenetic and the cladistic school) that were striving for cultural hegemony within the zoological community in the 1970's (and this is important as that debate would later have profound implications for the evolutionary interpretation of the Burgess Shale fossils), Manton was closest to the evolutionary school, though her thinking also contained a number of idiosyncrasies independent of evolutionary systematics. To understand this, it is necessary to keep in mind, that Manton's academic maturation process took place before the establishment of the Modern Synthesis. Originally, she was a student of

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28 See Schram 1993 for of an account of the relations between Manton and the British School of Carcinology, as well as Baron 2009, and in- for an account of the relations between Manton and the Cambridge team's early reconstructions.

29 Se e.g. Briggs 1978, p. 484 and Whittington 1978, p. 487. Apparently Briggs had a hard time convincing Manton about the credibiligy of his construction of the Crustacean *Canadaspis.*

30 According to Briggs (Brysse 2008, p. 303) Manton's particular belief concerning systematic had less impact on the work of the Cambridge team than her ideas on the origin of arthropods. As will be clear below, I believe that the actual interpretive practice of Cambridge team (or at least of Whittington and of Conway Morris) shows that they and Manton had more in common than what was probably explicitly realized at the time.

Herbert Graham Cannon (1897-1963). Together with William Thomas Calman (1871-1952), the third dominating figure of the British School, they all belonged to an intellectual tradition stemming from the rational morphologist D'Arcy Thompson. One of the key elements in the ontological assumptions of this tradition was an idealist belief in the existence of archetypical baupläne in the animal kingdom[31] – something that was expressed in Manton's 'polyphyletic theory' of the origin of the arthropods. As a consequence of her investigations of arthropod anatomy and locomotive functions, Manton came to the conclusion that the *Arthropoda* could be segregated into four major groups (*Crustacea, Chelicerata, Uniramia* and *Trilobita*) each of which had arisen separately from an annelid-like (or worm-shaped) life form - and that typical arthropod characters, such as segmented limbs and a calcified exoskeleton supposedly had originated several times from a soft-bodied stem form.[32]

This interpretation was based on a range of empirical and ontological claims concerning arthropod anatomy. The most pivotal of these was of course the claim that each of the four major arthropod groups were bound together by a set of characters that could be identified as a separate and distinct bauplan. But Manton also claimed these morphological designs or architectures were so distinct from one another that any transformation between them was deemed to be "impossible." The implicit presumption behind this claim was that each of these body plans posses some kind of *functional closure* that would make it impossible for a lineage to make the evolutionary shifts that proponents of the evolutionary school of systematic believed were necessary if a lineage was to enter a new adaptive zone.[33] Manton therefore placed each of the four major arthropod groups in separate phyla claiming that the "fundamental" difference between them was to be explained by four separate and independent origins.

Both Manton's belief in distinct and "fundamental" baupläne for each of the major arthropod groups, and her ideas on the origin of arthropods, was adopted by the Cambridge team in their treatment of the Burgess Shale fossils. When studies revealed

[31] Schram 1993, p. 321, p. 323. See also Baron 2009. p. 290-291.
[32] Manton 1977, p. 1; p. 487-488.
[33] See the previous note. As noted by Baron 2009, p. 291, this functional closure was only to be assigned to the arthropods (where Manton was a specialist herself). As should be clear from the precedent, Manton was most ready to give other groups (in this case annelids) the kind of evolutionary flexibility that she denied the arthropods.

that many Burgess Shale arthropods were in the possession of characters considered indicative of separate and incommensurable architectures, these idealist presuppositions about morphology resulted in proposed phylogenies that assigned each of the animals a separate and independent origin, from a segmented an soft-bodied annelid-like form; and with the implication that they each represented new and hithertho "unknown" baupläne.[34]

Manton's theory of the polyphyletic origin of the arthropods also formed the interpretative basis for Whittington's work with the reconstruction of the segmented animal *Opabinia regalis. Opabinia* lacked antenna, chaetae and segmented limbs, all considered "essential" arthropod characters, instead having several very "non-arthropod" features, like five eyes and a segmented trunk. On the basis of this unusual combination of characters, one that cannot be found in either annelids or arthropods, Whittington concluded that *Opabinia* was to be termed an "enigmatic animal" and taxonomically problematic with respect to existing phyla. He further suggested that *Opabinia* should be regarded as an independent descendant of the group of segmented animals from which, according to Manton, both the annelids and the major arthropod groups are derived.[35]

This practice was not limited to the treatment of the Burgess Shale arthropods. Conway Morris, who had been given the responsibility for the remaining invertebrates, managed to publish no less than five papers in 1976 and 1977, each of which described a new Burgess Shale animal as a case of taxonomic problematica, implying that they were all in the possession of unique anatomical designs.[36]

Indeed, it was through these studies, rather than the studies of the arthropods,[37] that the idea that Burgess Shale contained "weird wonders" was given form. Of the five animals described by Conway Morris, *Hallucigenia sparsa,* became the most prominent exemplar of the "bizarre" anatomical designs in the Burgess Shale fauna. In Conway Morris' original reconstruction (shown below) *Hallucigenia* is walking on seven pairs of stilt-like thorns and as having seven tentacles protruding upwards.[38]

[34] See Whittington 1979, p. 263 for an example of this kind of argumentation.
[35] Whittington 1975, p. 3; p. 41.
[36] Conway Morris 1976a, p. 707; 1976b, p. 213, 1977a, p. 271; 1977b, p. 626; 1977c, p. 834.
[37] Of which some, as in the case *Opabinia,* apparently turned out not to be arthropods.
[38] Conway Morris 1979 p. 336, p. 343; Conway Morris & Whittington 1979, p. 119). According to Conway Morris the name *Hallucigenia* was derived from its "bizarre and dream-like appearance" (Conway Morris 1977b, p. 624)

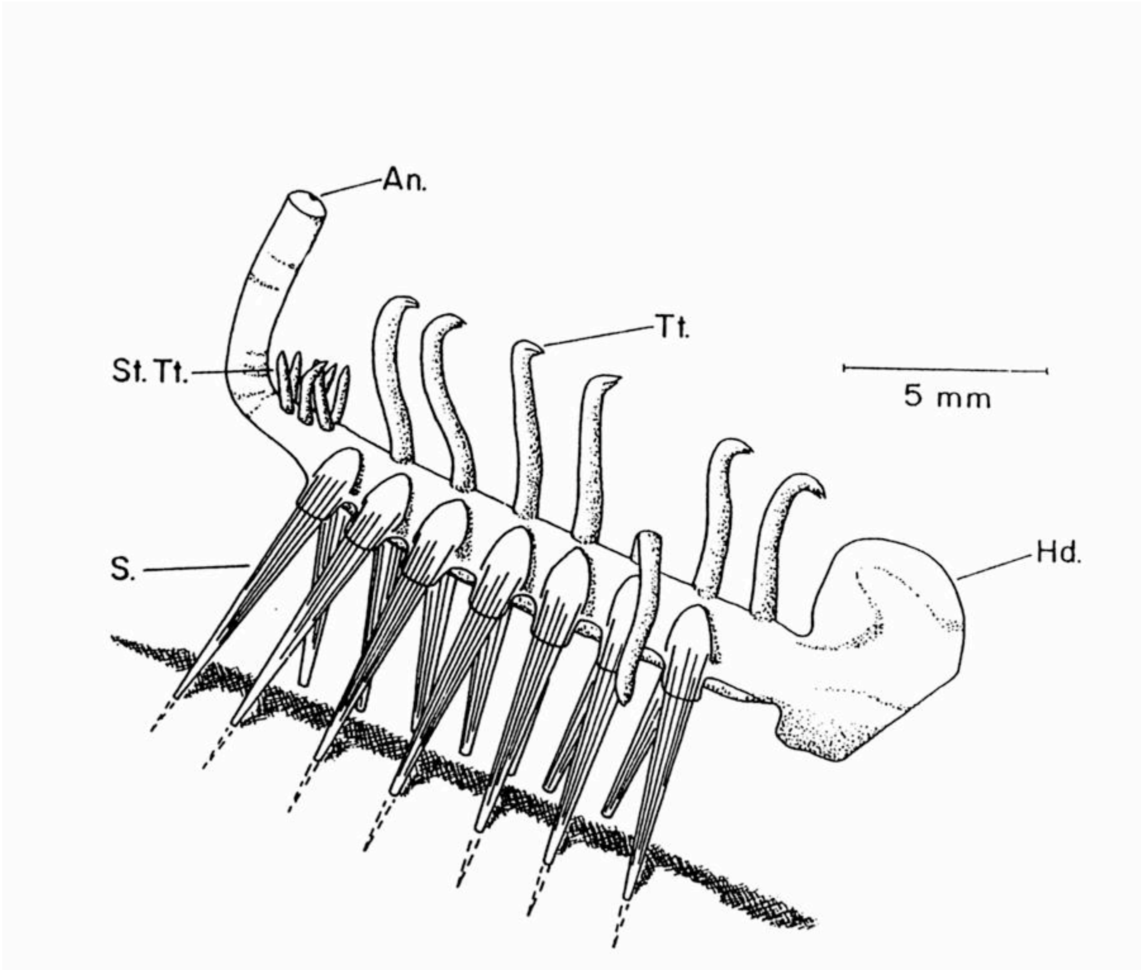

Figure 1: Conway Morris Original reconstruction of *Hallucigenia sparsa.* Conway Morris. 1977. p. 624.

The idea that the Burgess Shale fauna contained organisms with unique anatomical designs was launched in a popular paper in *Scientific American* jointly written by Conway Morris and Whittington in 1979. In this paper they claimed that the Burgess Shale, apart from containing members from known extant phyla, also contained ten or more representatives from hitherto unknown (and, since Cambrian presumably extinct) phyla.[39]

However, the Mantonian framework had even larger consequences for the interpretations of the Cambridge team (and especially Conway Morris and Whittington).[40] Because the Burgess Shale seemed to contain representatives of several special and unique anatomical body plans, Conway Morris and Whittington argued that

[39] Conway Morris and Whittington 1979, p. 110; p.116.
[40] As will be clear later, Briggs' biological interpretation of the Burgess Shale fauna deviated early from Whittington's and Conway Morris'.

the Cambrian faunas represented a time of extreme anatomical disparity. According to Conway Morris and Whittington this anatomical diversity was the result of a major evolutionary radiation in the beginning of the Cambrian. The image they portrayed of this radiation was that of many "experimentations in body plans," some of which later disappeared because of lack of success. Perhaps the most extreme consequence of the Mantonian framework drawn by members of the Cambridge team was Whittington's suggestion that metazoans (i.e. multi-cellular animals) in general had a polyphyletic origin, and that the apparent 'Cambrian Explosion' in anatomical disparity was to be explained as the result of the parallel evolution of many independent lineages. This conclusion made Manton's theory of the polyphyletic origin of arthropods a general principle for metazoan origin.[41]

Part II: Contingency and the Cambrian Disparity Debate:

The popular paper by Conway Morris and Whittington in the *Scientific American* augured a new phase in the history of the Burgess Shale studies – a period that coincided with the strong budget cut that hit British Universities under the Thatcher governments. During this period the Burgess Shale material was promoted by the Cambridge group as a cabinet of bizarre wonders with a special evolutionary significance.

The leading figure in this endeavor was Conway Morris, who wrote a series of papers arguing for the existence of a major evolutionary radiation at the Precambrian-Cambrian transformation. The result of this radiation had been a "experimentation" in new metazoan body plans and life forms. According to Conway Morris, this initial anatomical disparity had been reduced by later extinctions, during which most of these body plans had vanished.[42]

Conway Morris' interpretation of the causes of this sequence of events was formulated in a traditional ecological neo-Darwinian framework. Accordingly, Conway Morris explained the Cambrian radiation as the result of the ecological filling of empty niche space - a claim that he backed with a functional analysis that concluded that the trophic structures were more complex in Cambrian ecosystems than what was the case in older

[41] Conway Morris 1979, p. 343; Conway Morris and Whittington, 1979, p. 120; Whittington 1980, p. 145-146.
[42] Conway Morris 1979, p. 343; 1985a, p. 570; 1985b, p. 344; 1986, p. 425.

Precambrian ones; in particular, Conway Morris surmised that the Cambrian had a relatively sharp niche division with the presence of carnivores, detritivores and suspension feeders.[43]

This position was sharpened in a *Science* paper from October 1989 - a paper that was published almost synchronically with the publication of Stephen Jay Gould's *Wonderful Life* and the popular breakthrough of the Burgess Shale organisms in the public.[44] Following Segerstråle's vocabulary, this paper (*Burgess Shale Faunas and the Cambrian Explosion*) may be regarded as a 'trojan horse' for a polemic against the macroevolutionary research program that was promoted by Gould and his associates during the debates on theories of punctuated equilibria and species selection in the 1970's. The Cambrian scenario that Conway Morris defended in this paper was essentially a microevolutionary critique of that position. By arguing that the ecological filling of niches (by means of natural selection and adaptation) was an adequate explanation for the Cambrian radiation and the resulting anatomical disparity of that process, Conway Morris could at the same time conclude, that there was no need to postulate extra macroevolutionary processes, such as species selection, in order to explain the Cambrian radiation.[45]

Although Conway Morris advocated a view of the Cambrian radiation that was based on a traditional ecological neo-Darwinian perspective, he was not untouched by the critique of adaptationism that Gould and Lewontin had put forward a decade earlier. This is already clear from his monograph on the animal *Wiwaxia* from 1985. In a comparison of the adaptive potential of wiwaxiids (a group of soft bodied, scale-covered organisms) and mollusks, Conway Morris concluded that if life's tape were to be rerun, it would be quite possible that the former would have survived, and the latter gone extinct.[46] The "Replaying Life's Tape" thought experiment was addressed once again in the October 1989 issue of *Science.* On distance, Conway Morris believed that life in such a scenario would look much the same with various species occupying recognizable ecological roles

[43] Conway Morris 1985a, p. 570; p. 573; 1986, p. 435-436.
[44] There was probably also a breakthrough in the "scientific" public as well, as the Burgess Shale animal *Wiwaxia* hit the front page of the October 1989 issue of *Science* as an illustration of the paper by Conway Morris (1989)
[45] Conway Morris 1989, p. 345.
[46] Conway Morris 1985a, p. 572.

in the Cambrian ecosystem. However, the actors in this similar ecological theatre might themselves be totally different, and Conway Morris concluded that “a process of contingent diversification might produce a biota worthy of the finest science fiction”.[47]

Comparing the content of these two publications it would at first seem that by 1989, Gould and Conway Morris were very much in agreement in their evolutionary views. Both believed in a major metazoan radiation at the Precambrian/Cambrian border and ascribed to a polyphyletic view of the radiation of metazoan “body plans”.[48] Both also committed themselves to a view of the early Cambrian as a period of “evolutionary experimentation”, though Gould radicalized the notion of great Cambrian anatomical disparity in his claim that the Burgess Shale fauna *alone* contain greater anatomical disparity than all the recent metazoans taken together.[49] Furthermore, both Gould and Conway Morris seemed open to the possibility that contingency may produce radical different life forms than the ones found on Earth, and both of them used the famous metaphor of the “replaying of life’s tape” in order to suggest that life on Earth could have been dominated by different forms if time were rolled back to the Precambrian/Cambrian boundary and life allowed to evolve again.

However, a closer look at their arguments reveals that this similarity in metaphors in fact covered substantial theoretical disagreements. Whereas Gould perceived his adaptationist critique as part and parcel for a hierarchical theory of evolution, with the existence of an independent “decoupled” level of macroevolutionary processes, Conway Morris instead perceived it as an argument for the adequacy of traditional Darwinian explanation and only invoked contingency as an *ad hoc* explanation of the alien

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[47] See the previous note.

[48] It should be noted though that Conway Morris at the time of publication of the October 20th, 1989 number of *Science,* seems to distance himself somewhat from the strong essentialist equalization between phyla and body plans that the Mantonian framework entails. Whereas Gould speaks (in a Mantonian fashion) about a fall in the number of body plans after Cambrium, Conway Morris limits himself to speak about a fall in the “spectre of morphologies”. (Conway Morris 1989, p. 345).

[49] The use of the term *disparity* is Gould’s attempt to give a more precise metaphor for his claim about Burgess Shale anatomical variability. In Gould’s terminology this concept is to be separated from the traditional word *diversity* that he connects to the number of different species in a relevant sample. While Gould, like most biologists, believes that the number of species has risen since Cambrium, he claims that the disparity has fallen. In practice Gould estimates Burgess Shale disparity from the number of specimens that has been interpreted as representatives of new phyla or new major arthropod groups by the Cambridge group and its associates (e.g. Table 3.3 p. 210-211). But he also contends that the claim of higher Cambrian disparity is defendable from *any* anatomical criterion (Gould 1989, p. 23ff; 47-49; p. 209).

appearance of the Burgess Shale fauna.[50] Conway Morris' agenda in the 1980's was not primarily an effort to show that Cambrian life-forms were widely different from extant biotas, but to show that despite its alien appearance, Cambrian life were remarkably similar to ours, filling out the same ecological roles and having similar trophic structures.

In contrast, the contingency thesis advocated by in *Wonderful Life* has, at least to a certain extent, anti-uniformitarian tendencies. To Gould, the contingency concept functioned as a category for the unique historical coincidences that he believed to be essential for the historical course of life's evolution on Earth.[51]

Although finding that the conventional explanation of the Cambrian Explosion as a filling of empty niches, does capture important processes behind the Cambrian radiation, Gould did not believe it to be adequate to explain the origin of the enormous disparity that was allegedly to be found in the Burgess Shale material. Instead he believed that a unique sequence of the events led to the Cambrian radiation, and that part of the explanation behind the apparent explosion of life forms was a greater evolutionary potential of Cambrian metazoans as compared to later periods.[52] To Gould this overwhelming diversity of organismal forms in the Burgess Shale deposits, as compared to later faunas, was an empirical testimony to the scope of the Cambrian Explosion and a later extinction that led to the demise of most of the unique Cambrian anatomical designs.[53]

Gould's commitment to contingency as a powerful agent in evolutionary history is reflected in *Wonderful Life's* treatment of two other biotas – the so-called Vendian fauna

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[50] Unlike Gould (1989, p. 283) Conway Morris does not make a clear distinction between contingency and randomness in his original use of the concept. This, of course, begs the question of whether the authors actually have the same understanding of the meaning of contingency. Though a thorough analysis of the contingency concept is beyond the scope of this paper, I am inclined to answer 'no' to this question, as there is no reason to suppose that the early Conway Morris shared Gould's conception of contingency as a causal category for unique historical coincidences.

[51] Gould 1989, p. 284.

[52] As a possible a mechanism for this, Gould suggests that, contrary to the conventional view, Cambrian metazoan genomes were simpler and more flexible (Gould 1989, p. 230). Gould is clearly on thin ice here. To his defense it must be added that the molecular evidence on this area was scarce at the time (1989) of the publication of *Wonderful Life.* The idea of a greater evolutionary potential of Cambrian metazoans has recently been revived in the context of developmental plasticity by Newman & Müller (2006). However their account of the debate on the Cambrian radiation is curiously one-sided, giving no references to sources that are more recent than 1994, and uncritically accepting the scenario of the Cambrian radiation as an "explosion" in new body plans and anatomical design. As will be clear in the following account this is inadequate in face of the development of the Burgess Shale debate.

[53] Gould 1989, p. 49; p. 209, p. 304.

of Ediacara and the pre-Cambrian Tommotian fauna.[54] Gould suggested that both of these faunas should be regarded as earlier independent evolutionary experiments in multi-cellular life. In relation to the Ediacaran fauna Gould leaned on the paleontologist Adolf Seilacher's interpretation according to which these fossil should be interpreted as a separate group of multi-cellular organisms, having nothing to do with the origin of the metazoans.[55] Gould's interpretations of the Tommotian fauna was based on the presence of small (5 mm) hard bodied fossils of unknown zoological affinity and the archeocyathids – a group of sessile reef-forming cone-shaped organisms with double porous walls. Since their discovery, the taxonomic status of the archeocyatids has been much debated with the group being moved back and forth between different phyla. The majority view at the time of publication of *Wonderful Life* was that the archeaocyathids should be classified as a separate phylum. For Gould this convention offered support for viewing the Tommotian fauna as an early stage in the Cambrian explosion of body plans – with some anatomical designs that have disappeared by the time of Burgess Shale fauna.[56]

By the use of these examples Gould defended an interpretation of the pre-Cambrian/Cambrian transition as a period of comparatively "sudden" radiations and experimentations in new anatomical designs. For Gould this lent empirical support of contingency's decisive role in the major course of evolution.

This was done in a masterful hijacking of Conway Morris' "replaying the tape of life" metaphor. In the last chapter of *Wonderful Life,* Gould presented a series of thought-experiments that was to serve as counter-factuals to the actual history of life on Earth. By presenting a set of evolutionationary scenarios based on questions like 'what if the eukaryote cell had never evolved?' or 'what if the Vendian fauna hadn't become extinct?' Gould attempted to give an illustration of what life on Earth might have looked like, if the history of life was reset at various historical periods and run again with different outcomes – and to illustrate the potential impact of contingency on evolution by arguing

[54] In 1989 these two fauna types represented the only known traces of multicellular life before the Burgess Shale type faunas.
[55] Seilacher 1984. This position is in opposition to Glaessners (1984) traditional interpretation that regards the Ediacaran organism as early metazoans.
[56] Gould, 1989, p. 59, p. 226, p. 314-315; Rowland , 2001, p. 1065. Contemporary consensus has placed the *Archaeocyatha* as a major group within the *Porifera.*

that, if particular historical events had slightly different outcomes, life on Earth would have been radically different

The theoretical disagreements between Gould and Conway Morris are thus reflected both in their interpretation of the fossil data, and, perhaps most clearly, in their very different uses of contingency. To Conway Morris, the concept of contingency functioned as an addendum to the general processes that he regarded as the *explanans* of evolutionary biology. Gould, however, based his view of evolution on the ontological assumption that unique historical coincidences are essential causal agents in life's evolutionary history. For him, contingency becomes the decisive force in evolution. Such a position, however, implies that these causes are *particular* with respect to the historical sequence in question, and that general processes – or law-based explanations – are inadequate to understand the higher course of evolution.

The Cladistic Revolution in Arthropod Systematics and the Controversy on Diversity

The publication and success of *Wonderful Life* invited the public and popular breakthrough of the Burgess Shale fossils. This historical coincidence meant that public understanding of the Burgess Shale debate was to a large extent based on Gould's idiosyncrasies, and therefore, indirectly on Manton's theoretical framework. This was true despite a whole range of underlying disagreements about the primacy of adaptation, the possibility of equating evolution above and below the species level, and the role of historical contingency in evolution in the wild.

The systematic interpretations underwriting Gould's scenario of the Cambrian radiation was by this time getting into trouble, however, and theoretical developments outside the community of Anglo-Saxon paleontologists occupied with Cambrian fossils would soon force both Gould and Conway Morris to make substantial revisions in the way they defended their evolutionary views. Beginning in the 1970's, a controversy had been raging concerning the principles of classification within another scientific thought collective - the community of systematics.[57] Involved in this conflict were three major

[57] The historical development of this controversy, and epistemological issues involved are in themselves fascinating but beyond the scope of this paper. For extensive treatments of this subject, see Hull 1988; Schuh 2000; and Williams and Forey 2004. See also Suárez-Díaz and Anaya-Munoz 2008, for an analysis of the role of molecular data in constructing phyologenies.

systematic schools: the already mentioned school of evolutionary systematics (also known as the Mayr-Simpson school) which sought a biological classification based both on phylogenetic relations and on ecological and morphological similarities; the phenetic school that sought to base biological classification on measurable degrees of morphological similarity alone, and finally the cladist school (also known as the school of phylogenetic systematics) that sought to base biological classification on phylogenetic relations alone, using parsimony and monophyly as their primary guiding principles in systematic analysis.[58]

By the end of the 1980's it was becoming increasingly clear that the cladist school was going to emerge victorious from this controversy. As described by Brysse and Baron, this development turned out to have dramatic consequence for the Burgess Shale debate:[59] to a certain degree, Manton's idea of phyla being defined as having distinct origins had, until now, been able to coexist with the evolutionary school, whose systematic practice was based on the idea that major taxonomic groups shared 'adaptive zones'. This was true for an evolutionary taxonomist like George Gaylord Simpson (the author of the "adaptive zone" concept) and for a functional morphologist like Manton because both made *de facto* correlations between taxonomic divisions and adaptive bits of morphology.[60] The cladist school, however, contains several philosophical trends that are headed in direct opposite to the most prominent features of Manton's thinking. The most obvious cases for this are Manton's polyphyletic theory of arthropod origin and her essentialist notion of phyla being defined by the common possession of distinct body plans. As noted by Baron, the polyphyletic theory of arthropod origin conflicted directly with the one of the primary epistemic values of cladistic practice, namely the principle of parsimony. This principle prescribes that the simplest phylogenetic tree (i.e. the one with the *least* possible evolutionary character changes) should be preferred among possible alternatives. But following this principle, we would expect that typical arthropod characters like exoskeleton, segmented limbs etc. have a common phylogenetic origin.

[58] See Hull 1988, for an introduction to these schools and their background.
[59] See Brysse 2008, p. 303ff and Baron 2009, for a more thorough analysis of this development.
[60] Simpson would, of course, never have agreed with Manton's idealist characterization of archetypical arthropod body plans. As a proponent of evolutionary systematics, he acknowledged both that organisms change over time and included the notions of "pre-adaptive" and "post-adaptive" phases of evolution.

Hence, the principle of parsimony is therefore much more in accord with a monophyletic theory of arthropod origin, than with a polyphyletic theory.[61]

For various reasons, it was Derek Briggs, the third core member of the Cambridge team, who became the leading antagonist in the cladistic attack on Manton's taxomomic and evolutionary interpretations of the arthropods.[62] With a paper in the October 13, 1989 issue of *Science* – just a week before Conway Morris hit the front page of the same journal with *Wiwaxia* – Briggs and his associate Richard Fortey would be the first Anglo-Saxon paleontologists to publish a cladistic-based phylogenetic analysis of the Burgess Shale arthropods that included representatives of three of Manton's four major arthropod groups (*Uniramia* excepted).[63] Here, Briggs and Fortey, criticizing the theory of a polyphyletic origin of the arthropods, argued that the Cambrian arthropods should be regarded as morphological links between the major arthropod groups. This position was later expanded by Briggs, who attacked both Gould's view of the role of the arthropods in the Cambrian radiation and especially his contention that the Cambrian arthropods should be regarded as representatives of separate phyla with distinct body plans.[64]

It was not only from the systematic front that Gould's evolutionary scenario came under fire, however. Perhaps the greatest stroke against the image of the Burgess Shale fauna as a collection of weird evolutionary wonders was directed against Conway Morris' original reconstruction of *Hallucigenia sparsa.* As the result of new findings in the Chenjiang fauna (which is a Cambrian fossil fauna of the same type as the Burgess Shale), the paleontologists.Hou Xianguang and Lars Ramsköld published an alternative reconstruction of this animal, that literally turned it upside down. Their reconstruction is shown below, together with the original reconstruction of Conway Morris and a reconstruction of a representative of the fossil lobopods.

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[61] See Baron, 2009, p. 292-293.
[62] See Baron 2009, p. 292. Apparently Briggs was from the beginning somewhat skeptical towards a polyphyletic theory of polyphetic arthropod origin, and voiced this skepticism already in 1978 where the theory was presented at a symposium on invertebrate evolution. Whittington, 1979, p. 262; Manton and Anderson, 1979, p. 269; House, 1979, p. 485.
[63] Briggs and Fortey 1989, p. 242.
[64] Briggs 1990, p. 24ff.

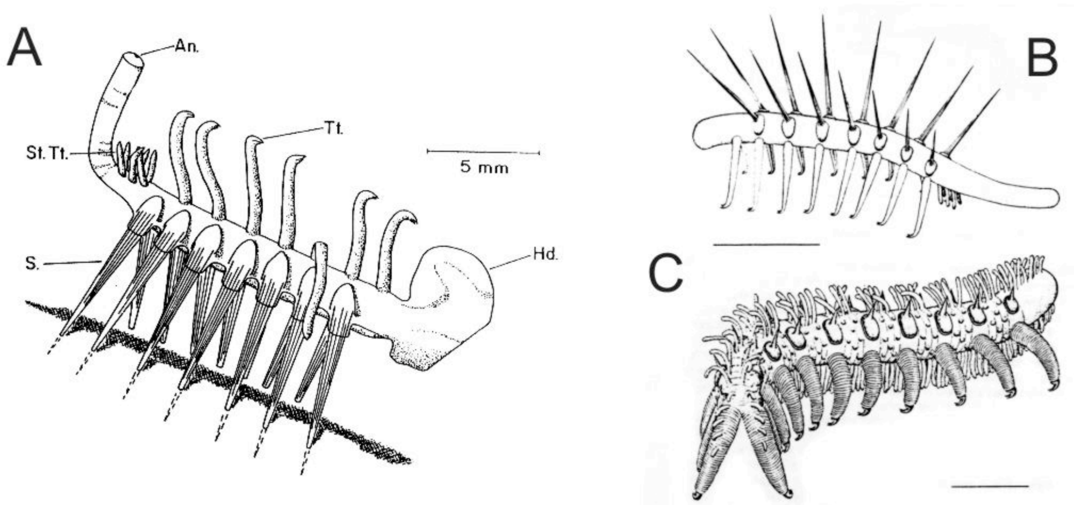

Figure 2. The original reconstruction of *Hallucigeina sparsa* (A) along with Ramsköld's and Hou's reconstruction (B) and a reconstruction of a lobopod (C). Taken from Conway Morris 1977b, p. 628, and from Ramsköld and Hou 1991, p. 227.

In the original reconstruction to the left (A) *Hallucigenia sparsa* is walking on seven pairs of stiltlike thorns with seven tentacles protruding upwards. In Ramsköld's and Hou's reconstruction (B) the animal is turned on its head, and the "stiltlike thorns" in Conway Morris' reconstruction is interpreted as seven pairs of spines on the animals back. The "seven tentacles" now appears to be the original specimens preserved half of seven pairs of limbs. The result is that while *Hallucigenia sparsa* may still seem to be a strange animal (controversy remains as to what is the front and back of the animal) it can be classified as belong to the lobopods (C), which the extant onychophores are regarded as modern representatives.

By the early 1990's, it was not only the Cambridge team's interpretation of the Burgess Shale arthropods that came under attack, but also their reconstructions of the remaining invertebrates. For Gould's claim for higher Cambrian disparity, this was a serious problem as it was connected to the ontological presumption that higher taxa could be defined by the common possession of basic body plans.

But in *Wonderful Life* Gould had also contended that his claim for higher Cambrian disparity is defendable from *any* anatomical criterion. And for this claim Briggs opened a back door for Gould by accepting that systematic arguments were not in themselves sufficient to reject Gould's Cambrian scenario. Though he did note that the claims were unfounded, Briggs also noted that it is difficult to find an "objective" estimate for morphological disparity, and that the subject needed further analysis.[65]

Gould was quick to take up the challenge. In a paper in a 1991 issue of *Paleobiology*, he argued that Briggs' and Fortey's cladistic analyses were irrelevant to the question of higher Cambrian disparity, and also that the question could only be solved by comparing the morphology of Cambrian and extant arthropods in a quantified morphological space. In such an analysis each animal is coded as a point in a multi-dimensional coordinate system where each dimension corresponds to a morphological character measure, and the distance between their representative points in the morphospace is then recorded.[66]

With this, the disparity debate entered a new phase - a phase that was characterized by attempt to make a quantitative *operationalisation* of the disparity metaphor. In this period, the discussion on Cambrian arthropod disparity was transformed from a systematic debate to a problem in theoretical morphology, and finally, into a technical debate about the validity and interpretation of various types of morphometric investigations. Briggs and his associates first attempted such a comparative analysis in a paper in *Science* in 1992 (*Morphological Disparity in the Cambrian*), and later discussed it in an exchange between the author and several critics, including Gould.[67]

The quantitative debate on disparity continued through the 1990's and is beyond the scope of this paper.[68] It may come as no surprise, however, that no consensus was reached between Gould and his adversaries concerning the comparative morphological disparity of Cambrian and extant arthropods.[69] But since the claim of greater Cambrian disparity is central to Gould's evolutionary scenario in *Wonderful Life,* it is up to proponents of this scenario to prove that Cambrian arthropods, in fact, contain body plans that are truly incomparable to more modern forms. It is therefore noteworthy that this claim has not, up till now, received decisive empirical support.

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[65] Gould 1989, p. 41, p. 209; Briggs 1990, p. 38.
[66] Gould 1991c, p. 420.
[67] Briggs *et al*. 1992a, p. 1671; Foote and Gould 1992, p. 1816; Lee 1992, p. 1816f; Briggs *et al.* 1992b, p. 1817.
[68] See e.g. Foote 1993, p. 185ff; Ridley 1993, p. 519ff; Gould 1993, p. 522f; Wills *et al.* 1994, p. 93ff; Fortey *et al.* 1996, p. 13ff; 1997, p. 429f.
[69] When Gould was asked to give his current opinion on the subject, during a visit to the University of Copenhagen in the autumn 2001 (some months before his deaths) he maintained that the disparity "even in the limited sample that is avalaible from Cambrium" was at least as high as the disparity of all extant arthropods taken together.

In the light of this unresolved, quite technical controversy, the overall development of the Burgess Shale debate in the 1990's must be considered a backlash for Gould on several fronts. The change of context facilitated by the cladistic revolution in systematics (particularly its methodological emphasis on monophyly) was a devastating blow to the taxonomic underpinning of Gould's Cambrian scenario in *Wonderful Life.* In order to defend his claims on the central role of contingency in evolution, Gould turned the disparity debate into a discussion on quantitive morphometrics – a move that itself perhaps is the most obvious illustration of the vulnerability of Gould's evolutionary scenario to the shift in standards as to what constitutes good scientific practice within the systematic community. The revisionary reconstruction of *Hallucgenia sparsa* that was based on the findings of Ramsköld and Hou in the Chenjiang fauna seemed to have facilitated this development.

The impact of this backlash reached not only Gould's specific Cambrian scenario as described in *Wonderful Life,* but the whole idea of a "Cambrian Explosion." This may be even further illustrated considering the development in two other areas of investigation, molecular systematics and micropaleontology. Though the use and reliability of the "molecular clock" as a dating method for the evolutionary origin of taxa has been widely debated even from its inception in the 1980's, the studies that were actually done using this method indicate a much older Precambrian origin of the metazoan body plan than was previously otherwise assumed. And finally, the technique of electron microcopy, put to use in the 1990's, disclosed a rich Precambrian fauna of very small animals, pushing the fossil evidence for metazoans back with several 100 million years.[70] The number of anomalies was rising.

Contingency vs. Convergence

As noted, the critique directed towards Gould by Briggs and his associates was a serious blow, especially because it collided with other inconvenient taxonomic and paleontological revisions of the Burgess Shale material. Despite the fact that this development rattled some of the central planks of Gould's larger argument, Briggs and his associates remained rather positive towards Gould's claim that contingency has

[70] Seilacher *et al*. 1998, p. 80; Chen *et al*. 2000, p. 4457; Xiao *et al*. 2000 p. 13689.

played a major role for the higher course of metazoan evolution, hypothesis. In one of their papers on disparity (*Disparity as an evolutionary index: a comparison of Cambrian and recent arthropods*), Wills, Briggs and Fortey regarded contingency to be a plausible factor in the explanation of the differential survival of certain Burgess Shale-genus as well as to why some morphological characters are stabilized during the history of evolution while others vary enormously.[71]

It was therefore not Briggs and his associates, but Conway Morris, who mounted the most radical attack on Gould's Cambrian contingency thesis in 1998. This was done in the counter-book *The Crucible of Creation* that can be regarded as a comprehensive criticism of all essential propositions in *Wonderful Life.*

Indeed, no stone was left unturned in this endeavor, and the book even included attacks on Gould's portrayal of Walcott's treatment of the Burgess Shale fossils and his atheist world view; Conway Morris seemed to object not only to Gould's science but also with his metaphysics. Indeed, *The Crucible of Creation* and *Wonderful Life* read side by side, makes them appear so entwined at times that it seems hard to tell them apart.[72]

What is clear, however, is that Conway Morris, despite several intellectual transformations, had retained his basic commitment to an ecological Darwinism that regards the Cambrian explosion to be explainable in familiar terms of general ecological processes like natural selection and the ecological filling of empty niche space. This commitment continued despite the fact that the Conway Morris writing in 1998 about seems to have very little in common with the Conway Morris of the 1970's when it comes to the Cambrian Explosion. Thus the Conway Morris of *The Crucible of Creation* denounces his own former opinion of the Cambrian radiation (now defended by Gould) as an explosion in metazoan body plan variability, as well as the claim of a later radical decimation of that disparity. Reverting to a position closer to Walcott's initial taxonomic interpretation than his own former work as part of the Cambridge group, Conway Morris instead argued in 1998 that most Cambrian fossils can either be accommodated into modern groups or interpreted as missing morphological links between them. Conway Morris extended this type of interpretation of the Ediacaran fauna, considered by Gould

[71] Wills *et al*. 1994, p. 122.
[72] Conway Morris, 1998 p. 38ff; p. 218.

to be a separate evolutionary experiment. Contrary to Gould, Conway Morris believed that the Ediacaran fossils are metazoan and regarded Martin Glaessner's interpretation as being basically correct.[73]

As to the ontological status of body plans Conway Morris distanced himself even further from the strong essentialist equivocation between phyla and body plans, getting rid of the remaining Mantonian elements of his thinking. For the Conway Morris of *The Crucible of Creation,* the body plan was by now transformed into a concept with a primarily *epistemological* content. The idea that phyla can be defined by the possession of common body plans was for the later Conway Morris merely a conceptual instrument that can be used to bring order to the complex problems of biological classification. But it was also an instrument that contains certain fallibilities. These are connected with the fact that this conceptualization creates a tension between a static notion of body plans and the dynamical character of organismic evolution. The most important consequence of this tension is that the practical delineation of body plans becomes, if not arbitrary, at least somewhat elastic. Thus, the allowed range of variation seems to be highly variable depending on the clade in question, being, for instance much larger in mollusks than in chaetognaths. The body plan concept can furthermore be applied at different scales in the taxonomic hierarchy. Hence, it is, according to Conway Morris, not only possible to recognize a common body plan for mollusks, but also to separate different groups within *Mollusca* each having a distinct body plan. The choice of phylogenetic scale is thus crucial for the decision about what constitutes a body plan. Instead of regarding body plans as metaphysical absolutes, claims of common shared body plans should be seen as reflection of the density of the clustering of these organisms in a quantitative morphospace—a purely theoretical representation of all possible body plans. Thus the mollusks represent such a clustering that, approached more closely, turns out to consist of several smaller clusters of cephalopods, gastropods, and bivalves. Likewise each of the approximately 35 metazoan phyla can be regarded as a clustering in morphospace. The characters used to diagnose phyla were, in Conway Morris' opinion, not principally

[73] Conway Morris 1998, p. 28f; p. 169f. Conway Morris' argumentation for the correctness of Glaessner's interpretation rests on the presence of the fossil *Thaumaptilon* in the Burgess Shale fauna, which Conway Morris believes to be a late representative of the Ediacaran fauna. According to Conway Morris *Thaumaptilon* is to be interpreted as a cnidarian. Conway Morris does not comment on Gould's interpretation of the Tommotian fauna.

different from the ones used to diagnose different classes of mollusks, and he therefore believed that Gould's and his own earlier claim of a 'Cambrian explosion' in body plans and weird designs to be a taxonomic artifact.[74]

If anything, these revisions served only to strengthen the platform for the basic evolutionary position that had been part and parcel of Conway Morris treatment of the Burgess Shale all along, however. Repeating this interpretation in *The Crucible of Creation,* Conway Morris argued that the Cambrian metazoan radiation is explainable in a traditional ecological Darwinian perspective as the result of the filling of empty niches and the emergence of an effective predation in Cambrian ecosystems. This predation then facilitated a series of evolutionary feedback mechanisms resulting in the appearance of a protective exoskeleton among prey organisms, and a rise in Cambrian diversity as the result of a limitation in the competition for resources. Thus, Conway Morris strongly disagreed with Gould's contention that other evolutionary forces were at play in the Cambrian radiation than today.[75]

In *The Crucible of Creation* Conway Morris' ecological Darwinism was developed into a platform for a full-scale attack on the contingency hypothesis itself, and on Gould's perception about what should be the cognitive goal of evolutionary explanations. While not denying that contingency can be central for the evolutionary success or failure of specific taxa, Conway Morris believed this to be a trivial point, and not especially illuminating for our understanding of evolution. Conway Morris believed that Gould's contingency hypothesis carries a much more serious flaw however. By directing our attention towards the inherent historical contingency in evolution, such a hypothesis risks hiding an underlying principal predictability in evolution that is much more important. Citing the parallel evolution of a South American marsupial saber-tooth tiger and a placental saber-tooth tiger on the northern hemisphere as a classical textbook example, Conway Morris argued that the abundance of evolutionary convergence demonstrate the existence of a set of ecological limitations to the biological properties that will become

[74] Conway Morris 1998, p. 169f.
[75] Of course, Gould might well accept this ecological-evolutionary scenario, and still argue that life would have evolved quite differently, had predation not evolved. This illustrates that although Gould's argument for the role of contingency were originally based on the empirical claim of higher Cambrian disparity, this is not a connection of logical necessity. The debate that connected contingency with Cambrian disparity was itself a contingent phenomenon.

dominant during evolution. In other words, evolution's many examples of convergence seem to indicate a rather fixed set of niches, as well as a limit to the possible morphological "solutions" to a set of functional problems (also a finite set) faced by all animals. Replaying life's tape, it may not be certain that Earth today would be populated by whales, but it would, according to Conway Morris, be certain that a large plankton-eating sea animal would one day occupy the oceans. By extension, Gould was wrong to claim that life on Earth could have evolved radically different if the history of evolution were allowed to be rerun from Cambrian. On the surface it would perhaps at first appear alien, but a closer investigation would reveal that these life forms were occupying similar recognizable ecological roles. Likewise "replaying life's tape" would invite the same biological properties—intelligence, for example—to inevitably appear because these properties will always confer a selective advantage in the struggle for existence.[76]

The publication of *The Crucible of Creation* led to a polemical discussion between several of the main figures involved in this debate, culminating in an exchange between Conway Morris and Gould in *Natural History Magazine,* december 1998. Entitled *Showdown on the Burgess Shale*, Gould accused Conway Morris of having a selective memory - a claim that was shared by Richard Fortey in a review of *The Crucible of Creation* for *The New York Review of Books.*[77]

This accusation may at first appear strange. Conway Morris made no attempt in either his book or in his *Natural History* paper to cover up the Cambridge group's earlier interpretation on the Burgess Shale fossils, including his own original reconstruction of *Hallucigenia,* as a collection of strange animals. On the contrary, Conway Morris took pain to explain, using a line of argumentation close to the one that was earlier used by Briggs, Fortey and Wills, why he now consider these earlier interpretations to be faulty.[78]

But a close reading of Fortey, as well as of Gould, discloses that this accusation is first and foremost directed against Conway Morris' conception of the role of contingency in evolution. Both Fortey and Gould contended, in their receival of *The Crucible of*

[76] Conway Morris 1998, p. 13, p. 139, p. 202f. A textbook use of the saber-tooth tigers example of evolutionary convergence can be found in Ridley 1996, p. 471.

[77] See Fortey 1998, and Conway Morris and Gould 1998. This exchange crystallized the positions of Gould and Conway Morris as two opposite poles that were not significantly changed before Gould's sudden death in 2002. Gould essentially confirmed this position in his last book *The Structure of Evolutionary Theory* (Gould 2001, p. 1160f).

[78] Conway Morris 1998, p. 54ff; p. 139.

Creation, that the earlier Conway Morris was much more open to possibility that contingency was a major factor in shaping the higher course of evolution. It is, of course, true that it was originally Conway Morris who introduced the metaphor of "replaying life's tape". It is also true that Conway Morris neglected to mention, both in *The Crucible of Creation* and in the exchange in the *Natural History Magazine* that his argument of convergence seems to lead in another direction. But at the same time it appears that especially Fortey[79] seems to be somewhat blind to the fact that Conway Morris, at least in writing, had not at any time abandoned neither the basic ecological Darwinism, nor the general process- or law-based approach to evolutionary explanations that has all along been the primary premise for his interpretations of the Burgess Shale fossils. In arguing against Gould's earlier claim from the 1970's that the higher course of evolution is governed by special macro-evolutionary processes like species selection, and against Gould's subsequent claim that the higher course of evolution is governed by historical contingency Conway Morris folded the Burgess Shale fossils into a traditional Darwinian interpretation and into a demonstration that the Cambrian biota, despite its alien appearance, has a number of properties in common with extant ecosystems.

Conclusion

Complexity seems to be the boon of philosophical accounts of science. Earlier generations of scholars attempted to bridge this problem by embedding the practice of the exemplary scientist into collective entities of thought known as paradigms; epistemes; styles of reasoning or even moral economies.[80] The weakness of such entities is of course, their porosity. As Ludwik Fleck pointed out long ago, an individual might belong to several "thought collectives" at once. As part of a research community, a scientist may belong to one collective, but as a member of a political party, a social class or a nation he belongs to others.[81]

[79] Gould seems to be less severe in his attacks on Conway Morris than Fortey on this point. In *Wonderful Life* Gould himself describes his evolutionary scenario as a "development" of ideas first presented by Conway Morris

[80] For an explication of these positions see Kuhn 1962 (paradigms); Foucault 1966/1994 (epistemes); Hacking 2000 (styles of reasoning); and Daston 1995 (moral economies)..

[81] Fleck 1934/1979, p. 45.

What Fleck did not address in his description of the thought collective, was that the semi-autonomous character of these entities means that a scientist may be a member of several *scientific* thought collectives. The scientific thought collectives relevant to the Burgess Shale controversies described in the above include (at a minimum) paleontology, evolutionary biology, systematics as well as carcinology and arthropod research. It might even be tempting to add the geographically limiting adjective ‘Anglo-Saxon’ to all of these collectives. Indeed several of these discussions appear geographically highly idiosyncratic considering for instance, that punctuationalist models seems to have played a much more predominant role in Soviet paleontology and evolutionary thinking before the 1970’s than in American paleontology or the fact that the majority of the (cladistically-oriented) German arthropod research community *never* bought into Manton’s ideas of a polyphyletic arthropod origin.[82]

As demonstrated in the previous section, navigating in a context of multiple scientific thought collectives is not an easy task. To some extent each of these collective has their own dynamic complete with fairly negotiated standards for investigation and explanation, theoretical background assumptions and certain peculiarities of practice. But the intellectual development in one of these collectives may “spill over” having far reaching consequences for the treatment of apparently independent epistemic problems that are subject to investigation in other communities. For the practicing scientist it is necessary to take this complex web of interactions into account in order to be able to navigate in the intricacies of such a situation.

Thus, both Gould and Conway Morris had to balance in a context of shifting standards for how to evaluate the legitimacy of various claims and evolutionary scenarios. For Gould, the difficulties that Manton’s theoretical framework encountered in the 1990’s, invited an attempt to turn his taxonomically based claims of higher Cambrian disparity into a discussion of the estimated distances in quantitative morphospace. For Conway Morris the same developments led him to denounce earlier claims of higher Cambrian disparity altogether. But despite these intellectual transformations there was also continuity in the thinking of this story’s main antagonists.

[82] See Gould and Lewontin 1977, p. 146, for a remark on punctuationalist thought in Soviet an American paleontology. The most prominent early german defence for phylogenetic systematics is of course Hennig, 1966.

For Conway Morris this continuity appears as a commitment to an ecological Darwinian account of the Cambrian radiation as a filling of empty niche space, and a belief that the higher course of evolution is explainable by within-population microevolutionary processes that remain robust when other events are substituted. For Gould this continuity appears in his commitment to a belief that unique historical events are essential causal agents and that (despite also showing an interest in the development of nomothethic explanations at a macroevolutionary level) the higher course of evolution can only be explained as the contingent result of a unique sequence of coincidences.

So far most studies of academic science[83] has had a tendency to treat the practicing scientist as members of a single (enclosed) thought collective that worked in isolation of other similar entities unless the discipline was in a state of crisis of paradigmatic proportions. The richness and complexity of the dynamics revealed here shows that this is not enough.

Acknowledgements: Thanks to Jens Høeg and Claus Emmeche for help and encouragement and constructive critique during the entire process of the making of this paper. Fred Schram provide helpful advice and access to private correspondence while Svend Lange provided lodging during a constructive stay in Amsterdam in 2002. An early draft of this paper were read and commented by Andrew Hamilton and Jane Maienschein and the Center for Biology and Society at the Arizona State University were the kind hosts during a three months stay in Tempe, Arizona. A special thank is due to Miranda Paton who made a very constructive and detailed criticism the manuscript. And finally thanks to the employees and associates at the Zoological Museum, the Biological Institute and Center for Philosophy of Nature and Science Studies at the University of Copenhagen for moral support and helpful critique. The responsibility for any shortcomings of this paper is, of course, mine alone.

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Section IV: Conclusion

This is not a thesis that aims to develop or advance a general account of methodology or theory-choice. General theories may be useful sources of understanding, modeling and explanation, or serve as heuristic guidelines, but are difficult to construct in a field like the history and philosophy of biology. Hence, it is probably in the specific case-stories that we find most of the interesting lessons. Many practitioners of behavioural ecology (and many biologists with a general interest in evolutionary problems), will probably enjoy (or be alarmed by) reading analyses arguing that some of the pivotal papers that led to the rejection of group selection by a majority of biologists were made on shaky arguments – and that this rejection was in fact founded more on the compability between the values of the authors of these papers and the dominant ideals of discipline, rather than the quality of the arguments presented. Likewise, many paleontologists or systematicists (and others interested in fossil research) may find interest in the account of how Briggs' were able to convince a majority of Anglo-Saxon arthropod researchers of the comparative advantage of a monophyletic approach (vs. a polyphyletic approach) to arthropod evolution despite presenting a set of arguments that from a purely analytical perspective appear inconsistent and unconvincing.

I believe however, that this comparative study shows some general points that *can* be made concerning the role of epistemic values in scientific controversies: Some of them are as following:

1) There is a relation of reciprocal underdetermination between epistemic values and other important variables in the scientific process: As noted in Section I, epistemic values logically underdetermine both theory-choice and concrete investigation procedures. Furthermore, the preference and application of epistemic values of the individual scientist are underdetermined by what can be considered to be the epistemic values of the collective. Scientific theories (themselves underdetermined by epistemic values) underdetermine factual beliefs – and factual beliefs underdetermine scientific theories. In short the important variables in a scientific argument are connected by appeal to contextual plausibility rather than absolute logical necessity. The previous investigations show several examples of this. The most obvious is the historical connection between the factual claim of higher Cambrian disparity and the contingency hypothesis – a connection that may itself be regarded as an instance of contingency. It was a historical (and geographical) coincidence that led the Burgess Shale fossils into the hands of group of Anglo Saxon paleontologists, who ended up interpreting them according to a local Mantonian, and with hindsight, rather exotic theoretical framework. But during the period where these reconstructions took place, there were, in other reserves, a theoretical framework available that would not have allowed the claim of higher Cambrian disparity – a claim that became so prominent a feature of the Cambridge group's interpretations. For instance, what would have happened if the first in-depth 3-dimensional reconstructions of the Burgess fossils instead had been made by German researchers that were at the time already adhering to phylogenetic systematics and monophyly? In such a counterfactual scenario, it seems likely that the Burgess Shale material would then have been approached from a monophyletic perspective right from the beginning. However, that would have removed the taxonomic underpinning for the claim of higher Cambrian disparity, on which Gould's evolutionary scenario in *Wonderful Life* was based. In this counterfactual scenario, there might never be a controversy on Cambrian disparity at all, and the whole debate concerning the evolutionary significance of the Burgess Shale fauna would have been radically different. Gould might still write a book on contingency, but the empirical focus of such a work would have had to be based on different material, like, for instance, the Cretacious/Tertiary mass extinction. Clearly, the historical connection in evolutionary biology between contingency and disparity is not a connection of logical necessity.

Another example of this general underdetermination lies in the fact that several of the participants in a discussion may share (and give the same epistemic priority to) a given value, but may nevertheless end up on opposites sides of the fence because they disagree about exactly how this value is to be implemented. One case of this can be found in the disagreement between Maynard Smith and Zahavi on the clarity and precision of formal models vs. verbal models. Maynard Smith, himself having experienced the analytical strength of mathematical modeling of biological problems under the tutorship of J. B. S. Haldane, advocated that formal models were superior to other forms of reasoning precisely because they had the virtues of clarity and precision. Zahavi, on the other hand, having already experienced how his own handicap hypothesis had been modeled on the wrong set of background assumptions, advocated *his* position from a view that tended to regard formal models as examples of a kind of reasoning that carried a inherent danger of muddling the issue.

This is something that may not only pertain to epistemic values as such, but also grander epistemic claims with a normative component. We see this in the various ways paleontologists has attempted to implement their claim that their discipline includes a "privileged historical perspective" by using strategies that were contradictory with respect to the epistemic ideals utilized. Thus one strategy (employed by Conway Morris and the early Gould) followed an appeasement policy towards a classical positivist and physicalist ideal of science, and attempts to demonstrate that paleontology has its own set of general 'historical' laws or principles. Another strategy, however (employed by the later Gould), outright rejects this ideal, instead attempting to place this 'privileged historical perspective' of paleontology in the idiographic study of unique historical coincidences.

2) Compatibility between the dominant values of the scientific community and that of the individual scientist makes life considerably easier: It goes without saying that it is easier to convince an audience of your position if they share your norms than if they oppose them. This may seem like a trivial point, but as the examples of the (too) early dismissal of the handicap hypothesis; and the fate of the Cambridge group's early taxonomic interpretation of the Burgess Shale arthropods shows, this is something that may skew the analytical ability of a scientific community to the extent that the majority of its member accepts propositions that are made on clearly unfounded or inconsistent grounds.

Thus, as shown in section II, one of the major papers that led to the temporary ostracizing of group selection among a majority of biologists (Maynard Smiths haystack paper), produced a rather flawed argument that held an unnecessary strong *a priori* bias against group selection (namely that in altruist groups that were subjected to selfish subversion from within, altruists would go extinct in one generation). Nevertheless this paper was long hailed as having a decisive influence on the demise of group selection, and was apparently not subjected to the same kind of critical scrutiny as Wynne-Edwards' work on group selection. As the analysis in Section II suggests, part of the explanation this difference is to be sought in the fact that Maynard Smith's paper, unlike Wynne-Edwards' publications, had the advantage of being in accord with the dominant epistemic ideals of the field (as expressed by a formal style of theorizing *sensu* Winther, 2006). This claim is supported by the fact that the *reappearance* of group selection as a viable position within evolutionary biology only took place *after* the defenders of group selection had already accepted the hegemony of a formal style of theorizing as "the way to do it".

A parallel example of this can be found in the way Briggs' paper on the monophyletic origin of arthropods was received by a scientific community with a newly gained preference for cladistics. Almost overnight, the theoretical upheaval that had been facilitated by the cladistic revolution in systematics, suddenly meant that a scientific position that had until now enjoyed reasonable credibility (i.e. Manton's polyphyletic theory of arthropod origin), was no longer feasible. By exploiting this momentum Briggs gained the benefit of being on the side with the angels in his attack on the theory of polyphyletic arthropod origin – and got away with employing a rather incoherent set of arguments in this attack (using a polemic that played with the implication that his opponents did not take a 'historical' perspective serious enough).

Does this mean that arguments that are otherwise epistemically sound, will fall on deaf ears, if they are put forward in a scientific environment that is hostile to their normative foundations? As noted earlier, I do not believe that this will necessarily be the case. A scientist may choose directly to address and criticize the normative foundations of a scientific practice. The most successful example of a group of scientist employing this strategy that has been mentioned in the previous pages are probably to be found among the founding fathers of population genetics, where especially Fisher and Haldane demonstrated an early willingness to defend their formal approach at a time where it was much less common and accepted than what was later to be the case. Among the scientists whose publications are subjected to a more thorough scrutiny, however, this strategy are followed (with mixed success) by Zahavi in his defense of the handicap hypothesis, and by Gould in his defense of the contingency hypothesis. Zahavi, operating under the hegemony of a formal style of theorizing defended his own approach by directly addressing and criticizing the virtues of certainty and clarity that other biologists ascribed to formal modeling. However, although he himself probably felt vindicated in this defense, as the handicap hypothesis, after initial resistance from biologists employing formal models, finally became widely accepted, adherents of a formal style of theorizing could interpret this development as confirming their view that formal and mathematical modeling was the right approach to settle evolutionary questions, as the final acceptance of the handicap effect by a majority of biologists was only gained when Alan Grafen and others managed to construct a successful formal modeling of the phenomena. Likewise, while the contingency thesis has received considerable attention among philosophers of biology and humanistic scholars, it has generated much less attention among practitioners of evolutionary biology, in addition to being strongly contested by paleontologists such as Conway Morris. The difference between success and failure for this strategy is probably to be found in the ability of the maverick position to provide new and alternative research programs. The dominant epistemic values of a scientific thought collective are embedded within the scientific practice of that collective. The fruitfulness of that practice must be addressed (and viable alternatives provided) if an argument for changing values is to be successful.

3) The study of the actions of individual scientists in scientific controversies constitutes an important level of analysis in the investigation of epistemic values. Here, interesting phenomena occurs that may otherwise go unnoticed when focusing exclusively on the level of the collective (or supra-collective). At the level of the individual, the encapsulated domain of the scientific community shows itself to be quite porous. It turns out, in fact, that scientific communities are not intellectually isolated islands. Occasionally, a stranded canoe does get through the waves with new ideas or knowledge that may show up to be pivotal for the practices in the local habitat. The advent and hardening of the modern synthesis completely transformed the problem of division of labour among social insects. No longer was it to be regarded primarily as a case against the possibility of the inheritance of acquired characters. In the new selectionist regime that followed, the division of labour problem was transformed into a conflict between kin- and group selectionist accounts of the evolution of apparently altruistic behaviour among insect workers. Thus a theoretical upheaval otherwise unrelated to the subject, completely transformed, not only the discussion of division of labour problem, but even the way the problem was conceived at all.

Although it was in a comparable manner unrelated to the epistemic problem at hand the cladistic revolution in systematics had a similar dramatic effect on the Burgess Shale debates. Its methodological emphasis on monophyly was a devastating blow to Manton's claims of arthropod polyphyly – and, hence, to the taxonomic underpinning of the Cambrian scenario that Gould employed in order to defend his contingency hypothesis. As a result of this development, Gould had to resort to a defensive maneuver that turned the disparity debate into a discussion on morphometrics – at the same time denying that he had ever claimed that disparity was to be based on anything else. Conway Morris (who had not, unlike Gould, invested scientific capital in defending a strong claim concerning the role of contingency in evolution) responded to the same development by denouncing earlier claims of higher Cambrian disparity altogether.

One of the important analytical possibilities inherent in an approach that takes the actions of individual scientists as its focal point of analysis, is that it may, to a higher extent than analyses focusing more exclusively on the scientific collective, allow the investigator to couple the analysis of epistemic values with other important sociological variables that may play an important role in scientific controversies, such as, for instance, scientific prestige and authority.

A comparative analysis of the roles played by Gould in the Burgess Shale debates and by Maynard Smith in the debates on group selection, altruism and the handicap hypothesis (probably the two most prominent evolutionary biologists that were among the major players in the events described in Section II and III) shows both of these variable to be important for understanding the developments of the controversies. In both cases we have a situation where leading scientists of the field are strong advocates of a specific epistemic ideal, and, in the pursuit this ideal, actually ends up leading their field astray, at least for a period of time. In his own words Maynard Smith's initial attitude to the handicap hypothesis was one of 'cynicism' precisely because it was expressed in words rather than in a mathematical model, and therefore did not live up to the epistemic standards concerning models of which Maynard Smith was an outspoken proponent. Indeed Maynard Smith's adherence to formal modeling was so strong that he, well aware of his own status as a high ranking scientific authority within evolutionary biology, was later troubled by the possibility that he single-handedly delayed the acceptance of the handicap principle for over a decade. It might, of course, also be argued that Maynard Smith's initial resistance to the handicap hypothesis was actually beneficial to its later widespread acceptance. Probably, the most devastating thing that can happen to an idea is that it is ignored in complete silence. By his outspoken resistance to the handicap hypothesis, Maynard Smith also drew public attention to it, thereby attracting the interests of other scientists that were eager to subject the handicap hypothesis to critical scrutiny. In the end, this attention helped Zahavi's cause when Alan Grafen was able to use game-theoretic modeling to reach a positive verdict of the theoretical viability of the handicap hypothesis

Gould was able to draw similar widespread scientific public attention to the Cambrian animals of the Burgess Shale, when he, with publication of *Wonderful Life* connected this extinct fauna to his own contingency thesis. Like Maynard Smith, Gould had by the time already established himself as a major figure in contemporary evolutionary biology. However, compared to Maynard Smith, Gould's claim to fame came not only from his work on problems in paleontology and evolutionary biology (although this is not to say that these were insignificant – Gould can, for instance, rightly be hailed as one of the founding fathers of modern theoretical morphology). Having also pursued a career as a historian of science,[84] besides that of an evolutionary biologist, his fame as a scholar extended well beyond the domain of evolutionary biology. By entering the debate on evolutionary interpretation of the Burgess Shale fossils (which had hitherto been 'confined' to a fairly sectarian community of carcinologists and invertebrate paleontologists) Gould not only made the fossils famous far beyond the border of paleontology. By turning the Cambridge group into the main characters in his narrative about the taxonomic reinterpretation of these fossils, he also helped the spurring the careers of some of the staunchest critics of his interpretation of the evolutionary

[84] The most well-known works by Gould as a historian of science are probably *Ontogeny and Phylogeny* (1977) and *The Mismeasure of Man* (1981).

significance of the Burgess Shale. One might, therefore with equal right, claim that Gould's scientific authority has in fact promoted ideas that he vehemently opposed, especially when it comes to the evolutionary interpretations (and nomothetic aspirations) of his adversary, Simon Conway Morris.

This development has also led to the paradoxical situation, that while the credibility of many of claims of *Wonderful Life* has suffered from the thorough scrutiny they were subsequently exposed to *within* the paleontological community, many biologists and other scholars *outside* this community may have a wrong perception of the state of affairs because they have read Gould's book without encountering the work of his less famous critics.[85]

Comparing the actions of Maynard Smith and Gould, one does also find interesting differences, however. For one thing, Maynard Smith had the advantage, as a prominent advocate of formal modeling, of being in accordance with the dominant epistemic ideal of his domain of inquiry. Gould (or rather, the later Gould) was not. While Maynard Smith could call on the authority that comes with being part of the majority view, Gould, like Zahavi, repeatedly played the role of a dissenter, although often with great success. It may be that the difference between majority and dissenting views may partly explain the disparate attitudes that Maynard Smith and Gould exhibited when their claims were faced with serious problems. Despite initially having expressed strong resistance towards the handicap hypothesis, Maynard Smith was able to retreat from this position when it was no longer tenable, without the loss of scientific prestige. Gould, however, when attacked for the claim of greater Cambrian disparity, did not flinge from this claim, despite that fact that the intellectual developments in field of inquiry,

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[85] An example of this, mentioned in Section III can be found in the 2006 paper *Genes and Form* (from the anthology *Genes in Development. Re-reading the molecular paradigm* ed. by Eva Neumann-Held and Cristoph Rehmann-Sutter) by Stuart A. Newman and Gerd B. Müller - two senior biologists with a strong interest in problems of development. In fact, developmental biology may be one domain where this situation may persist for some time because Gould 1) as the author of *Ontogey and Phylogeny* (1977) is known here as an important scholar; and 2) developmental biologists can usually safely conduct their research on, for instance, cell differentiation without having to deal with the methodological problems of systematics that were so important for the development of the Burgess Shale debate.

produced such a backlash during the 1990's that it became almost untenable. Zahavi exhibited a similar behaviour, albeit with more success than Gould, when he experienced the negative assessment of the handicap hypothesis that came from the earliest attempt to model it. It may be that it is more difficult to retract from an dissenting position than from a majority position. By going against the perceived consensus the dissenter has already invested a large amount of scientific prestige in claiming that everybody else is wrong. That capital may be lost, if it turns out that this investment was made on faulty premises. Taking the majority position, one does not make such a risky investment, however. One simply assumes that the perceived consensus is right until proven otherwise. As in many other instances of life, there is safety in numbers.

Where does this leave Simon Conway Morris? In relation to the majority/dissent distinction, Conway Morris was in the situation that he (at least originally) was not in the possession of the same scientific authority, as his adversary when he was still establishing himself in the 1980's. In this sense *he* played the role the underdog – a role that is otherwise often associated with the dissenting position. However, at the same time Conway Morris has attacking Gould's macroevolutionary research program, and, later, his contingency thesis from an orthodox Darwinian position. In this sense, Conway Morris was actually defending a majority view against a minority position. This situation makes it difficult to analyse the behaviour exhibited by Conway Morris along these line until one realizes that it is actually a combination of 'majority resilience' and 'underdog stubbornness'. No doubt Conway Morris was simply following the majority view when he chose to abandon Mantons theory of polyphyletic arthropod origin and the association idea of basic arthropod baupläne (as will be remembered it was Briggs, and not Conway Morris who first pioneered the use of cladistic methods as the means to investigate arthropod relations within the community of Anglo Saxon invertebrate paleontogists). In no way did this retraction endanger Conway Morris' arguments that the Cambrian radiation can be explained by the same ecological principles of natural selection and niches filling that are operant in extant faunas – in fact it rather served to strengthen it. However, when defending these evolutionary views Conway Morris has shown no willingness to flinge. In fact, it seems that his persistence with these arguments has actually grown over time – although it should be added that Conway Morris has yet to face the kind of difficulties that Zahavi and Gould experienced with their scientific agendas concerning the handicap hypothesis and the empirical foundation for the contingency thesis.

The analyses in the previous paragraphs relate the actions of individual scientists in scientific controversies to considerations concerning their social roles in the scientific communities of which they are a part. They illustrate both why the study of individual actions constitutes an important level of analysis in the investigation of epistemic values, and also why it must be complemented by other studies in a multilevel approach to their role in scientific practice. By placing individual researchers' actions and their situational application of epistemic values in the context of their social role in the communities of which they are members, we bring in, once again, the perspective of the scientific collective as a way of understanding scientist's behaviour. However, it is only by the inclusion into these studies the phenomenon of individual idiosynkracy, and by considering the specific social status and authority of this or that scientist that we may be able to make sense of the disparate behaviours of scientists when they are faced with apparently similar dilemmas of decision-making (although these dilemmas may in fact not look so similar when put under closer scrutiny). As with many subjects, the devil is in the detail.

As a final thought, one may ask whether the investigation of epistemic values has anything to say about the larger themes of the unification or disunificatíon of the sciences. As described in Section I, it was the unifying ambitions of the early universalist attempts to establish a general scientific method, that first drew attention to the role of epistemic values as methodological criteria of judgment. As noted earlier this is not a thesis that aims to develop or advance a general account of methodology or theory-choice, and neither does it address the subject of unification *per se.* However, it has been an inherent part of the approach of this thesis that the application of epistemic values is a non-trivial affair. In my opinion, the existence of a relation of reciprocal underdetermination between epistemic values and other important epistemic variables that has been confirmed by this study bodes ill for any universalist notion that seeks to establish its unification of the sciences on a uniform application of epistemic values. I also fail to see what such a project would achieve, should it actually reach its goal. If epistemic values underdetermine theory-choice, then we need the dissent that is created by disagreements about how these values are to be applied. Only by discussing these various uses will we get the chance to evaluate them critically. And the constant critical evaluation of the choice and application of methodological criteria *is* needed in scientific communities. As some of the cases that has been the subject of analysis here also illustrate, the fact that a controversy may reach closure and consensus does not necessarily mean that it has been settled in a way, where we may claim with justified confidence that it was the most sound arguments that won the debate. Epistemic progress, understood as the strengthening of the empirical and argumentative justifications for our factuals beliefs, has to be fought for. It does not come automatically.

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Danish Resumé: Denne afhandling omhandler epistemiske værdiers (forstået som metodologiske bedømmelseskriterier) rolle i evolutionsbiologi: hvordan de konkret anvendes; hvordan de kommer i konflikt; og hvordan deres anvendelse forandres som følge af den intellektuelle udvikling i forskellige videnskabelige domæner. Undersøgelsen er baseret på studier af videnskabelige kontroverser inden for adfærdsøkologi og palæontologi. Det centrale omdrejningspunkt for undersøgelsen af adfærdsøkologien er de videnskabelige diskussioner omkring en række internt forbundne biologiske problemer relateret til oprindelsen og opretholdelsen af biologisk arbejdsdeling, altruistisk adfærd i naturen; muligheden for gruppeselektion og den såkaldte handikap-hypotese for biologisk signalering. Det centrale omdrejnigspunkt for undersøgelsen af palæeontologien er et sæt af videnskabelige problemer, der alle er forbundet til diskussionerne om den evolutionære tolkning og betydning af de kambriske fossiler fra Burgess Shale faunaen, herunder diskussionerne om deres systematiske placering, deres morfologiske disparitet, og den historiske eventualitets rolle i udviklingshistorien.

På baggrund af et sammenlignende studie af publikationer forbundet med forskellige videnskabelige kontroverser indenfor disse to områder, fremsætter afhandlingen tre generelle påstande omkring epistemiske værdiers rolle i naturvidenskab, der er støttet empirisk i de belyste cases: 1) Der eksisterer et forhold af gensidig underdeterminering mellem epistemiske værdier og andre vigtige variable i den videnskabelige proces; 2) Det er betragteligt nemmere for den enkelte forsker at overbevise andre forskere om sine videnskabelige konklusioner, hvis de er baseret på det gældende epistemiske ideal inden for det videnskabelige kollektiv, forskeren er medlem af, end hvis de er i konflikt med dette ideal; og 3) Individuelle forskeres handlinger udgør et vigtigt og selvstændigt niveau i analysen af epistemiske værdier – et niveau, som rummer interessante fænomener, der ellers ville gå ubemærket hen, såfremt man udelukkende fokuserede på det videnskabelige kollektiv.

Endelig konkluderer afhandlingen, at det omtalte forhold af gensidig underdeterminering mellem epistemiske værdier og andre variable i den videnskabelige proces udgør en alvorlig forhindring for universalistiske forsøg på at opnå en enhedsvidenskab, gennem opstillingen af et universelt gældende sæt af epistemiske

normer – samt at et sådant forehavende endog kan være kontraproduktivt for udviklignen af videnskabelige erkendelse. De konflikter, der bliver skabt af forskeres uenigheder omkring hvordan epistemiske værdier skal tolkes og anvendes, er nødvendige for at sikre en kritisk refleksion over de beslutninger, der bliver baseret på disse værdier. Det er kun ved åbent at diskutere disse værdier, at vi bliver i stand til at vurdere deres betydning, og eventuelt ændre praksis, såfremt det bliver tydeligt, at de bliver anvendt uhensigtsmæssigt.

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